ASSESSMENT OF CHARACTER VARIATION IN THE CRANIA AND TEETH OF MODERN ARTIODACTYLS FOR BETTER SPECIES DIAGNOSIS IN THE FOSSIL RECORD

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A DISSERTATION

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Title: Assessment of Character Variation in the Crania and Teeth of Modern Artiodactyls for Better Species Diagnosis in the Fossil Record

Accurately distinguishing species in the fossil record is difficult when the extent of osteological variation in many modern animals is unknown. Research into intraspecific variation has been conducted in a number of groups, but has not been conducted for systematics use in most modern artiodactyls. In this dissertation I quantify intraspecific variation of teeth in 14 species of modern artiodactyl, then test how accurately cranial characters diagnose modern, sympatric species of duikers, and use this information to reassess the artiodactyl diversity of a fossil group: the superfamily Merycoidodontoidea in the John Day Fossil Beds. Ultimately, variation is not constant between orders or different size classes, is influenced by morphology, size, and dimorphism, and this variation should be incorporated into fossil diagnoses to avoid both overconfidence of diagnosis and under-recognition of possible intraspecific variation. This dissertation includes previously unpublished co-authored material, as Chapters II and III were coauthored with Dr. Edward Byrd Davis.

This dissertation contains additional supplemental files, including excel formatted versions of Appendix F, Appendix I, and the data for Chapter III. There is also a nexus file of data for Chapter IV.

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DEDICATION

To my mother, who always encouraged me to grow up to be a nerd, and to my husband Logan and my best friend Amy, who worked together to keep me sane.

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CHAPTER I

INTRODUCTION

With the advent of large online databases and new statistical software, big-data paleontology has become a rich platform for studies in evolutionary theory and ecology. Databases like Neotoma and MIOMAP contain geographic, temporal and faunal information available for free download and use (Grimm 2008, Carrasco et al. 2009) and these big databases have led to complex synthesis works. Recent big-data projects have overturned major theories – e.g. showing that the latitudinal gradient has not been stagnant over time (Marcot et al. 2016), that annual precipitation has driven diversity patterns for the last 50 million years (Fraser et al. 2014), or that the late Pleistocene extinction was a complicated, regionally driven event (Emery-Wetherell et al. In Revision). Big-data projects contribute to our understanding of species dynamics across large timescales and in the face of enormous climate change – information which serves to greatly improve conservation strategies (Dietl and Flessa 2011, McGuire and Davis 2014). Ours is the first epoch dominated by the habitat disturbances caused by a single species, and the influence of humans across the landscape has caused massive habitat fragmentation, invasion of new species, climate change, and the Earth's next great extinction (Barnosky 2014). Climate change is not a new concept to our planet – glaciations and hot-houses are well-documented in the geological record just as at least some organismal responses to these perturbations are recorded in the fossil record. Understanding how animals evolved and changed in response to environmental alteration in the past can help create biologically defensible conservation strategies for the future (Dietl and Flessa 2011, McGuire and Davis 2014).

But big-data studies are only as good as their underlying data points, and paleontological studies of species diversity typically assume that paleontological species can be compared at

consistent scale to modern animals though in many cases, this assumption is false (Alroy 2002, Prothero 2014). Even in modern species, the true definition of a species is not constant or necessarily consistent between different organisms or workers (i.e. Frost and Hillis 1990, Rosselló-Mora and Amann 2001, Agapow et al. 2004). Though there is definition conflict, modern species can still be diagnosed using a variety of methods that are not available to paleontologists, e.g. inability to reproduce (Biological Species Concept), geographic barriers that cause genetic isolation but may not be obvious in the fossil record (Genetic Species Concept), or occupation of different niche spaces that may not be reflected in bone structure (Ecological Species Concept) (Mayr 1940, Van Valen 1976, Baker and Bradley 2006a). Instead, fossil vertebrates are diagnosed almost exclusively by osteological characters. Osteological morphology should reflect genetic differences (Harvati and Weaver 2006, Jedensjö et al. 2013, Hlusko et al. 2016), but it may not reflect species differences at the same scale as say, the genetic species concept (Baker and Bradley 2006a). Furthermore sexual dimorphism, ontogenetic change and individual variation all influence bone structure; without recognition of natural intraspecific bone vaiation in different mammalian groups, some diagnostic paleontological characters may be more representative of intraspecific variation than diagnostic of different species. Genetic drift and post-depositional deformation can also cause substantial variation amoung individuals, possibly higher in the fossil record than in modern samples (e.g. Guthrie 1970, Stevens and Stevens 2005). Systematics that do not take these factors into account can be over-diagnosed, yielding results that are inaccurate in large-scale studies.

To resolve this problem, considerable systematic revisions need to be conducted to bring fossil species into line with modern species and with each other. Yet parameters of expected intraspecific osteological variation have only been determined for a small number of modern

groups, particularly rodents, primates, and carnivores (Gingerich and Schoeninger 1979, Gingerich and Winkler 1979, Pengilly 1984, Cope 1993, Bell and Repenning 1999, Plavcan and Cope 2001, Caumul and Polly 2005). Modern artiodactyls in particular have very few studies parameterizing their osteological variation in a manner that is replicable for fossil systematics, instead studying dimorphism and geographic osteological variation (e.g. Endo et al. 1998, Subbotin et al. 2007) without describing infraspecific limits of that variation in a manner that is replicable for systematic studies.

In this dissertation, I will parameterize intraspecific osteological variation in 14 species of extant artiodactyls, and apply the resulting species concept in the fossil record to resolve subsections of the group Merycoidodontoidea. Merycoidodontoidea (more commonly known as oreodonts) was an abundant group of herbivores in the North American Cenozoic which survived 40 million years of climate change and biome turnover (Scott 1915, Lander 1998). Oreodonts were mid-sized herbivores found in nearly 100 formations across North America, and in some they were the most abundant large mammalian fossil found (Thorpe 1937a, 1937b, Alroy et al. 1998).

Merycoidodontoidea is typically divided into two families, the morphologically homogenous Agriochoeridae and more diverse Merycoidodontidae (Lander 1998) (Figure 0.1).

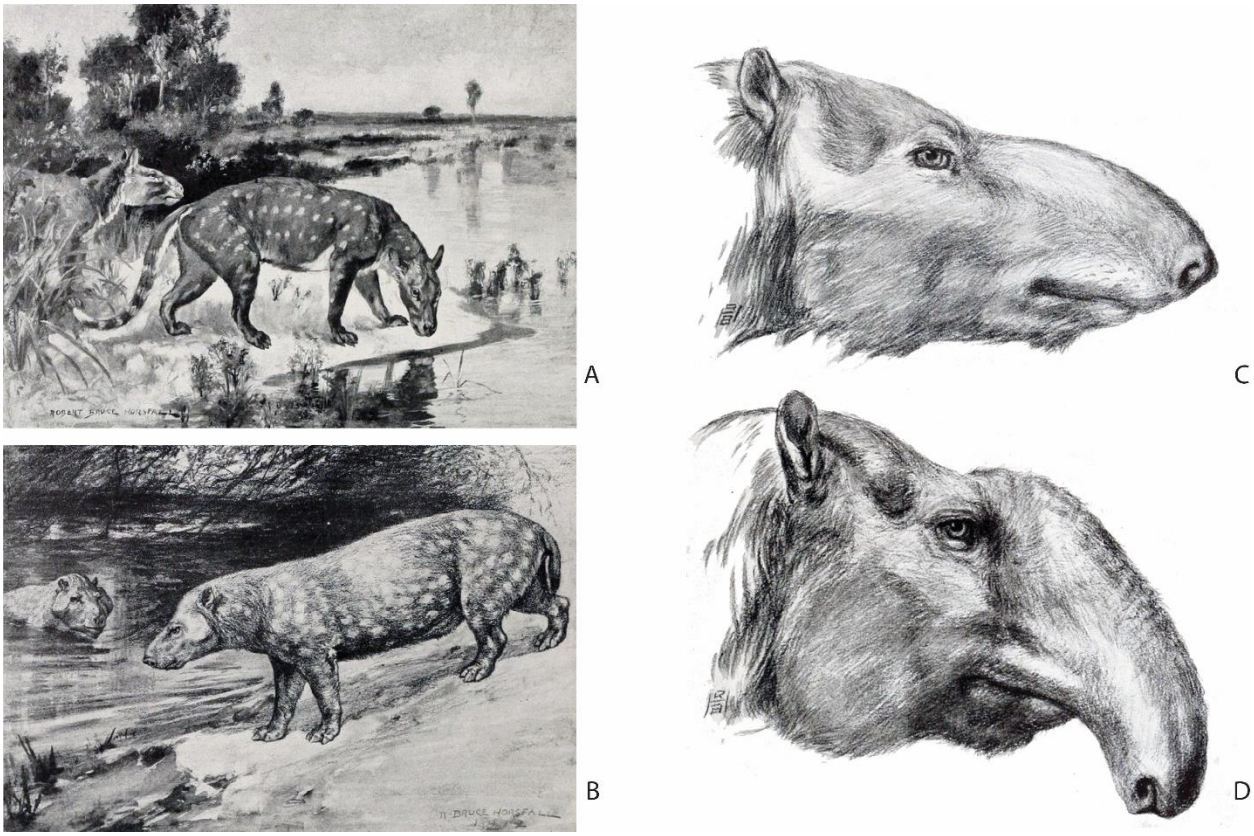

Figure 0.1: Different body forms of Merycoidodontoidea. A) Agriochoerus. B) Promerycochoerus. C) Merycochoerus proprius, showing initial trunk development. D) Brachycrus laticeps, showing full trunk developement. Images from Scott 1915, reproductions of Robert Bruce Horsefall's images for the Carnegie Museum.

Members of Agriochoeridae lacked a pre-orbital fossa and have an incomplete postorbital constriction, and are often considered ancestral to Merycoidodontidae (Lander 1998, Ludtke 2007). Members of Agriochoeridae were restricted to North America, and lived from the Uintan through the early Arikareean (~46 - 30 ma) (Ludtke 2007). Morphological diversity of this group was minimal, restricted primarily to size and dental morphology, though some genera developed clawed ungual phalanges (Ludtke 2007). Morphological analysis of the clawed taxa suggests their adaptation for a semi-arboreal lifestyle, though isotopic analysis of *Agriochoerus* in the White River Formation showed δC^{13} values more consistent with feeding in an open habitat (Coombs 1983, Boardman and Secord 2013). Three genera are currently recognized of

Agriochoeridae, all of which coexisted temporally but not necessarily geographically (Ludtke 2007).

Merycoidodontidae is a considerably larger group with more variation in body forms, including both greater variation in size than Agriochoeridae and several lineages with nasal retraction (Figure 1 C-D) (Schultz and Falkenbach 1940, Lander 1998). Merycoidodontidae were present in North America from the early late Duchesnean to the late Hemphillian, and had also spread to Central America by the Middle Miocene (MacFadden and Higgins 2004, Macfadden 2006). Merycoidodontidae occupied many different niches, often in the same locality: of the 19 currently-recognized genera, up to 10 coexisted during the early Miocene (Thorpe 1937a, Lander 1998).

As part of their great morphological diversity, oreodonts share morphologies with many modern endangered ungulates including camelids, suids, and tapirids (Douglass 1906, Thorpe 1937a, Lander 1998, Stevens and Stevens 2007), and the factors affecting oreodont success through time could provide helpful conservation strategies for these groups (Dietl and Flessa 2011, Rick and Lockwood 2013, Dietl et al. 2015). Yet current oreodont taxa are diagnosed by continuous, overlapping character states, have inadequate published descriptions, and few illustrations or figures that elucidate unique morphologies and as a result, their role in the paleoecology of the North American Cenozoic is obscured. For example, inadequate descriptions of the numerous smaller oreodont species from the John Day Formation made it impossible to separate out many specimens below the family level, leaving an isotopic analysis overlumped and unable to answer how divergent niche-space was within John Day oreodonts (Kohn and Fremd 2007).

To maximize the utility of oreodonts in paleoecological and evolutionary studies, their systematics must be revised to be replicable and consistent with modern artiodactyl standards – and before that can happen, parameters need to be established from modern artiodactyl osteology. In this dissertation, I have summarized variation and tested for some important possible common causes of variation, co-authored with Dr. Edward Byrd Davis. I have used classification analyses to determine the scale at which species can be identified by cranial material, as well as which parts of the skull may be maximally useful for diagnosis, co-authored with Dr. Edward Byrd Davis. Finally, I have used these newly defined parameters to untangle a systematic snarl from the John Day Formation of Central Oregon: the taxonomy of eporeodontine oreodonts, one of the most abundant fossils found in the region. To untangle oreodont systematics I have generated 3D models for, measured, and landmarked 307 specimens representing 21 different species of modern artiodactyls. These species were selected as phylogenetic, ecological, and morphological analogues for Merycoidodontoidea, but the osteological variation discussed in this dissertation applies to many fossil artiodactyl groups. Resolving the systematics of fossil artiodactyls is vital for understanding their evolutionary and ecological trajectories, especially given their economic importance (Bodmer et al. 1994, Juste et al. 1995). Understanding the long-term evolutionary trends in Merycoidodontoidea and other fossil artiodactyls can better inform conservation efforts of this economically and ecologically important order world-wide.

CHAPTER II

DENTAL VARIATION DOES NOT DIAGNOSE MODERN ARTIODACTYLS: IMPLICATIONS FOR THE SYSTEMATICS OF MERYCOIDODONTOIDEA

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Abstract

Dental measurements are frequently used to diagnose the fossil species of Merycoidodontoidea and other extinct artiodactyls, but have not been tested for effective diagnosis of modern artiodactyls. Our study finds that dental measurements poorly diagnose modern artiodactyls, with some species of *Cephalophus* correctly classified less than half the time by Discriminant Function Analysis. Poor classification power of artiodactyl dentition may be a result of high dental variation, which is generally higher than in primates, carnivores, rodents, and even elephants, with molar coefficients of variation ranging up to 18% (*Camelus bactrianus*). The most variable tooth in artiodactyls is M1, which is conversely the least variable tooth in primates and carnivores. Our study also found that the relationship between standard deviation and average measurement length (commonly represented by the coefficient of variation) is not completely linear across different size classes of artiodactyls. The higher-than-expected coefficients of variation for artiodactyls imply that many fossil taxa may be over-split,

but the low utility of dental measurements in separating sympatric species also suggests that dental measurements are not effective for resolving species diagnoses. We advocate a systematic revision of Merycoidodontoidea and many other fossil artiodactyl groups with lower emphasis on dental measurements and better accounting for patterns of variation in selenodont dentition.

Keywords

Variation, artiodactyl, discriminant function analysis, dental morphology, merycoidodontidae

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 qualitative dental morphology, quantitative dental measurements are often the only method for diagnosing artiodactyls at the species level (e.g. Phleger and Putnam 1942; Gustafson 1986; Stevens and Stevens 2005). Therefore, equivalence between fossil selenodont artiodactyl systematics and the modern biological species concept depends on whether the cut-off a palaeosystematist uses for 'more than one species' is consistent with intraspecific variation in modern artiodactyls. Simpson and Roe (1939) suggested a 10% rule of thumb for distinguishing intraspecific from interspecific variation in mammals, but this rule not been tested explicitly across most mammals, including Artiodactyla. Simpson and Roe (1939) 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.

Papers exploring osteological and dental variation have been published in only a handful of extant mammalian groups, in particular carnivores (Pengilly 1984, Roth 1992, Polly 1998),

elephants (Roth 1992), primates (Gingerich and Schoeninger 1979, Cope 1993), and rodents (Austin and Stangl 1995, Carrasco 2004). Artiodactyls in particular have been the subject of very few systematic dental variation studies, with quantification of only 5 different modern species (Vrba 1970, Stevens and Stevens 2005, Carranza and Pérez-Barbería 2007, Natsume et al. 2008). There have been qualitative or geographic studies of dental variation in a number of different artiodactyls (e.g.Robinette et al. 1957, Hewison et al. 1999, Veiberg et al. 2007, Anezaki et al. 2008), but rarely are data or variation values reported and so these studies are of minimal use for paleosystematists. Without modern-derived parameters for normal intraspecific variation, the systematics literature for fossil artiodactyls contains many contradictions, a point exemplified by the extinct superfamily Merycoidodontoidea. Merycoidodontoidea has experienced 4 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 1937a, Schultz and Falkenbach 1968, Lander 1976, 1998, Ludtke 2007, Stevens and Stevens 2007). Such divergent systematic 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 2.1). Yet divergent systematics are difficult to avoid when fundamental questions of variation and the species concept remain unanswered, and only subjective criteria exists for researchers to delimit species. To begin filling this gap, our study tests whether dental measurements of the kind typically used in merycoidodontoid systematics are adequate for species-level diagnosis, and how wear, sexual dimorphism and dental function influence these dental measurements.

We analysed artiodactyl dental variation in species selected as analogues for Merycoidodontoidea. Our dataset more than doubles the current published literature on variation

in dental measurements, allowing us to test several questions about the adequacy of dental material for diagnosis and the factors influencing character choice.

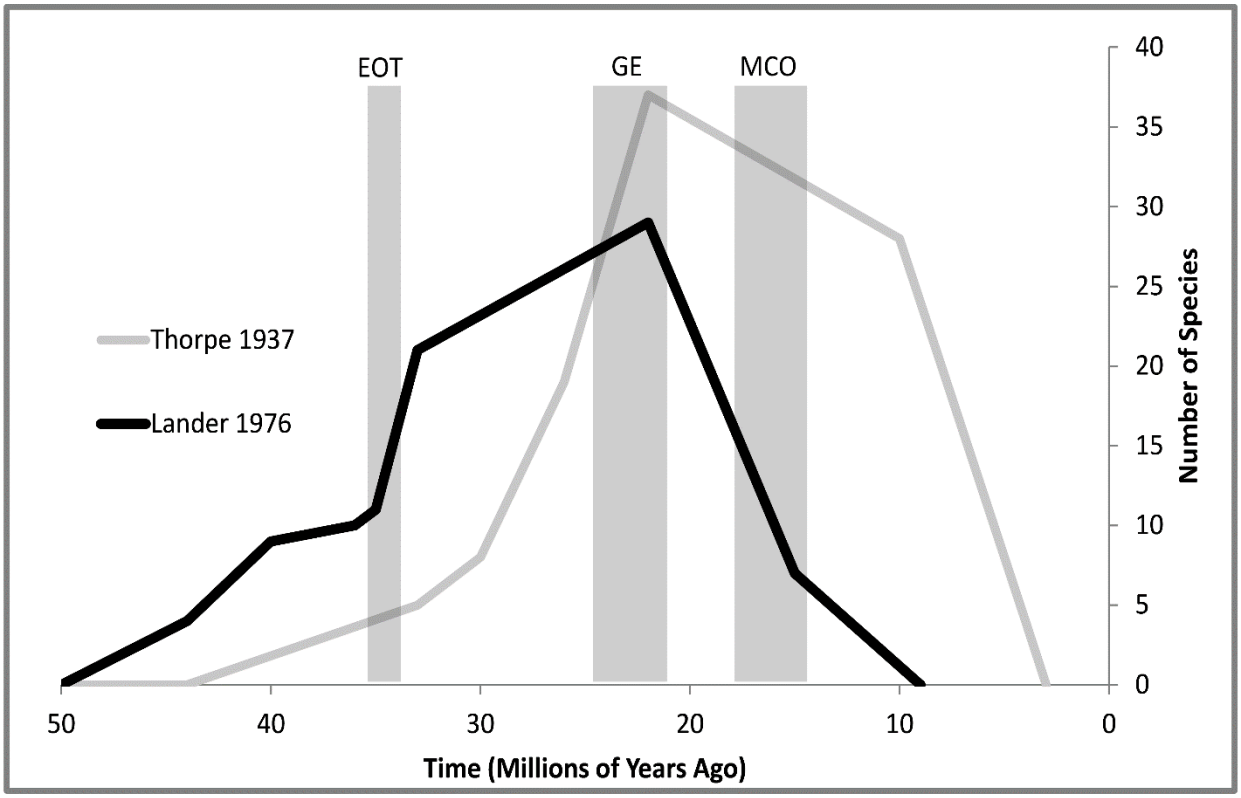

Figure 2.1: Oreodont diversity through time by worker (Thorpe 1967 vs Lander 1998). Time bins show important North American climactic and ecological turnover events, including Eocene-Oligocene Extinction (EOT), beginning of grassland expansions (GE), and the Mid-Miocene Climactic Optimum (MMCO) (Zachos et al. 2001, Strömberg 2011).

Tooth size is correlated with body size (Janis 1990), a pattern assumed to be constrained by natural selection because of the important role of teeth in feeding. Dental size is also highly heritable (Bader 1965), so 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 have tested these assumptions using discriminant function analysis to determine whether dental measurements of the chewing teeth are distinct enough to diagnose species in groups of modern duikers, muntjaks, and camelids.

Though we are testing the robustness of dental material for species separation with prior knowledge of species divisions, palaeontologists work on samples of unknown numbers of species. Given that higher variation increases the likelihood that a palaeosystematist 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. The teeth of many artiodactyls have larger occlusal surfaces than base measurements, and sufficient wear could potentially increase dental variation in a sample. Artiodactyls are also frequently size-dimorphic (Pérez-Barbería and Gordon 2000a, Carranza and Pérez-Barbería 2007), and if this dimorphism is reflected in dental measurements then overlapping distributions of males and females could be misconstrued as more than one species. Tooth function may also affect variation – teeth with less involvement in chewing may be more variable and potentially less useful for systematic analyses (Gingerich and Schoeninger 1979, Roth 1992). We used linear regressions of height versus widths or length of teeth to test for the influence of wear on variation. We also used 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 Palaeontology Laboratory at 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 3rd upper incisor (I3), 2nd upper premolar (P2) and upper canine (C1) of camelids.

Species

As abbreviated in figures and tables: *Camelus bactrianus* (bact), *Camelus dromedarius* (drom), *Lama guanaco* (guan), *Vicugna vicugna* (vicu), *Hylochoerus meinertzhageni* (hylo), *Muntiacus 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 and Methods

Measurements

We made and measured 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. To ensure compatibility between Photoscan and digital calliper measurements, we checked for significant differences between identical dental measurements on 3 specimens of *Ovis ovis* using an F test (Zar 1999). We used 3 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 and improvements in the software, our more recent 3D models are far better than earlier models. To determine whether our methodologies were comparable, we used *t*-tests in MS Excel to compare different measurements between our subsets

(Winston 2009). We also tested our measurement variance for significant differences from small measurements on small species, to explore whether our methodological error overwhelmed intraspecific variation in small organisms. When measuring we made certain to measure the maximum lengths and widths of the tooth, following criteria used by Lander and Hanson (2006), Ludtke (2007) and other oreodont palaeontologists. We kept our measurements parallel to the palate, to avoid inflating measurements on uneven occlusal surfaces. Measurements are provided in supplementary tables 1.1 and 1.2.

Discriminant Function Analysis

We used both linear and quadratic discriminant function analysis to test for classification success of modern species using dental measurements. We ran our linear discriminant function analyses (DFA) in R, and included jacknife verification as a more robust measure for evaluating DFA success (DeGusta and Vrba 2003, Meloro 2011). High multicollinearity in our dataset prevented use of the full complement of dental measurements using quadratic DFA, so we subsampled for two sets of analyses by length vs. width measurements.

Variation Tests

Our DFA had low classification success with dental measurements, which may have resulted from the high dental variation in our sample. 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 <10% variation within species (Simpson and Roe 1939). We found considerably higher variation 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 Valkenburgh 1997), but because body size is correlated with chewing area, size dimorphism can also affect chewing teeth (Carranza and Pérez-Barbería 2007). Only our bovid and cervid species had identified sex and of those, only *Ovis* and *Muntiacus* show any size dimorphism (Pérez-Barbería and Gordon 2000b). We had too few females to test for size dimorphism in *Muntiacus*, so we proceeded to test for size dimorphism only with *Ovis dalli* molars.

We tested camelid and suid caniniform teeth and *Ovis dalli* molars for dental size-dimorphism using *t*-tests, where sex is known *a priori*, and a series of distribution tests where sex of individuals is not already known. We tested distributions using 1) the Shapiro-Wilk test to detect deviation from normal distributions, 2) the Hartigan's Dip test for multimodality, and 3) Finite Mixture Analysis models 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 (Hartigan and Hartigan 1985, Villasenor Alva and Estrada 2009, Young et al. 2015). By using both *t*-tests and distribution tests, we could determine if the detection likelihood of sexual dimorphism in a sample of unknown sex distribution favourably compares to detection likelihood in samples of known sex.

2) Age-Related Dental Wear. Our measurements were taken on the maximal length and width of the tooth: for length, this was typically at the occlusal surface, and for width it was often at the base. Because artiodactyl teeth are wider at the occlusal surface than at the root, progressive

wear should yield progressively smaller measurements (Figure 2.2B). This change through wear may influence the size of certain dental measurements, and increase overall dental variation.

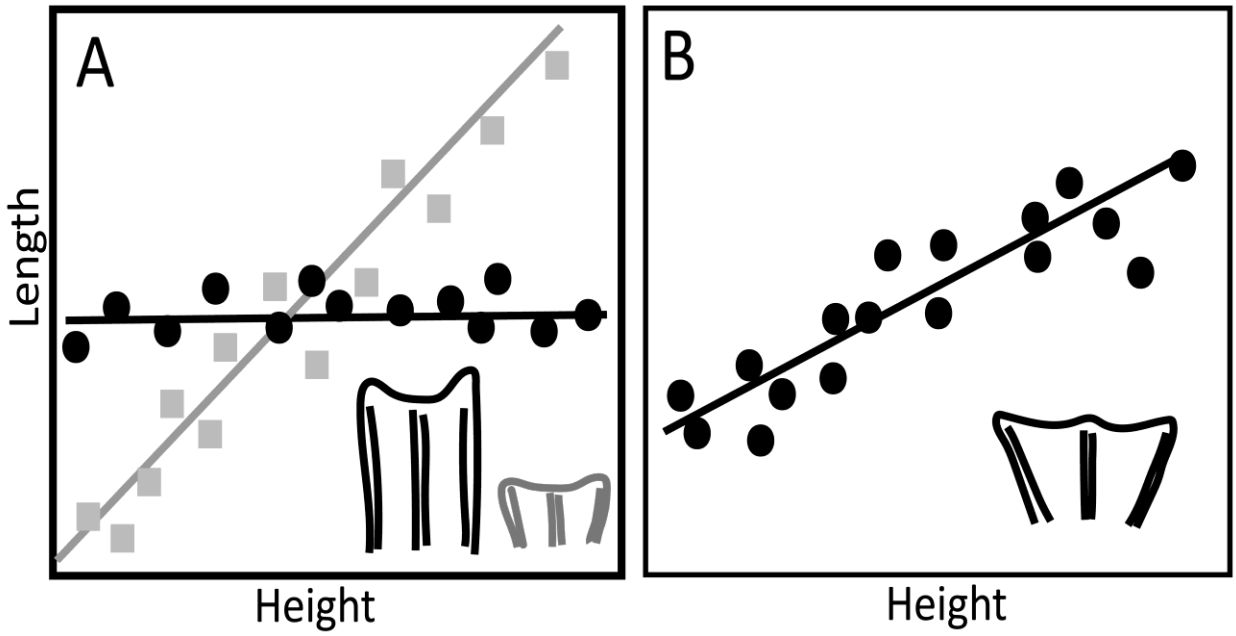

Figure 2.2. Simplified representative relationships between crown length and crown height if A. wear does not affect crown length, or B. wear does affect crown length.

There is inherent covariance between tooth height and length or width (bigger teeth are also taller teeth), but if wear is not a complicating factor then occlusal size and tooth height should be proportionally linked: either zero slope, in the case of teeth that flare at the occlusal surface, or a linear relationship with an intercept of zero (Figure 2.2A). If the relationship between height and length or width is strongly influenced by wear then there should be significant correlation and a non-zero intercept (Figure 2.2B). If the change in the tooth shape through wear is not consistent (trumpet-shaped teeth, for example), there may be a non-linear relationship present as well. None of our taxa presented a trumpet-shaped and nonlinear morphology, but this may be a concern for other groups. We used the crown height of the first

molar as an age proxy because M1 has the longest wear series preserved in our sample, capturing the greatest potential time series of change in length and width.

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 Z tests to test for significant differences in CV values between multi- and single-species samples (Zar 1999). We also used a CV correction factor for data that had <8 measurements, as CV is known to underestimate variance in small sample sizes (Sokal and Rohlf 1995).

The advantage of CVs is their status as a unitless measure of variation that removes the effect of absolute scale (Lovie 2005). Our dataset returned significantly higher single-species CV values than we expected for large taxa, causing us to suspect that CV may not perform as uniformly across size classes as expected, and that a nonlinear relationship might better fit our data. 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 effects 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, or a linear model with an intercept significantly different from 0 (anisometric variation) would best model the relationship between standard deviation and mean.

Significance Tests

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).

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 wild specimens were not 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 callipers (.00254 cm) (Suzuki and Matsumoto 1986). Measurement variance was not significantly different between 3D model measurements and digital calliper measurements ($p = 0.24$), but the actual measurements were significantly different for 2 of 16 measurements ($p < 0.5$). Finding significance in 2 of 16 tests should happen by chance about 19% of the time (cumulative binomial probability of 0.19). Our results therefore indicate that digital callipers and Photoscan measurements are comparable.

*Table 1.1 Individual species coefficients of variation, and coefficients of variation in genus-level mixtures (*Muntiacus, Camelus, *Mix 1:* Cephalophus *and* Philantomba, *Mix 2: Mid-size*d Cephalophus *species, Mix3 (Lamini):* Lama *and* Vicugna*). Asterisks indicate where samples <8 had the coefficent of variation correction factor applied. Duiker characters with variation smaller than measurement uncertainty of Photoscan are indicated by grey fill, and by digital callipers indicated by +.*

	hylo	**bact**	**drom**	**vicu**	**guan**	**dors**	**leuc**	**nigi**	**silv**	**weyn**	**phil**	**munt**	**reev**	**ovis**	**Muntiacus**	**Camelus**	**Mix 1**	**Mix 2**	**Lamini**
H C1	59.3																		
L C1	26.6	39.6	26.2	26.4	28.5							28.1*	43.5*		34.2	37.9			31.3
L I3				28.0	25.6														28.7
L P2		28.3	33.7			7.6	8.5	5.5+	8.5	6.0+	5.5+	11.6	4.7*	15.7	13.2	32.1	26.3	10.0	
L P3	15.5	13.1	9.0	20.9*	26.2	10.9	8.5	6.6+	8.9	10.2	8.5+	11.4	4.0*	9.1	12.9	11.9	25.4	10.0	30.2
L P4	14.5	9.3	7.5	10.6	9.3	7.3	8.6	8.1	8.5	6.8	8.1+	16.8	8.6*	9.3	18.0	8.7	24.5	9.3	16.9
L M1	10.8	17.0	18.1	18.2	11.7	11.7	11.7	11.0	10.4	13.1	9.9+	12.5	10.9	12.2	14.1	18.7	25.6	11.0	17.1
L M2	11.9	14.0	13.9	14.2	14.4	10.2	9.5	8.5	7.4	10.4	8.0	14.4	8.0	8.8	14.5	14.6	24.7	8.8	17.1
L M3	4.8	6.3	8.3	4.8	11.9	8.9	9.1	7.5	5.5	6.5	7.4	10.7	5.4*	7.9	12.9	8.0	25.0	7.7	16.2
T C1	34.7	41.8	37.1	23.1	29.6							19.4*	49.3*		34.8	45.9			34.0
T P2		28.4	25.6	25.3	35.6	9.4	6.9	8.4	9.0	10.5	11.2+	14.8	7.0*	8.6	15.3	32.3	28.5	9.5	37.7
T P3	18.8	11.2	9.5	14.7*	20.9	7.9	4.8	7.3	9.4	6.8	11.4	9.7	6.2*	8.9	11.9	10.7	30.3	10.9	20.2
T P4	16.9	7.2	12.5	16.1	19.0	6.6	6.4+	6.9	5.3	7.0	9.2	9.8	4.7*	5.8	12.5	9.9	27.6	6.8	24.8
T M1	14.0	8.0	13.1	9.9	11.9	9.0	6.5	6.4	5.5	6.0	8.2	10.3	10.4	7.3	14.2	10.1	25.9	7.9	18.0
T M2	13.7	6.3	14.1	14.8	10.4	6.8	8.6	7.0	5.0	6.1	6.6	9.9	7.3	8.0	12.4	9.9	25.4	7.4	20.1
T M3	13.1	8.3	18.1	10.6	9.6	6.3	7.6	8.0	6.4	6.6	6.2+	11.3	4.8*	6.5	12.0	13.6	24.2	8.4	17.1
Premolar row	27.9	8.1	6.3	15.0	13.7	6.8	7.6	5.3	7.4	3.4	6.0	9.7	5.0*	11.8	13.1	7.4	25.7	8.4	21.0
Molar row	11.0	7.8	13.8	10.0	10.0	6.8	5.6	5.7	5.5	6.1	5.2	12.0	14.6*	5.5	14.7	11.1	23.7	6.2	16.3
Tooth row	7.7	5.9	7.9	12.7	11.2	5.2	5.4	3.9	5.5	3.1	4.9	10.4	5.6*	6.1	12.8	7.3	24.8	5.5	17.1

Although Photoscan measurements are not incomparable to digital calliper measurements, our methodological uncertainty sometimes was larger than the measured uncertainty for several of the smaller characters of smaller duiker species. We found that 38 of 96 measurements had measured uncertainty that was significantly smaller ($p < 0.05$) than our Photoscan uncertainty (cumulative binomial probability of <.001), while only 9 were less

variable than our digital calliper measurement uncertainty (cumulative binomial probability of 0.05; Table 2.1).

Small measurements were more susceptible to this phenomenon. The influence of our digital calliper uncertainty is consistent with the findings of Polly (1998), which found that the natural variation of small measurements are often overwhelmed by measurement uncertainty. Measurement uncertainty occurs regardless of measurement system, but the threshold is much lower because of the greater uncertainty in Photoscan.

Despite the higher variation of Photoscan models, the measured variation of our small measurements is still small: the smallest premolars (*Cephalophus* and *Philantomba*) were less variable than the large premolars in our dataset (Table 2.1). The higher uncertainty of Agisoft Photoscan therefore does not eradicate the trends present in our data but may inflate our variation, and our CV values should be considered maximum CVs for our smaller measurements and smaller specimens.

Discriminant Function Analysis

The percentage of specimens correctly classified by dental measurements (Table 2.2) ranged from 40% (*Camelus bactrianus, Cephalophus nigifirons*, and *Cephalophus weynsi*) up to 100% (*Cephalophus silvicultor* and *Philantomba monticola).* Overall classification rates within family ranged from 52% to 82% accuracy (Table 2.2). Higher percentages resulted from species with dramatic size differences: *Cephalophus silvicultor*, part of the lineage of giant duikers (50 kg), was easy to distinguish dentally from the dwarf duiker *Philantomba monticola* of around 5kg (Prins and Reitsma 1989). Artiodactyls of similar mass were more difficult to distinguish, and it

seems that DFA of dental measurements is more likely to diagnose distinct size classes than true biological species.

Table 2.2. 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

The poor performance of DFA may be influenced by the considerable variation in artiodactyl dental measurements (Table 2.1). 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 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 higher even than several molar measurements of elephants, which were previously presumed to be the uppermost limit of natural dental variation (Roth 1992).

Pattern of Variation

For primates, the least variable dental measurement is the length of M1 (Gingerich 1974, 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 2.3). 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 variation: 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 2.4). 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 retain the smallest CVs, suggesting that the overall character stability of duiker dentition is a trait rather than a methodological artifact.

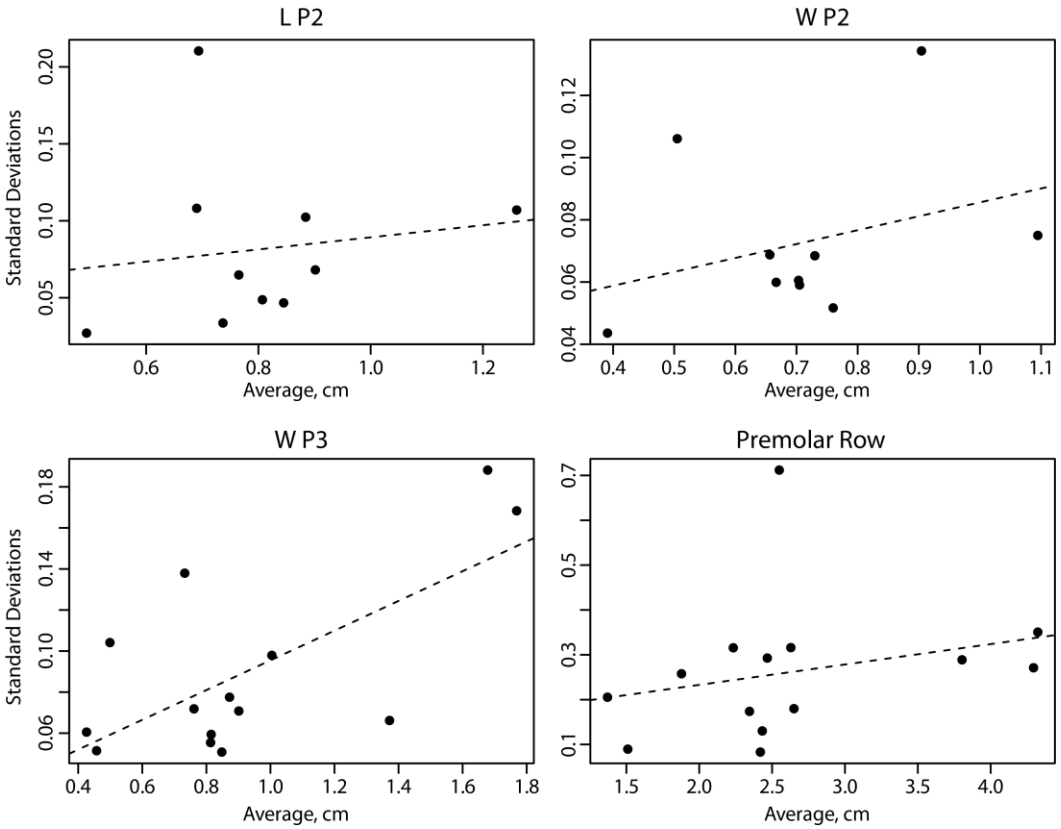

Figure 2.3. Nonsignificant linear regressions of standard deviation and average.

Low variation may relate to diet – many duikers are predominantly frugivorous (Hofmann and Roth 2003), and could require less muscle force for mastication, resulting in a longer functional tooth row that includes premolars. The shorter functional tooth row of most artiodactyls is related to masseter placement - the masseter is prevented from moving forward because it would reduce gape and, in turn, limit functionality of incisors and canines (Greaves 1978). Unlike *Muntiacus*, *Hylochoerus* and the camelid species in our sample, duikers have no upper incisors and no canines, so gape may not be as important, allowing anterior migration of the masseter and increasing overall functionality of the duiker tooth row, minimizing overall dental variation. Though a complete examination of this hypothesis is outside the scope of this

paper, the anteriormost part of the zygomatic arch roots ahead of M2 in our duiker species, which is further anterior than in the other skulls of our sample.

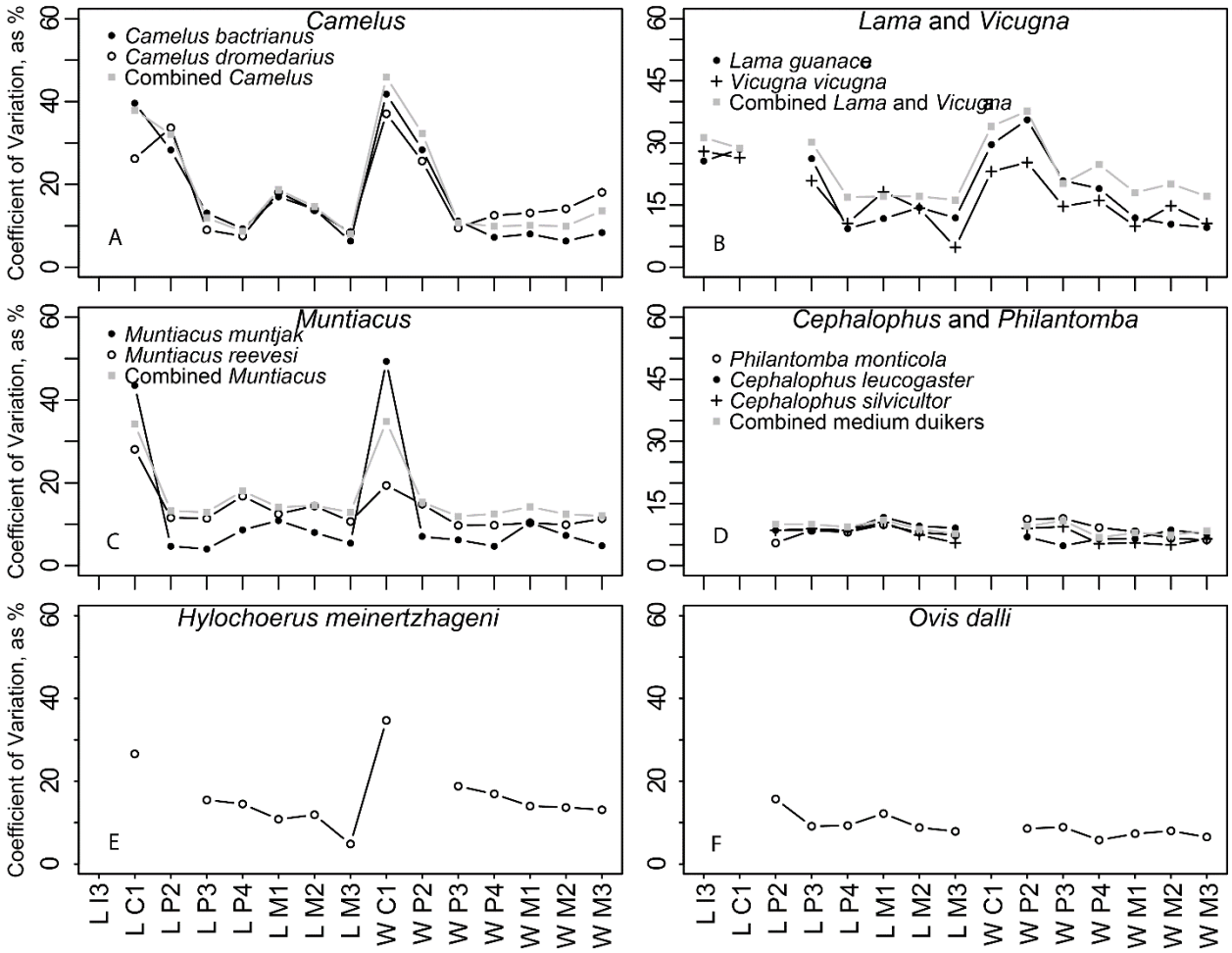

Figure 2.4. Variation in dental measurements of different species, including lengths and widths. Combined samples of Camelus, Muntiacus, Lama and Vicugna, and Cephalophus leucogaster, nigrifrons, dorsalis and weynsi are included on their respective graph

The lowered functionality of premolars can explain their higher variation in most artiodactyls, but it does not explain the high variation of M1. We tested two other possible causes of higher variation in molars: age-related dental wear, and sexual dimorphism.

Influence of Age-Related Wear on Dental Variation

One of the possible explanations for such high variation in artiodactyl teeth may relate to the influence of wear on tooth dimensions. Artiodactyl teeth often have a larger occlusal surface than base and as the tooth wears, the length decreases (Figure 2.2). However, this relationship should wear anisometrically: because the tooth shape is not a perfect triangle – it is truncated at the base, rather than coming to a point - there will still be length present even when the crown is almost absent (a non-zero intercept). Therefore, teeth affected by wear should show an anisometric relationship between standard deviation and mean (Figure 2.2B). Teeth that are trapezoidal but have minimal effect of wear (brachydont teeth or teeth that resist wear) may still have a degree of proportionality that could create a significant relationship between height and length among many individuals, but this should display covariance, not dependence, and pass through the intercept at 0 (Figure 2.2A, gray squares).

We found significant correlation between height and length of M1 for most species (Table 2.3). 11 of 17 regressions had slopes significantly different from zero (each with $p < 0.05$), and all regressions had intercepts significantly different from zero (Table 2.3). The correlation between length of the molars and M1 height (our age proxy) was stronger in the anterior teeth 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 in molar width: 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 2.3).

Table 2.3. 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
	pIntercept	*<.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
	pIntercept	*<.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
	pIntercept	*<.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
	pIntercept	*<.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
	pIntercept	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*

Table 2.3, continued.

		bact	drom	guan	vicu	hylo	dors	leuco	dilv	nigi	weyn	phil	munt	reev	ovis
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
	pIntercept	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*

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 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.

Width measurements tell a different story. The correlation between height of M1 and width of different molars is negative: older teeth are wider teeth. Because our measurements were taken on the maximum width, which was typically at the base of the tooth, the negative correlation of width and height may be a result of cryptic eruption: if a tooth appeared fully erupted but was not, we would have underestimated the width.

Sexual Dimorphism

Another possible reason for high variation in artiodactyl dentition is the presence of sexual size dimorphism. Our *t*-tests for sexual dimorphism were significant for M1 L, but not for any other measurement of *Ovis dalli* (Table 2.4). Our Shapiro-Wilk tests were not significant, indicating no deviation from normality in *Ovis dalli* molars, though the *p*-value for M1 L did approach significance ($p = 0.08$, Table 2.4). 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 2.4). Finally, our mixture analysis could not reject the null, single distribution hypothesis for any of our univariate molar measurements in *Ovis dalli*.

Table 2.4. 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 one 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

Several of our caniniform values had significant Shapiro-Wilk results, but none showed signs of multimodality according to Hartigan's Dip test (Table 2.5). 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 2 distributions 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 2.5. 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 gray.

		Shapiro-Wilk	Hartigan's	>1	>2
C. dromedarius	C1 L	*0.01*	0.99	*0.05*	0.38
	C1 W	*0.01*	0.46	*0.03*	0.35
	P2 L	0.95	0.91	0.98	
	P2 W	*0.01*	0.71	0.41	
	Multivariate			0.78	
C. bactrianus	C1 L	0.47	0.97	0.88	
	C1 W		0.85	0.82	
	P2 L	0.11	0.47	0.16	
	P2 T	0.34	0.06	0.31	
	Multivariate			0.07	
Hylochoerus	C1 L	0.40	0.45	0.76	
	C1 W	0.47	0.40	0.45	
	C1 Height	*0.01*	0.89	0.40	
	Multivariate			0.61	

Coefficients of Variation

Camels were significantly larger than the rest of our artiodactyls and had larger relative variation, which caused us to suspect that perhaps CV was not truly removing the influence of size in our sample. We tested for inadequate compensation by CV by evaluating the relationship between standard deviation and mean within measurement types.

Table 2.6. Regression Coefficients for Average and Standard deviations. Significant p-values are italicized and highlighted in gray. 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)	R^2	NLS intercept	NLS slope	change in AIC	AIC relative liklihood
All Characters	-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	-0.10	0.01	0.40	-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*	0.20	*<.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
T P2	0.04	0.27	0.04	0.37	0.28	-0.01	<.01	0.43	0.02	0.99
T P3	0.02	0.34	0.07	*0.01*	0.25	0.41	<.01	0.81	0.45	0.80
T P4	-0.01	0.83	0.10	*<.001*	0.91	0.51	<.01	1.06	0.00	1.00
T M1	-0.03	0.28	0.12	*<.001*	0.39	0.74	<.01	1.20	0.10	0.95
T M2	-0.04	0.39	0.12	*<.001*	0.51	0.62	<.01	1.19	0.17	0.92
T M3	-0.12	*0.02*	0.18	*<.001*	*0.01*	0.77	<.01	1.77	-1.26	0.53
Premolars	0.14	0.30	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
Caniniform Teeth	-0.01	0.59	0.31	*<.001*	*<.001*	0.90	<.01	1.03	0.04	0.98

For most measurements, the relationship between standard deviation and mean was proportional and best described by a linear relationship with a zero intercept (Table 2.6). M1 L, M2 L, M3 T, and length of the molar row all had intercepts that were significantly different from zero (Table 2.6). 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 significantly different from zero, indicating no linear relationship between standard deviation and size in this dataset (Figure 2.3). 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 2.6). 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 <0.0001). When we excluded camels, we found that the anisometric relationship disappeared for M1 L and M2 L (Table 2.7). Anisometry was still present in the length of the molar row and width of M3 with or without camels.

Table 2.7. Regression Coefficients for Average and Standard deviations, without Camelus species. Significant p-values are italicized and highlighted in gray. 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)	R^2	NLS intercept	NLS slope	change in AIC	AIC liklihood
All Characters	0.01	0.38	0.11	*<.001*	0.30	0.56	0.11	0.98	0.02	1.01
L P2	0.05	0.55	0.04	0.69	0.54	-0.10	0.09	0.40	-0.02	0.99
L P3	-0.02	0.75	0.15	0.12	0.59	0.15	0.12	1.15	0.05	1.03
L P4	-0.03	0.29	0.14	*<.01*	0.29	0.59	0.10	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	1.08
L M2	-0.06	0.14	0.15	*<.001*	0.06	0.79	0.09	1.34	0.11	1.05
L M3	0.04	0.25	0.05	*0.01*	*0.01*	0.48	0.09	0.71	-0.77	0.68
T P2	0.04	0.27	0.04	0.37	0.28	-0.01	0.08	0.43	0.01	1.01
T P3	0.08	*0.01*	<.01	0.94	*0.01*	-0.10	0.08	0.01	0.00	1.00
T P4	-0.01	0.93	0.10	0.19	0.98	0.08	0.10	0.99	0.01	1.00
T M1	-0.04	0.47	0.12	*0.01*	0.63	0.44	0.08	1.30	0.06	1.03
T M2	-0.07	0.21	0.14	*<.01*	0.30	0.55	0.07	1.56	-0.03	0.98
T 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	1.07
Caniniform Teeth	-0.01	0.60	0.29	*<.001*	*<.001*	0.91	0.27	1.06	-0.20	0.91

These non-proportional relationships between standard deviation and mean are contrary to the correlation predicted by Simpson and Roe (1939), who suggested that larger measurements

and larger animals should have correspondingly 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 2.4); presumably the influence of measurement error overwhelms any linear trend. However, our results also suggest that large endmembers are responsible for some of the non-proportionality. Our measurements were, on the whole, much larger than those conducted by Polly (1998) because our study organisms were larger. CV may poorly account 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: 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 predominantly became isometric again. *Camelus* had a strong relationship between age and size in these measurements, and was an endmember; further research should be conducted with additional large ungulates to see whether our anisometric trend is truly size bias in CV, or if camels are simply inordinately variable.

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.

t-Tests for Significant Differences in Coefficients of Variation

It is clear that dental measurements are inadequate for separation in DFA, but DFA is rarely employed by palaeontologists because of the lack of appropriate and known training sets. Given the high variation in our artiodactyl samples, how likely would a palaeontologist be to reject a single-species hypothesis for a sample of dental material? *t*-tests are often used to detect whether a CV is significantly increased as a result of multiple species in a sample (Sokal and Braumann 1980, Cope and Lacy 1992, Cope 1993). Our six species of duikers are sympatric and have highly overlapping ranges, all co-occurring in the lowland forests of the Congo (Johnston and Anthony 2012). Our sample had one species of the giant duiker clade (*Cephalophus silvicultor),* and one of the dwarf duiker clade, (*Philantomba monticola)* as well as four mid-sized duikers from the East African Red clade. The giant and dwarf duikers were obviously different from the rest of the sample, and so we only combined the four species of similarly-sized duiker (*C. dorsalis, C. nigrifrons, C. leucogaster* and *C. weynsi*).

Using a *t*-test, we compared CV values from the combined sample of four mid-size duikers versus single-species CV values (Table 2.8). Only three measurements had combined CV values that were significantly larger than any single-species CV value (probability cut-off of $p < 0.05$, Table 2.8). The highest number of significant values within a species was only 2 of 17 (cumulative binomial probability of $p = .17$). Given that significant *p*-values occur randomly one time in twenty, a palaeontologist would reasonably need to find significance in 3 of 15 *t*-tests before rejecting a single-species hypothesis (cumulative binomial probability of $p < .05$), a

threshold not exceeded by any of our duiker species models. In this case, the CVs of dental measurements alone are not adequate to detect the presence of a lumped sample of four species. Several workers (e.g. Kelley and Plavcan 1998; Plavcan and Cope 2001) have suggested other tests like the Levene's test may prove more fruitful when looking at possibly combined samples.

Table 2.8. t-values for comparisons between two species mixtures (Cephalophus and Miniochoerus) and multiple single-species CVs. Significant t-values (p<.05) are highlighted in gray. Combined muzzles of juveniles and adults, and only adult muzzle values are both reported.

Multispecies Mix:	*Cephalophus dorsalis, leucogaster, nigifirons, weynsi*						*Miniochoerus affinis & gracilis*				
Single Species Comparison:	**weyn**	**silv**	**nigi**	**leuc**	**dors**	**phil**	**munt**	**nigi**	**vicu**	**taya**	**dico**
L P2	0.85	0.16	1.12	0.16	0.33	1.12					
L P3	-0.01	0.17	0.64	0.12	-0.06	0.18					
L P4	0.44	0.08	0.15	0.09	0.32	0.15					
L M1	-0.10	-0.05	0.00	0.04	-0.04	0.10	0.01	-0.02	2.62	1.31	0.94
L M2	-0.13	-0.07	0.03	0.21	-0.11	0.10					
L M3	0.24	-0.14	0.04	0.64	-0.12	0.05					
Premolars	*3.24*	0.10	0.83	0.14	0.27	0.52	-0.21	1.37	-0.27	1.32	0.88
Molars	0.04	0.18	0.13	0.21	-0.11	0.34	-0.06	1.27	-0.02	*3.96*	0.98
Tooth row	*2.03*	0.03	0.87	0.01	0.10	0.21	-0.06	*3.57*	-0.23	*2.96*	*2.07*
T P2	-0.07	0.44	0.13	0.05	0.01	-0.11					
T P3	0.70	*2.09*	0.54	0.13	0.39	-0.04					
T P4	-0.04	0.07	-0.02	0.39	0.02	-0.23					
T M1	0.46	0.27	0.33	0.67	-0.11	-0.04					
T M2	0.28	-0.13	0.08	0.81	0.11	0.15					
T M3	0.33	0.12	0.05	0.42	0.45	0.49	0.01	0.33	0.05	0.82	0.68

Implications for Merycoidodontoidea

Variation is overall higher in our sample of artiodactyls than in published samples of carnivores or primates, but variation depends on the species in question. Duikers and camels do not vary in the same ways nor with the same numerical values, both as a consequence of differing

morphology (and thus different dental wear effects) and as a consequence of differing size (as the coefficient of variation does not perfectly remove size effects). When picking a modern analogue for a variation analysis of a fossil group, it is therefore important to pick modern taxa with a similar influence of wear and size as is present in a fossil sample.

There are two analyses of Merycoidodontoidea that compare dental variation of fossil samples to the variation of modern analogues: Phleger and Putnum (1942) and Stevens and Stevens (2005). Phleger and Putnam (1942) compared species of the genus *Miniochoerus* to modern and extinct lions, which is unlikely to be an appropriate analogue group for oreodonts given the strong occluding constrains on felid dentition. Stevens and Stevens (2005) used the peccaries *Dicotyles tajacu* and *Tayassu pecari*, which have the benefit of being artiodactyls similar in body form to members of Merycoidodontoidea. Peccaries have bunodont dentition, which wears differently from the selenodont dentition of *Miniochoerus affinis* and *M. gracilis*, the two small-bodied merycoidodonts from the White River Group considered by Stevens and Stevens (2005).

Miniochoerus has selenodont dentition with prominent para, meso- and metastyles (Schultz and Falkenbach 1956). These styles are angled to such an extent that unworn surfaces would be greater in extent than worn surfaces, and age-related wear should influence tooth length as it does in *Camelus*. We compared CVs of *Miniochoerus* specimens to the similarly-sized dentition of *Vicugna vicugna*, *Muntiacus muntjak*, and *Cephalophus nigrifrons* as well as the reported CVs of peccaries from Stevens and Stevens (2005). Stevens and Stevens (2005) report a combined *Miniochoerus* M3 width CV of 11.47, a value similar to our modern taxa. Given the possibility of significant *p*-values by chance, we would need 2 out of 5 measurements to have significantly different variance to confidently reject a single-species hypothesis. Only

Tayassu pecari had significantly lower variance in two measurements than the *Miniochoerus* sample did. Only for *Tayassu pecari* would we have been confident in rejecting a single-species hypothesis (Table 2.8). Stevens and Stevens (2005), using *Tayassu* as their model, rejected a single-species hypothesis and described two co-occurring species: *M. affinis,* and *M. gracilis.*

It is important to choose comparative taxa carefully. The body form of *Miniochoerus* has a great deal in common with suids, but the teeth are more similar those of selenodont artiodactyls than the omnivorous, bunodont peccary species chosen as analogous by Stevens and Stevens (2005) or the carnivorous *Smilodon, Felis*, and jaguar chosen by Phleger and Putnam (1942). No character state separates *M. affinis* from *M. gracilis* (Phleger and Putnam 1942), and they co-occur. Their distributions of measurements overlap, and without any discrete morphological characters there is no evidence upon which to separate them into two distinct size classes (Phleger and Putnam 1942, Schultz and Falkenbach 1956, Gustafson 1986). The species of *Miniochoerus* as reported by Stevens and Stevens (2005) are also diagnosed by character divisions that are not statistically meaningful. As we have also found that cryptic diversity is present but undetectable in dental samples of modern duikers, it is possible that more than one species of *Miniochoerus* exists. Regardless, these species are still not diagnosable via reported characters, and should be reexamined.

Conclusion

Dental measurements in artiodactyls are not sufficient for identification at the species level when using DFA or, in some cases, Z tests of the coefficient of variation. Some artiodactyl dentition - camels in particular - 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. The artiodactyl pattern of higher variation in premolars may result from a decrease in functional constraints in the anterior of the chewing battery. Premolar rows are more variable than either molar rows or overall toothrow lengths, partly as a result of high quantitative variation in premolars but also as a result of rotated, replicated, or absent teeth.

For molars, the story is more complicated: while variation decreases in lengths of each subsequently posterior molar, variation increases posteriorly in widths. Increased variation in molar lengths results from changes through wear: older teeth are more worn and smaller. For widths the increase in variation posteriorly may result from undetected eruption differences. Both molar variation patterns result from the morphology of certain selenodont teeth: M1 is longer at the occlusal surface than at the base, while M3 is wider at the base than at the occlusal surface. With the exception of duikers, selenodont molars show measurement changes through wear and wear-related size change should be considered when selecting analogous taxa for comparisons to fossil populations. It is not simply enough to measure teeth at the base, because widths are still highly variable at the base of the tooth. Duikers demonstrated overall low variation with minimal differences throughout the toothrow, possibly as a result of the differing functional constraint of frugivory and a low reliance on gape.

Sexual dimorphism is another complicating factor that may increase variation in dental measurements. 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 (Carranza and Pérez-Barbería 2007). 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 in fossil samples using statistical techniques.

When selecting a modern analog it is important to select an analogue that is morphologically similar but also similar in size as our research shows that CV may not adjust for size differences between different taxa. Phylogenetic relatedness should also come into play when choosing an appropriate analogue – camels and duikers vary differently, which can inform a paleosystematist's decision to accept or reject a single-species hypothesis. Once a palaeosystematist has selected one or more appropriate comparative taxa, their next step should be to use significance tests for differences in variation. We found that combined CVs of *Minochoerus gracilis* and *affinis* reported by Stevens and Stevens (2005) were not significantly higher than the modern single-sample CVs of any selenodont taxa of similar body size. This may also result from the conservative nature of the *t*-test for CV data - other workers have reported that CV significance tests are prone to rejecting multispecies hypotheses (Kelley and Plavcan 1998, Plavcan and Cope 2001). Similarly, we found that we were unable to reject a single-species hypothesis for a multi-species sample of similarly-sized sympatric duikers.

Though variable within species, artiodactyl dentition is conserved between species and did not diagnose taxa via DFA or demonstrate multi-species groups via *t*-tests in our sample. Dental measurements may be generally too conservative to reveal multispecies samples of artiodactyls.

Supplementary Table Captions

Table S1.1. Lengths and widths of premolars and molars. Acronyms: L, Length; W.

Table S1.2. Measured data of incisors, canines, premolar row, toothrow and molar row.

Acronyms: L, Length; W, Width, H, Height. Measurement uncertainty also listed.

CHAPTER III

CRANIAL LANDMARKS OF DUIKER ANTELOPE DIAGNOSE GEOGRAPHY, NOT PHYLOGENY

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Abstract

Vertebrate paleontologists have been naming fossil mammal species for centuries, but how well cranial morphology diagnoses artiodactyl and other vertebrate species has not been thoroughly tested. We can test the accuracy and resolution of osteological diagnosis by comparing extant species to species diagnosis made using their skulls. For this study we chose a "worst case" scenario for paleontologists: duiker antelope, an abundant group of African artiodactyls with similar morphologies, recent divergence, and overlapping ranges. Our study uses geometric morphometric analyses to determine A) whether overall cranial shape of duiker antelope can be used to identify duiker species through classification analysis, and B) whether cluster analysis of cranial material creates clusters similar to those defined by coat pattern and DNA. Correct classification percentage ranged between 22% and 71%, and misclassification specimens were primarily misidentified as taxa that overlapped in range, rather than as sister taxa. Cluster analysis showed only 3 distinct groupings rather than the 10 species included, suggesting that paleontological studies of these and other similar taxa would underestimate

paleodiversity. We advocate using the term "species complex" to describe any fossil sample where variation exceeds what would be expected by a single species sample, yet yields no diagnostically different characters.

Introduction

Skulls are a current gold standard for fossil artiodactyl holotypes, but while cranial morphology is adapted for the complicated rigors of feeding, breathing, sexual selection, sensory reception, and species recognition, it is possible that these differences may not diagnose species with the same fine-scale detail as DNA or other modern techniques. The field of genetics has opened up difficult questions in modern systematics, and even neontologists struggle to accurately diagnose cryptic, sympatric mammalian species (Baker and Bradley 2006b, Colyn et al. 2010). Defining the species concept for fossil animals has been similarly difficult, and is a patchwork of differently scaled levels of definition specificity (Agapow et al. 2004, Forey et al. 2004). The inconsistency of the fossil species concept has led to opposing systematics revisions of many fossil mammals – for example, the extinct artiodactyl superfamily Merycoidodontoidea has between 88 and 290 diagnosable taxa according to different systematists (Schultz and Falkenbach 1968, Lander 1998, Stevens and Stevens 2007). Opposing fossil species concepts have gridlocked studies of the ecology and evolution of Merycoidodontoidea, and because the osteological characters used have not been evaluated for diagnostic power in modern artiodactyls it is hard to say whether any one of these revisions is more accurate than the other.

Species should be diagnosed at a level which is comparable to modern diversity. Standing in the way of this goal is the fact that few modern artiodactyls have been diagnosed using osteological characters without the benefit of soft tissues. Artiodactyl skeletal diagnosis is

particularly understudied, with variation studies conducted in only a handful of species (e.g. Vrba 1987, Stevens and Stevens 2005, Carranza and Pérez-Barbería 2007, Natsume et al. 2008). Artiodactyls are abundant, often sexually dimorphic, and have many overlapping species utilizing the same resources – a difficult scenario for diagnosis in the fossil record. Duiker antelope (Cephalophinae, Bovidae, Artiodactyla) are a paleontological worst-case scenario even among artiodactyls. The systematics of duikers are contentious, with cryptic species (Colyn et al. 2010), elevated and demoted subspecies (Groves and Grubb 2011), and considerable evidence for reticulation and introgression (Johnston 2011). To complicate matters further, duikers are highly sympatric with as many as 8 species of duiker overlapping in range (IUCN 2016). Despite considerable overlap, duikers are ecologically very homogenous: with the exception of *Sylvicapra,* duikers are frugivores that occasionally also eat leaves (Kendrick et al. 2009). Larger duikers eat correspondingly larger fruit, but there are otherwise few dietary differences even in sympatric duikers (Hofmann and Roth 2003). Behavioral rather than dietary differences define duiker niche space, primarily through differences in activity patterns and range sizes (Newing 1994, Bowland and Perrin 1995).

Would the atypical diversity of duikers be detected if only their skulls were present, or would it be underestimated? Are the characters employed by artiodactyl paleontologists legitimate morphological markers of species diversity, or do they capture a different landscape of subgroups altogether? Accurately articulating fossil species diversity is not a mere "stamp collecting" expedition, but a fundamental underpinning of broad-scale ecological and evolutionary studies. As a prime example of the utility of the fossil record, prehistoric extinctions are now being used to inform modern conservation efforts through the growing field of

Conservation Paleobiology (Dietl and Flessa 2011, Gavin et al. 2014, McGuire and Davis 2014, Maguire et al. 2015).

For paleobiological studies to be maximally informative for modern conservation efforts, diagnosis of fossil species must be comparable to extant taxa. We tested the adequacy of cranial characters for diagnosing sympatric duiker species using a 3D geometric morphometrics approach that captured the characters used to diagnose fossil taxa. We used characters commonly used in artiodactyl systematics with an emphasis on the diagnostic characters of Merycoidodontoidea (Thorpe 1937b, Schultz and Falkenbach 1968, Stevens and Stevens 2005, 2007), an extinct group with sympatry and morphology similar to modern duikers. By determining the accuracy of species diagnosis using cranial characters, we can better understand how morphologically-defined fossil artiodactyl species compare to biologically-defined modern artiodactyls.

Abbreviations and Terminology

Specimens: *Cephalophus callipygus* (CALL), *Cephalophus dorsalis* (DORS), *Cephalophus leucogaster* (LEUC), *Cephalophus natalensis* (NAT), *Cephalophus nigrifrons* (NIG), *Cephalophus rufiliatus* (RUF), *Cephalophus silvicultor* (SILV), *Cephalophus weynsi* (WEYN), *Philantomba monticola* (MONT) and *Philantomba maxwelli* (MAX).

Museums: American Museum of Natural History (AMNH), Museum of Comparative Zoology (MCZ), and Museum of Vertebrate Zoology (MVZ).

Materials and Methods

Specimens: Our sample consisted of 79 dentally mature crania representing 10 species, two genera: *Cephalophus callipygus*, *Cephalophus dorsalis*, *Cephalophus leucogaster*, *Cephalophus*

natalensis, Cephalophus nigrifrons, Cephalophus rufiliatus, Cephalophus silvicultor, Cephalophus weynsi, Philantomba monticola and *Philantomba maxwelli (Table S2.1).* We used taxonomy from the IUCN redlist (IUCN 2016), but biological species are often contentious and *C. weynsi* and *C. callipygus* are frequently synonymized into *C. callipygus* by some workers (Groves and Grubb 2011, Johnston 2011). Additionally, the poorly recorded geographic data for several of our specimens means that our sample of *Philantomba* could contain specimens of recently-described *P. walteri*, a new species previously considered a geographic variant of *P. monticola* (Colyn et al. 2010).

3D Models: We made dorsal and ventral 3D surface models of crania using 3D photogrammetry in Agisoft Photoscan (Agisoft 2013, Mallison and Wings 2014). We placed 44 landmarks (Figure 3.1) using Landmark Editor (Wiley 2007) and combined dorsal and ventral landmarks using the freeware program DVLR (Raaum 2006). We performed a general Procrustes analysis in the package 'geomorph' in R (Adams and Otárola-Castillo 2013) to align specimens for analysis (Supplementary Table 3.1).

Dimensional Reduction: Principal components analysis (PCA) reduces the high dimensionality of 3D geometric morphometrics data into data more easily interpreted by classification analyses (Adams et al. 2004). PCA axes maximize the variance among either individuals (basic PCA) or species groups (among-groups PCA). We imported our landmarks and performed classic PCA using the package 'geomorph' in R (Adams and Otárola-Castillo 2013). We used the 'multigroup' package to perform an among-groups PCA (Eslami et al. 2014, 2015).

Classification Data Subsets: Size is often included in species diagnosis, but morphometrics data removes scale to analyze pure shape. We achieved scale by multiplying our PCA data by skull length (prosthion to inion). We then used subsets of scaled and unscaled data using PCA and among-group PCA to see which method was the most accurate in our subsequent classification analyses.

Classification Analysis: The first 17 principle components (PCs) accounted for 99% of the variance in our sample, so we used them in our classification. We performed a linear discriminant function analysis with jackknife cross-validation using the R package 'MASS' (Ripley et al. 2015) and a random forest analysis using the package 'randomForest' (Liaw et al. 2009). Discriminant function analysis is a commonly applied classification method with a number of underlying assumptions, including low-to-no multicollinearity and multivariate normality, while Random Forest Analysis is a newer non-parametric method with fewer assumptions (Liaw and Wiener 2002). We used both methods to compare prediction accuracy; while DFA is a more common statistical method in paleontology (Reed 1998, Fraser and Theodor 2011, Davis and McHorse 2013), the binary decision tree classification procedure of Random Forest is very similar to the "keying out" process used intuitively by taxonomists, and may more accurately replicate identification decision-making.

We compared misclassified specimens to a consensus phylogenetic tree of duikers from 10k trees (Figure 3.2), and to overlapping geographic ranges downloaded from the IUCN Redlist (IUCN 2016). If specimens were misclassified as their sister taxa, we considered them a phylogenetic misclassification. If specimens were not misclassified as their sister taxa but were misclassified as another duiker which had a geographically overlapping range, we considered

that a geographic misclassification. Most of our specimens were missing precise locality information, so finer-scale geographic examination was not possible. In some cases, specimens were misclassified as a duiker that had neither overlapping ranges nor was closely related.

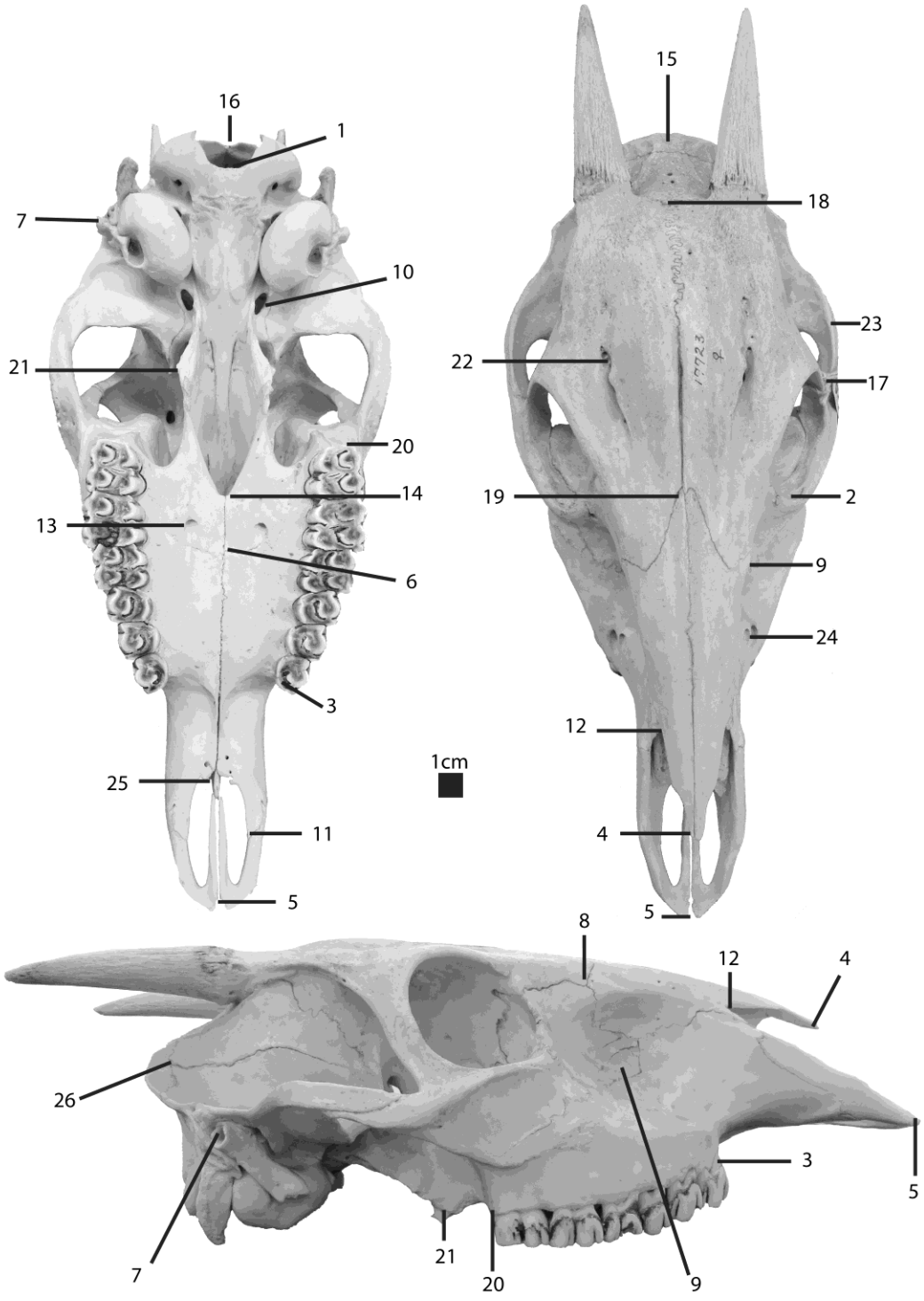

Figure 3.1. Skull of MCZ 17723 Cephalophus silvicultor, showing landmarks used in study. Anatomical landmark names from (White et al. 2011). 1) Basion; 2) Anteriormost surface of orbit; 3) Anterior of P2, labial surface; 4) Rhinion; 5) Prosthion; 6) Ante

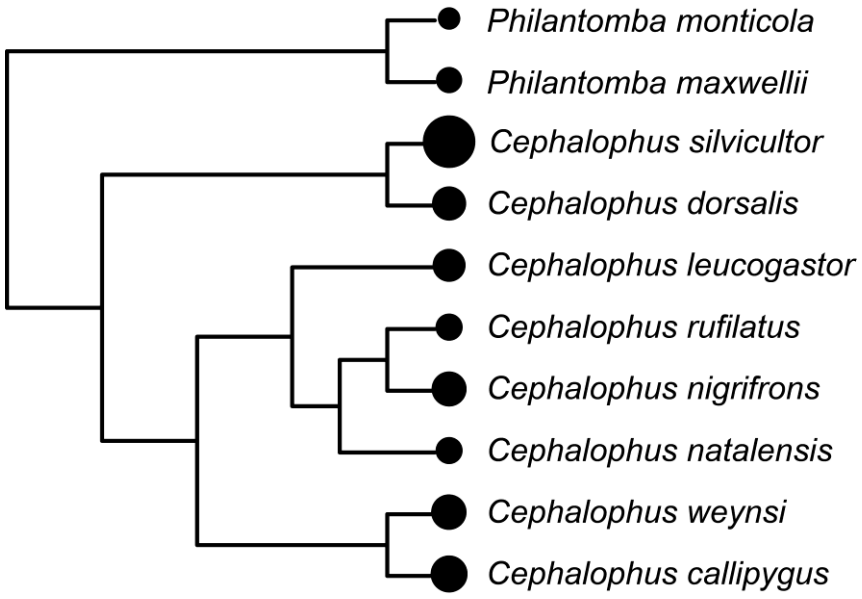

Figure 3.2. Phylogenetic consensus tree from 10K trees (Arnold et al. 2010). Tips are scaled to relative skull length.

Cluster Analysis: Cluster analysis is sometimes used by paleontologists to determine the number of discrete multivariate groups of fossil taxa (Valentine and Peddicord 1967, Shi 1993). We used hierarchical clustering methods for our coordinate data using 'pvclust' in R, and distribution clustering methods for our skull lengths using 'mclust' in R (Fraley and Raftery 2006, Suzuki and Shimodaira 2006). The results of clustering analysis vary by methodology (Blashfield 1976), so we tested combinations of the different algorithms and distance measurements offered in 'pvclust' to determine whether any method could potentially mimic biological species. Paleontologists sometimes use pure size variables, so we also conducted a univariate bootstrapped distribution analysis in 'mclust' to investigate whether size alone could diagnose biological species.

Convergent Evolution: To visually evaluate convergence of landmarked characters between taxa, we created a phylomorphospace plot of species average PC scores using the package

'phytools' in R (Revell 2012). A phylomorphospace plot projects a tree into morphospace, so that morphologically similar taxa are plotted near each other. Projecting phylogenetic relationships and morphological affinities simultaneously makes it easier to visualize trait convergence.

Results

The most largest eigenvalues for the first 5 PC axes were related to the position of prosthion, inion, basion, dacryon, and the infraorbital and supraorbital foramina (see Figure 3.1 for anatomy). These characters capture the overall length, height, and width of the skull – in essence, the first five PC axes seem to be capturing either allometry or overall skull shape rather than specific placement of features. Almost all of the characters with high eigenvectors in any PC axis were from the dorsal side of the skull; ventral characters were highly conserved among species.

Cranial landmarks showed minimal ability to discriminate species, ranging from 22% correct identification to a maximum of 71% (Table 3.1). Discriminant function analysis performed generally better than Random Forest analysis. Adding size back into coordinates dramatically decreased the performance of both DFA and RF. Specimens that were incorrectly identified were more likely to be identified as a species that shared overlapping ranges but was not a sister species (Table 3.1, Table 3.2).

Table 3.1. Classification summaries from discriminant function analyses and random forest analyses, showing percentage of specimens identified correctly, percentage incorrectly identified as their sister taxa, and percentage incorrectly identified as a geographically overlapping species. Each column represents a different data format: principal components analysis (PCA), PCA scores scaled by size, among-group PCA (agPCA), and agPCA scores scaled by size.

Discriminant Function Analysis				
	PCA	PCA*size	agPCA	agPCA*size
% correct	70.89	68.35	22.78	24.05
% geographic	56.52	56.00	81.97	75.00
% phylogenetic	34.78	32.00	4.92	10.00

Random Forest Analysis				
	PCA	PCA*size	agPCA	agPCA*size
% correct	56.96	49.37	32.91	22.78
% geographic	70.59	75.00	92.45	88.52
% phylogenetic	20.59	15.00	3.77	4.92

Table 3.2. Classifications from discriminant function and random forest analyses. Each row shows the number of specimens classified in that category (correctly, or incorrectly as a duiker with overlapping geographic range, as a sister species, or as a species that was neither geographically overlapping nor closely related) Each column corresponds to a subdivision of data and analysis type: principal components analysis data, PCA data scaled by size, among-group PCA data, and among group PCA scaled by size. All four data types were tested using Discriminant Function analysis and Random Forest analysis. For example, the first row shows the number of C. callipygus *specimens identified as* C. callipygus, *(which is the correct identification, as described by the column headed Classification Type). For discriminant function analysis, PCA, PCA scaled by size, and among-group PCA scaled by size did not classify any specimens of* C. callipygus *as* C. callipygus. *Among-group PCA without size correctly classified one individual. Under Random Forest Analysis, none of the four data types correctly classified* C. callipygus.

			Discriminant Function Analysis				Random Forest Analysis			
Actual Species	Identified As	Classification Type	PCA	PCA *Size	agPCA	agPCA *Size	PCA	PCA *Size	agPCA	agPCA *Size
CALL	CALL	Correct	0	0	1	2	0	0	0	0
DORS	DORS	Correct	11	10	7	6	10	10	0	2
LEUC	LEUC	Correct	20	20	9	10	20	20	16	16
MAX	MAX	Correct	4	2	0	0	1	1	2	0
MONT	MONT	Correct	2	4	0	0	1	1	0	0
NAT	NAT	Correct	3	3	0	0	0	0	0	0
NIG	NIG	Correct	5	5	0	0	2	0	1	0
RUF	RUF	Correct	0	0	0	0	0	0	0	0
SILV	SILV	Correct	2	2	0	0	3	1	0	0
WEYN	WEYN	Correct	9	8	1	1	8	6	7	0

Table 3.2, continued.

Actual Species	Identified As	Classification Type	Discriminant Function Analysis				Random Forest Analysis			
			PCA	PCA *Size	agPCA	agPCA *Size	PCA	PCA *Size	agPCA	agPCA *Size
CALL	DORS	Geographic	0	0	1	0	1	0	1	0
CALL	LEUC	Geographic	1	1	1	1	2	2	4	5
CALL	MONT	Geographic	0	0	1	0	0	0	0	0
CALL	NIG	Geographic	1	1	1	0	1	1	0	0
CALL	SILV	Geographic	0	0	0	1	0	0	0	0
DORS	CALL	Geographic	0	0	0	0	0	0	0	0
DORS	LEUC	Geographic	0	0	1	1	2	1	10	10
DORS	MAX	Geographic	0	1	0	0	0	0	0	0
DORS	MONT	Geographic	1	1	1	0	0	0	0	0
DORS	NIG	Geographic	0	0	0	0	0	0	0	0
DORS	RUF	Geographic	0	0	0	1	0	0	0	0
DORS	WEYN	Geographic	0	0	1	1	0	1	2	0
LEUC	CALL	Geographic	2	2	2	1	0	0	0	0
LEUC	DORS	Geographic	0	0	2	1	1	0	2	4
LEUC	MAX	Geographic	0	0	1	2	0	0	0	0
LEUC	MONT	Geographic	0	0	2	1	0	0	0	0
LEUC	NIG	Geographic	0	0	1	1	0	0	0	0
LEUC	RUF	Geographic	0	0	0	0	0	0	0	0
LEUC	SILV	Geographic	0	0	2	2	0	0	0	0
LEUC	WEYN	Geographic	0	0	3	4	1	2	4	2
MAX	CALL	Geographic	0	1	0	0	0	0	0	0
MAX	NIG	Geographic	0	0	0	0	0	1	0	0
MAX	RUF	Geographic	0	0	0	0	0	0	0	0
MAX	SILV	Geographic	0	0	0	0	0	0	1	0
MONT	CALL	Geographic	0	0	0	0	0	0	0	0
MONT	DORS	Geographic	0	0	1	1	0	0	1	0
MONT	LEUC	Geographic	0	0	2	2	1	3	2	1
MONT	NAT	Geographic	0	0	0	0	0	0	0	0
MONT	NIG	Geographic	0	0	0	0	0	0	1	0
MONT	RUF	Geographic	0	0	0	0	0	0	0	0
MONT	SILV	Geographic	1	0	1	0	1	0	0	2
MONT	WEYN	Geographic	0	0	1	1	1	0	1	1
NAT	DORS	Geographic	0	0	0	0	0	0	1	2
NAT	MONT	Geographic	0	0	0	0	0	0	0	0
NIG	CALL	Geographic	1	1	2	1	1	1	0	0
NIG	DORS	Geographic	0	0	0	0	0	0	1	1
NIG	LEUC	Geographic	0	0	3	3	3	3	2	3
NIG	MAX	Geographic	0	1	0	1	0	1	0	1
NIG	MONT	Geographic	1	0	1	1	0	0	1	0
NIG	SILV	Geographic	0	0	0	1	0	0	0	0
NIG	WEYN	Geographic	0	0	1	0	1	2	2	2
RUF	DORS	Geographic	0	0	0	0	1	0	0	0
RUF	LEUC	Geographic	0	0	0	0	1	2	2	2
RUF	MAX	Geographic	0	0	0	1	0	0	0	0
RUF	MONT	Geographic	0	0	1	0	0	0	0	0
RUF	SILV	Geographic	0	0	1	1	0	0	0	0
RUF	WEYN	Geographic	0	0	0	0	0	0	0	0
SILV	CALL	Geographic	3	2	0	0	0	1	0	0
SILV	DORS	Geographic	0	0	1	1	1	2	1	2
SILV	LEUC	Geographic	0	1	4	3	1	2	3	4
SILV	MAX	Geographic	0	0	0	1	0	0	1	0
SILV	MONT	Geographic	0	0	0	0	0	0	0	0
SILV	NIG	Geographic	0	0	1	1	0	0	1	0
SILV	RUF	Geographic	0	0	0	0	0	0	0	0

Table 3.2, Continued.

			Discriminant Function Analysis				Random Forest Analysis			
Actual Species	Identified As	Classification Type	PCA	PCA *Size	agPCA	agPCA *Size	PCA	PCA *Size	agPCA	agPCA *Size
SILV	WEYN	Geographic	1	1	0	0	1	0	0	0
WEYN	DORS	Geographic	0	0	1	2	0	0	2	9
WEYN	LEUC	Geographic	0	1	8	5	3	5	2	2
WEYN	MONT	Geographic	0	0	0	0	0	0	0	0
WEYN	NIG	Geographic	0	0	1	1	0	0	1	1
WEYN	RUF	Geographic	0	0	0	0	0	0	0	0
WEYN	SILV	Geographic	1	0	0	1	0	0	0	0
CALL	MAX	Other	0	0	0	0	0	0	0	0
CALL	NAT	Other	0	0	0	0	0	0	0	0
CALL	RUF	Other	1	1	0	0	0	0	0	0
DORS	NAT	Other	0	0	2	2	0	0	0	0
MAX	LEUC	Other	0	0	2	3	2	3	1	2
MAX	NAT	Other	0	0	0	0	0	0	0	0
MAX	WEYN	Other	0	0	1	2	0	0	0	2
NAT	CALL	Other	0	0	0	0	0	0	0	0
NAT	MAX	Other	0	0	1	0	0	0	0	0
NAT	SILV	Other	0	0	0	0	0	0	0	0
NAT	WEYN	Other	0	0	1	1	0	0	1	0
RUF	CALL	Other	1	1	0	0	0	0	0	0
SILV	NAT	Other	0	0	0	0	0	0	0	0
WEYN	MAX	Other	0	1	0	0	0	0	0	0
WEYN	NAT	Other	0	0	1	1	1	1	0	0
CALL	WEYN	Phylogenetic	2	2	0	1	1	2	0	0
DORS	SILV	Phylogenetic	0	0	0	1	0	0	0	0
LEUC	NAT	Phylogenetic	0	0	0	0	0	0	0	0
MAX	DORS	Phylogenetic	0	0	1	0	0	0	0	1
MAX	MONT	Phylogenetic	0	2	0	0	1	0	0	0
MONT	MAX	Phylogenetic	2	0	0	0	1	0	0	0
NAT	LEUC	Phylogenetic	1	1	1	2	4	4	2	2
NAT	NIG	Phylogenetic	0	0	1	1	0	0	0	0
NAT	RUF	Phylogenetic	0	0	0	0	0	0	0	0
NIG	NAT	Phylogenetic	0	0	0	0	0	0	0	0
NIG	RUF	Phylogenetic	0	0	0	0	0	0	0	0
RUF	NAT	Phylogenetic	1	1	0	0	0	0	0	0
RUF	NIG	Phylogenetic	0	0	0	0	0	0	0	0
WEYN	CALL	Phylogenetic	2	2	0	1	0	0	0	0

Cluster analyses of this data were similarly inaccurate. The best cluster analysis of our coordinate data employed the Ward method and found 9 clusters; all others failed to separate taxa into distinct groups. Though the Ward analysis found close to the 10 species that were included, the 9 clusters were all mixed-species samples, and only half of the specimens were even included in the 9 clusters (Figure 3.3). A similar low-level of resolution was found by a distribution clustering analysis of skull lengths, which detected 3 solid clusters (Figure 3.3).

The poor resolution of cluster analyses and classification analyses suggests that the influence of geography is a stronger influence on cranial morphology of duikers than phylogeny or size. Convergent evolution is visible in our phylomorphospace plot (Figure 3.5). The first two PCs show allometric shape change, with smaller species closer together, but PC3-PC8 reveal that morphological data also shows strong convergence between groups of different size (i.e. SILV and NIG, SILV and CALL). The convergent evolution of duiker cranial morphology confirms the strong geographic overprint in our landmark data suggested by our classification and clustering analyses.

Discussion

Neither cluster analysis nor either of our classification methods had high accuracy in replicating extant species using geometric morphometrics, and accuracy was decreased even further when size was included as a factor. Misclassified specimens were identified predominantly as geographically overlapping taxa rather than sister taxa. Therefore, duiker cranial morphometrics are more influenced by geography than shared evolutionary history (Figure 3.5). Convergent morphological evolution in duikers has led to such similar cranial morphologies that members of the dwarf duiker clade *Philantomba* were identified by the DFA as members of the giant duiker clade (Table 3.2, Figure 3.3), though DNA evidence points to their having split 8 million years ago (Johnston 2011).

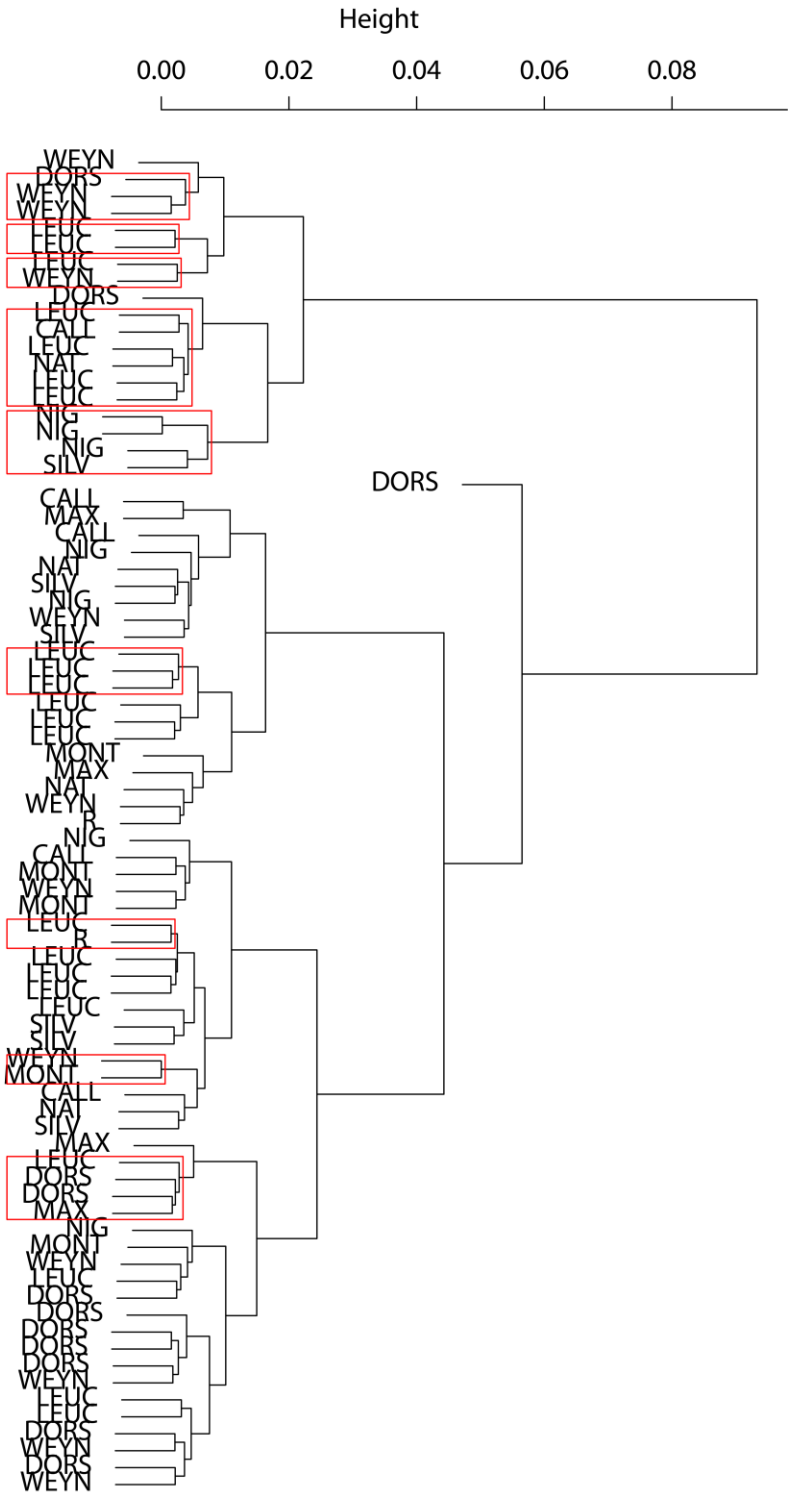

Figure 3.3. Best-performing cluster analysis (correlation, Ward cluster method). Red boxes are supported at p <.05.

Cranial shape is often influenced by diet in artiodactyls (Janis and Thomason 1995, Fraser and Theodor 2011, Tennant 2013), and in duikers, the morphological similarity we have documented likely reflects their uniform diets. Duikers are predominantly frugivorous, and different species of duikers consume the same fruit. Instead, niche space among duikers is defined by behavioral adaptations: differences in range size, activity patterns, and size of fruit selected (Newing 1994). Such behavioral niche space divergence does not necessitate diagnostically different cranial morphology, but can lead to stronger pattern in geographic convergent evolution (Figure 3.4)

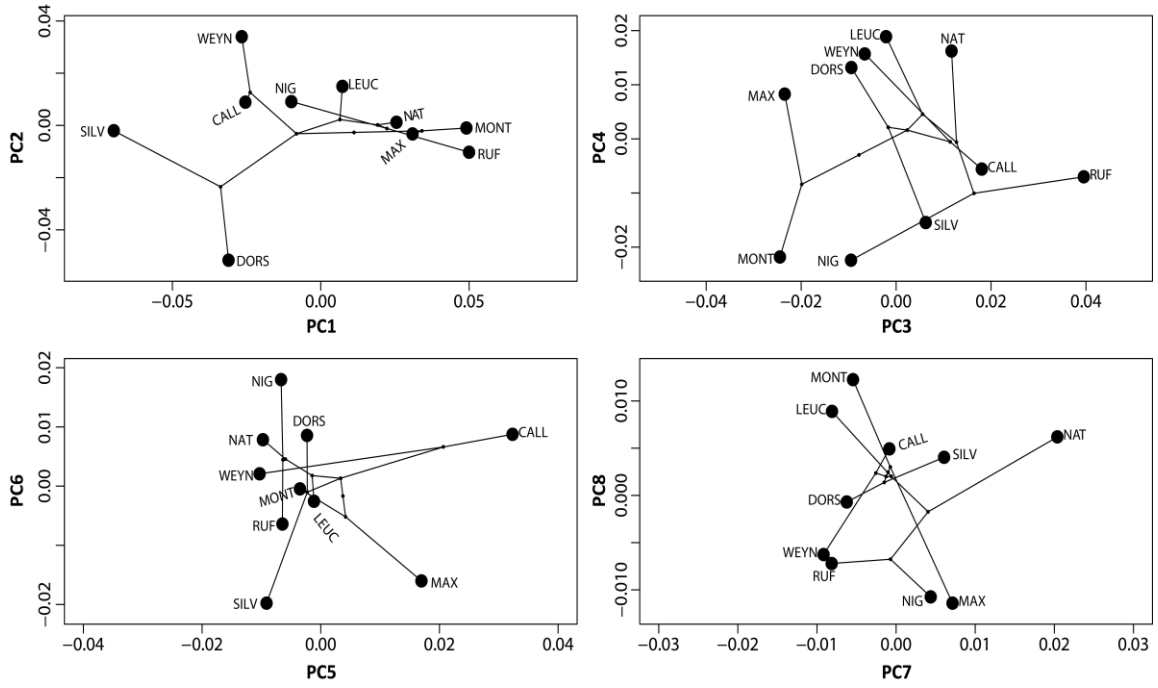

Figure 3.4. Phylogram of principle coordinate scores showing shape convergence in Philantomba (MONT and MAX) and several species of Cephalophus.

Duikers are difficult to distinguish cranially, but they are tropical rainforest specialists – this may be the type of taxonomic tangle that is confined to highly productive rainforest environments. If so, that is unlikely to affect many fossil mammal taxa – rainforest soils are

highly acidic and do not preserve bone well (Retallack 2008). However, duikers are not the only artiodactyl with complicated sympatric species relationships – muntjaks (*Muntiacus* spp.) and dik-diks (*Madoqua* spp.) are both similarly diverse and overlapping (Allard et al. 1992, XiRan et al. 2002, Gilbert et al. 2006). Muntjaks live in areas of similarly poor fossilization likelihood (evergreen and montane forests), but dik-diks live in bushlands – and these environments are particularly likely to fossilize well (Retallack 1991, 2008). Highly diverse artiodactyl samples are therefore potentially preserved in the fossil record – the trick will be to recognize them.

Diet is only one possible reason for different cranial morphology: species identification needs can also cause diversity in cranial shape. Though horns are used for species identification of many bovids, they are variably present within duiker species and their morphology is relatively homogenous and rarely used for diagnosis (Colyn et al. 2010). The horns of duikers are used for ramming and, given their irregular appearance, seem to serve little purpose in species identification (Ralls 1975, Lundrigan 1996). Instead of cranial differences, duikers rely on scent to recognize one another: the large pre-orbital gland produces compounds that are unique between sympatric species (Burger et al. 1988, Bowland and Perrin 1995).

Modern artiodactyls with large scent glands use pheromones to discern species, sex, and age of other artiodactyls (Lawson et al. 2001) – a form of species identification that does not necessitate diagnostic cranial differences. To accommodate their large pre-orbital scent glands, all duikers, muntjaks, and dik-diks possess large pre-orbital fossae. Similar fossae occur in many fossil ungulates, including several species of fossil horse (Forsten 1983), amynodonts (Wall 1980) and Merycoidodontoidea (Schultz and Falkenbach 1968). If segregation by scent plays a role in artiodactyl speciation, then samples of fossil taxa with large pre-orbital fossae may hold hidden diversity.

Once the potential for cryptic morphological species is recognized in a fossil sample, how should those taxa be reported? There are two current approaches: to group all indistinguishable taxa together, or to split them using character states that are continuous or polymorphic within a sample. In the case of Merycoidodontoidea, most researchers have chosen the second option, with multiple species diagnosed in the same locality using characters that may not be diagnostic of species but rather subspecies, or possibly even reflect individual variation (Schultz and Falkenbach 1968, Lander 1998, Stevens and Stevens 2005, Ludtke 2007). This leads to an issue of replicability: other researchers with partial specimens or polymorphic samples from other regions must choose which taxonomy to use. Such inconsistency in identification can artificially increase the beta diversity between sites, simply by a researcher's systematics preferences. Given the increasing number of studies that assume identifications are comparable between workers (Barnosky 2001, Qian et al. 2009, Quental and Marshall 2013, Fraser et al. 2014), we would not advocate over-splitting using small polymorphic characters in otherwise indistinguishable taxa.

Conversely, lumping can lead to under-recognition of the diversity within an assemblage. By obscuring cryptic diversity, or diversity that is recognizable but not diagnosable (i.e. high variation without discernable bins), paleontologists are setting up a system that seems to have increased in diversity over time when it may have decreased or stayed steady. Our study demonstrates that cranial morphometrics would under-predict alpha diversity in modern duikers; comparing a conservative fossil sample to a finer-scale modern sample would thus necessitate either finding morphology that better identifies species, or some form of rarefaction to that compensates for fossil under-diagnosis (Carrasco 2013). A lumped species on its own does not connote information about hidden diversity, requiring that any paleontologist be intimately familiar with the group in question before they know to compensate for different levels of

resolution. By lumping cryptic diversity under the heading of species, systematists risk misinterpretation of their replicable taxonomic unit as being the equivalent of DNA-driven diagnoses.

To avoid confusion, we advocate using the term "species complex" to denote fossil samples whose distributions are suggestive of multiple species which cannot currently be diagnosed. For example, were the data presented in this paper an unidentified fossil sample, we would characterize the fossils as three species complexes – a small, medium, and large group, as recognized by our distribution cluster analysis (Figure 3.5).

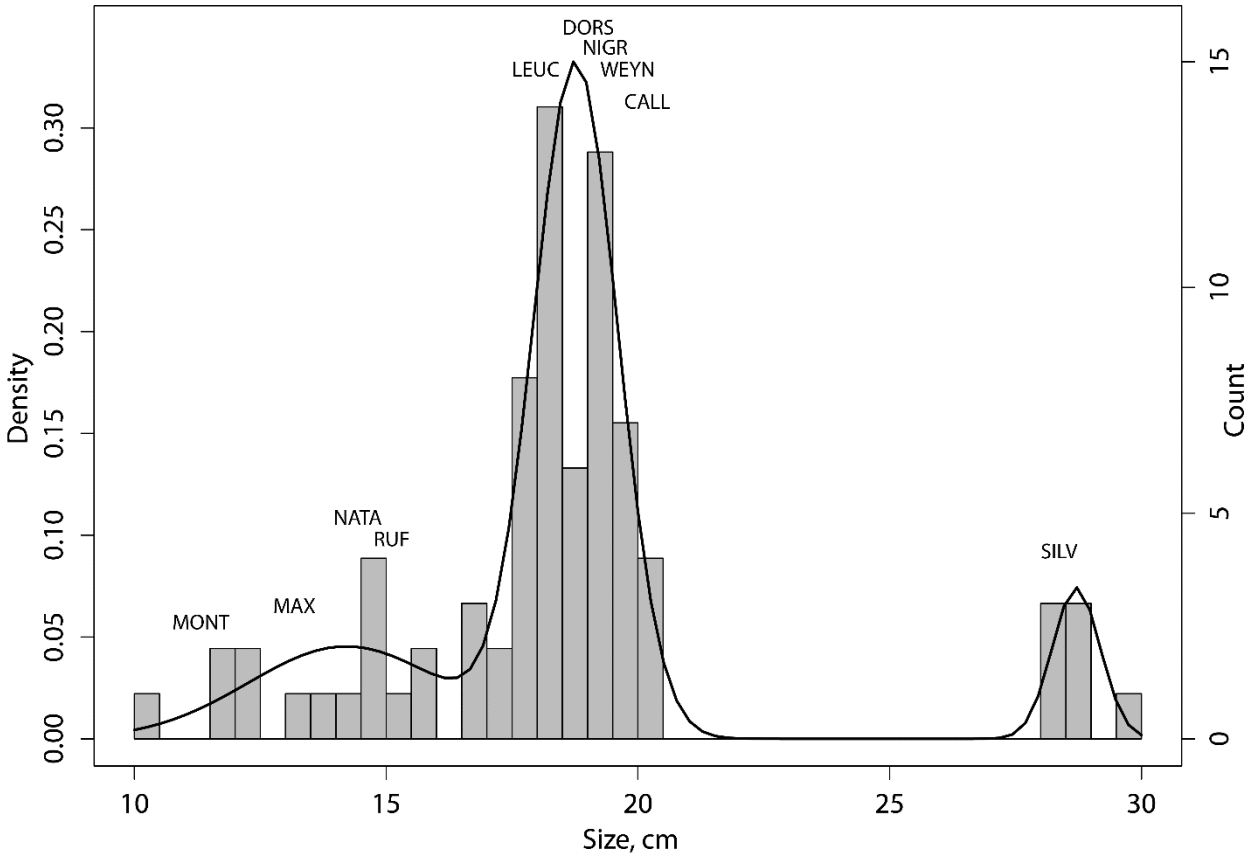

Figure 3.5. Histogram of skull length (cm), with density diagram derived from cluster analysis showing 3 recognized clusters. Species labels placed at mean skull length.

The poor resolution of landmark data for classification mimics the resolution of size classes found in duiker teeth (Emery-Wetherell and Davis, *Submitted),* and though it underrepresents the diversity present, the use of the word 'complex' explicitly acknowledges the possible presence of more than one species per size group. Instead of over-splitting by non-replicable characters, or over-lumping without recognition of possible increased diversity, the use of "species complex" for morphologically cryptic species preserves and recognizes hidden diversity without using artificial divisions or characters.

Conclusion

Convergent evolution of cranial morphometrics in duiker antelope overwhelms species-diagnosis ability of the morphologies we tested here, obscuring the true diversity that is recognized using DNA and coat color for identification. This cranial "blur" of species may be difficult to detect in the fossil record using conventional techniques; cluster analysis of cranial morphometrics did not adequately replicate species groups, and a distribution of skull sizes found only three main groups rather than 10. Modern artiodactyl sympatric species clusters also occur in evergreen montane forests and bushlands – sympatric speciation is not confined to poorly-fossilized tropical rainforest environments and should be considered as a possibility in any environment.

A unifying character of modern sympatric species clusters of artiodactyls is the presence of large pre-orbital glands (and correspondingly large pre-orbital fossae). Pre-orbital fossae are found in many fossil ungulates, including the highly diverse and abundant group Merycoidodontoidea. In modern artiodactyls, facial scent glands are used for territory marking, bonding within groups, and can facilitate detection of age, sex, and species (Dubost 1980, Burger

et al. 1988, Newing 1994). Some groups of artiodactyls, then, may circumvent the need for species identification using unique cranial features by instead possessing unique systems of scent communication. The presence of a large pre-orbital fossa should be considered a red flag for cryptic species, particularly when accompanied by greater-than-anticipated character variation.

Our analyses show that cranial morphometrics perform poorly in separating cryptic species of duikers. Any attempt to use small-scale character variation to separate out species in our dataset could easily lead to misclassification (Figure 3.3, Figure 3.4). Instead of splitting when diagnostic characters are not available, we advocate adopting the terminology of "species complex." This does not force the issue of over-splitting, yet retains information of hidden species diversity. By using clear terminology rather than potentially arbitrary division, we can increase the chance that future workers will recognize hidden patterns of diversity present in isotope or other niche-space studies without being enmeshed in irreplicable systematics. Preservation and translation of information should be the ultimate goal of any systematist, and use of "species complex" in suspect fossil taxa will preserve and pass on maximally verifiable information. By recognizing the limitations of fossil systematics, we can create fossil species divisions that are useful, informative, and applicable in the paleobiological studies that compare modern and fossil assemblages.

Supplementary Table Captions

Table S2.1. General Procrustes rotated landmark data. Contains ID, Genus, Clade, Species, Sex, and size data as well as landmarks. Included as additional file, not as appendix because of size constraints.

CHAPTER IV

EXTRAORDINARY TO CRYPTIC DIVERSITY: A REVISION OF THE EPOREODONTINE OREODONTS OF THE TURTLE COVE MEMBER, JOHN DAY FORMATION, OREGON

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Abstract

Up to 10 species of mid-sized oreodont have been diagnosed in the John Day Formation of Central Oregon, a figure more than twice the number of native artiodactyl species that reside in Modern Oregon. The unusual diversity of oreodonts could either represent greater past diversity, or taxonomic oversplitting. To evaluate these possibilities, I used finite mixture analysis and Hartigen's dip test to measure multimodality and multicomponent distributions in continuous characters of oreodont skulls, and a phylogenetic analysis of specimens to detect phylogenetic clustering in discrete characters. I also compared variation of continuous and discrete characters to levels of variation in those same characters of modern artiodactyls. All continuous characters were normal in multivariate and univariate distributions. However, the variation of the depth of the pre-orbital fossa was unusually high when compared to that of extant samples. In this oreodont sample, there was no statistically supportable way to diagnose more than one species using the pre-orbital fossa, but the high variation of the pre-orbital fossa

suggests the presence of more than one species. I thus rename the 10 species of mid-size oreodont in John Day, and all previously recognized members of *Eporeodon,* as a species complex: *Eporeodon bullatus.* Ultimately, further temporal resolution and collection may resolve *Eporeodon bullatus* into two or more diagnosable taxa, but the current material is inadequate for such precision.

Introduction

Though Oregon today is home to only four native artiodactyl species, the paleontological record contains a far different picture of artiodactyl diversity – for example, the paleosols of the of the John Day Formation contain the fossils of 22 different artiodactyl species (Fremd et al. 1997, Lander 1998, Albright III et al. 2008). Such high artiodactyl diversity is akin to modern diversity in the tropical forests of Africa, where as many as 27 species of artiodactyl overlap in range (IUCN 2016), but the climate recorded in the Oligocene of Oregon was subhumid and temperate environment, very similar to the Willamette Valley today (Bestland et al. 1997). In a world of changing climate and declining diversity, knowing what environments and ecosystems supported greater diversity in the past is becoming increasingly important (Louys 2012). Yet the incredible diversity of artiodactyls in the John Day Formation and other fossil localities may be related not solely to ecological differences, but to differences in species concept: paleontologically recognized species are not always comparable to extant standards (Alroy 2002).

In particular, the high diversity of the John Day Formation is driven by the large number of oreodont taxa present (Superfamily Merycoidodontoidea). These species are treated very differently by different researchers – for just the mid-sized oreodonts there are up to 10 species, four genera, and two subfamilies identified – all restricted to the John Day formation (Schultz

and Falkenbach 1968). Yet the diversity of John Day oreodonts is debated: Lander (1998) reports only 4 species and 3 genera. Thus the artiodactyl diversity in the 30 million-year-old John Day Formation is either extraordinarily high or typical for post-Pleistocene extinction North American artiodactyl communities, painting different pictures of diversity through time.

The opposing end member systematics of John Day result from differing standards of systematics, commonly referred to as "splitting" or "lumping" taxa (Morrison et al. 2009). The relative paucity of extant species diagnosed via cranial osteology has compounded the problem with systematics of fossil artiodactyls, for few studies provide osteological definitions for extant species. Larger sample sizes of fossil taxa capture a broader spectrum of possible variation, and without available data on expected modern variation the sheer abundance of oreodont crania has added considerable noise to their systematics. Collection in the John Day began in the mid 1800s, and by 1906 the first revision of oreodonts was published (Douglass 1906). Even 50 years after their discovery, the extensive variation and character continuity of oreodonts had led to systematic confusion.

The taxonomic debate over oreodonts has been spurred by each worker's emphasis on different osteological characters. In this study I analyzed the variation of mid-sized oreodonts of the John Day formation. Excluded from this study are the smaller oreodont genera (*Oreodontoides, Paroreodon, Merychyus)* and large oreodont genera (*Promerycochoerus, Merycochoerus, Hypsiops* and *Ticholeptus).* Though these oreodont taxa also warrant examination, analyzing and describing an additional 15 species was beyond the scope of this study. Similarly, I have excluded Agriochoeridae from this paper, as it will be the topic of a separate upcoming study.

To bring oreodonts systematics into agreement with extant standards, I have compared variation in this fossil sample to single-species samples of modern artiodactyls, drawing on the variation summaries described in chapters 1 and 2 of this dissertation. In particular, my questions for this study reflect diagnostic capacity of the characters used to split the mid-size oreodonts of the John Day formation into multiple species. To be used for diagnosis, characters should reflect biological differences (rather than improper preparation, or postmortem compression), represent interspecific rather than intraspecific variation, and be capable of separating the majority of specimens into species (though with continuous characters there may always be some un-diagnosable specimens where distributions overlap).

As discussed in Chapter II and III, sympatric species often are similar in size and overlap in their character distributions; without *a priori* knowledge of species, some sympatric artiodactyls can be nearly impossible to distinguish. In some cases, multi-species samples can be identifiable without being diagnosable – that is, variation in a character may be too high for one species, but distributions are too close to properly diagnose two or more species within it (Cope and Lacy 1992, Davis and Calède 2012).

In this study I evaluated the nature of character distributions of John Day eporeodontine oreodonts, the correlation between characters, and the capacity for discrete characters of oreodonts to detect phylogenetically related clusters in and outside John Day. Signs of multimodal distributions, unusually high variation in comparison to modern artiodactyls, and replicable phylogenetic clusters would all be signs that there was more than one species of mid-size oreodont in John Day – even if those species were not necessarily diagnosable from one another.

Abbreviations and Terminology

I follow Bärmann and Rössner (2011)for dental terminology with the exception of several pieces of terminology that are unique to oreodonts and not addressed in that paper. Fossettes are the labial surfaces of each cone (Lander and Hanson 2006). Molar ribs refer to linear crenulations of the fossette's enamel. What Lander (1998) refers to as the lacrimal fossa I call the pre-orbital fossa, as this is the common term in modern artiodactyls.

Museum abbreviations are as follows: American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), University of Oregon Museum of Natural and Cultural History (UOMNH), Thomas Condon Museum of Paleontology collections at the John Day Fossil Beds National Monument (JODA), Carnegie Museum of Natural History (CM), Yale Peabody Museum (YPM), Museum of Comparative Zoology at Harvard (MCZ).

Systematics

Class Mammalia Linneaeus 1758

Order Artiodactyla Owen 1848

Superfamily Merycoidodontoidea Hay 1902

Family Merycoidodontidae Thorpe 1929

Genus *Eporeodon*, Marsh 1875

Remarks — The genus *Eucrotaphus* has priority, but the holotype of *Eucrotaphus jacksoni* was a broken section of the cranium with bullae and no teeth (Figured in Leidy 1852, pl VII Fig 1-6). The absence of teeth and similarity between the basicranial region of *Eucrotaphus* and *Agriochoerus*

makes these two genera indistinguishable. In the absence of diagnostic characters, the name *Eucrotaphus* is a *nomen dubium.*

Type Species — *Eporeodon occidentalis,* Marsh 1875. Type specimen is from John Day, Oregon. This is the type for the genus, but *Oreodon bullatus* Leidy 1869 has presidence for species name.

Diagnosis — As in *Promerycochoerus* but differing from *Merychyus, Paroreodon* and *Oreodontoides,* the styles on the upper molars taper upwards from the base. Differs from *Merycoidodon* but similar to *Promerycochoerus* in having well-rounded and inflated auditory bullae that may be conical or laterally compressed, or nearly perfectly spherical. Possesses large, round pre-orbital fossae. Differs from *Promerycochoerus* by less prominent upward hooking of the zygomatic arches, by having well-defined, sharp, and thin outer edges of the zygomatic arch rather than rounded and thick, and by having an elongated auditory meatus that may start as a thin ridge or transition abruptly into a wide trumpet shape. Differs from *Merychyus* and *Pareoroeodon* in having thick post-glenoid processes. Differs from *Promerycochoerus, Hypsiops, Merychyus,* and *Paroreodon* in having large stylids on the lower molars. Differs from *Merycoides* in having small incisive foramina. Differs from *Merycoides* by having nasal retraction only to P1, no deeper, and by having thin rather than thick premaxillae. Differs from *Promerycochoerus* but similar to *Merycoides* in having unfused premaxillae.

Eporeodon bullatus Leidy 1869

Figures 4.1-4.4

Remarks — Though *Oreodon major* is an older name than *Eporeodon bullatus,* the type specimen of *Eporeodon bullatus* is the first to contain both teeth and bullae, which are necessary to tell the difference between *Eporeodon* and either *Agriochoerus* (teeth), or *Merycoidodon* (bullae). The holotype of *Oreodon major* contains only teeth, and though subsequent authors have placed it into *Eporeodon,* there is no evidence that the holotype truly is different from *Merycoidodon.*

1869 *Oreodon bullatus;* Leidy, p. 106.

1869 *Oreodon major;* Leidy, p. 99.

1873 *Oreodon occidentalis;* Marsh, p. 409.

1875 *Eporeodon occidentalis;* Marsh p. 250.

1884 *Eucrotaphus jacksoni;* Cope p. 517.

1884 *Eucrotaphus major;* Cope p. 519.

1884 *Eucrotaphus trigonocephalus*; Cope p. 514.

1902 *Eucrotaphus helenae*; Douglass, p. 265

1907 *Eucrotaphus dickinsonensis* Douglass, p. 99, pl. 22.

1921 *Eporeodon bullatus*; Thorpe, p. 104.

1921 *Eporeodon condoni*; Thorpe, p. 104, figs. 6-8.

1921 *Eporeodon leptacanthus leptacanthus;* Thorpe, p. 97.

1921 *Eporeodon leptacanthus pacificus;* Thorpe, p. 99.

1921 *Eporeodon longifrons*; Thorpe, p. 103.

1921 *Eporeodon major*; Thorpe, p. 103.

1921 *Eporeodon occidentalis;* Thorpe, p. 96, figs. 1-3.

1921 *Eporeodon perbullatus;* Thorpe, p. 106, figs. 9-10.

1921 *Eporeodon trigonocephalus parvus;* Thorpe, p. 101, figs. 4-5.

1921 *Eporeodon trigonocephalus;* Thorpe, p. 101.

1924 *Eporeodon bullatus*; Thorpe, p. 65, figs. 28-30.

1924 *Eporeodon condoni*; Thorpe, p. 66, figs. 31-33.

1924 *Eporeodon dickinsonensis;* Thorpe, p 68, fig. 34.

1924 *Eporeodon helenae*; Thorpe p.69.

1924 *Eporeodon leptacanthus;* Thorpe, p. 70.

1924 *Eporeodon longifrons perbullatus*; Thorpe, p. 72, figs. 35-37.

1924 *Eporeodon longifrons*; Thorpe, p. 71.

1924 *Eporeodon major*; Thorpe, p. 74, figs. 38-39.

1924 *Eporeodon occidentalis;* Thorpe, p. 81, figs. 41-43.

1924 *Eporeodon pacificus;* Thrope, p. 83.

1924 *Eporeodon parvus;* Thorpe, p. 84, figs. 44-45.

1924 *Eporeodon socialis*; Thorpe p. 86, figs. 46-64.

1924 *Eporeodon thurstoni;* Thorpe p. 96.

1924 *Eporeodon trigonocephalus;* Thorpe, p. 96.

1924 *Eucrotaphus jacksoni;* Thorpe p. 61.

1931 *Eporeodon socialis*; Thorpe p. 7, figs. 1-22.

1940 *Eporeodon meagherensis;* Koerner, p. 845, pl. 2, figs. 1-3

1954 *Subdesmatochoerus socialis dakotensis*, Schultz and Falkenbach, p.223, figs. 18-21

1954 *Subdesmatochoerus socialis*, Schultz and Falkenbach, p.220, figs. 18-21

1968 *Dayohyus trigonocephalus;* Schultz and Falkenbach, p. 216, figs. 28-29.

1968 *Eporeodon (Paraeporeodon) longifrons perbullatus;* Schultz and Falkenbach, p. 210, figs. 25-27, 30.

1968 *Eporeodon (Paraeporeodon) longifrons;* Schultz and Falkenbach, p. 207, figs. 25-27, 30.

1968 *Pseudogenetochoerus condoni*; Schultz and Falkenbach, p. 159, fig. 16.

1968 *Dayohyus wortmani;* Schultz and Falkenbach, p. 217, figs. 28-30.

1968 *Epigenetochoerus parvus;* Schultz and Falkenbach, p. 164, figs. 19-23.

1968 *Eporeodon (Paraeporeodon) leptacanthus;* Schultz and Falkenbach, p. 213, figs. 25-27, 30.

1968 *Eporeodon (Paraeporeodon) pacificus;* Schultz and Falkenbach, p. 205, figs. 25-27, 30.

1968 *Eporeodon davisi;* Schultz and Falkenbach, p. 203, fig. 24.

1968 *Eporeodon occidentalis;* Schultz and Falkenbach, p. 201, figs. 24, 30.

1968 *Genetochoerus (Osbornohyus) dickinsonensis;* Schultz and Falkenbach, p. 154, figs. 14-16, 19-20, 22.

1968 *Otinohyus bullatus;* Schultz and Falkenbach, p. 118, fig. 11.

1968 *Otinohyus hybridus helenae;* Schultz and Falkenbach, p. 131, fig. 11.

1968 *Paramerycoidodon (Barbourochoerus) major;* Schultz and Falkenbach, p. 92, figs. 7-9, 19-23.

1968 *Paramerycoidodon (Gregoryochoerus) meagherensis;* Schultz and Falkenbach, p. 103, figs. 7-9

1968 *Pseudogenetochoerus covensis;* Schultz and Falkenbach, p. 161, fig. 16.

1998 *Eporeodon major;* Lander p. 413.

1998 *Eporeodon occidentalis major;* Lander p.412.

1998 *Eporeodon occidentalis;* Lander p. 412.

1998 *Eucrotaphus jacksoni;* Lander p. 412.

1998 *Eucrotaphus trigonocephalus;* Lander p. 412.

2007 *Eporeodon occidentalis;* Stevens and Stevens p. 163, fig. 12.4A.

2007 *Eporeodon pacificus;* Stevens and Stevens p. 163.

2007 *Eporeodon thurstoni;* Stevens and Stevens p. 163.

Holotype— YPM 10142, Skull with RP4-M3, LM3. Broken anterior to P3 alveolus. Zygomatic arches are missing.

Description — The superior incisors are spatulate and increase in size posteriorly. The superior canine is larger in width and anteroposterior measurements than *Agriochoerus, Paroreodon, Merychyus* or *Oreodontoides,* though similar in size to small individuals of *Promerycochoerus* or *Hypsiops.* The posterior surface of the canine is flat, as in all oreodonts, giving it a D shape in occlusal outline. The anterolingual surface of the canine often displays wear from contact with the lower canine. The incisive foramina terminate anterior to the canine, unlike in *Agriochoerus* where they terminate posterior to the canine. These incisive foramina are small and slitlike, not rounded as in *Merycoides* or *Promerycochoerus.* The diastema between the canine and first premolar is variable in size (CV of 31.8) but always smaller than the anteroposterior measurement of the first molar.

The first upper premolar is simple without a lingual cone, triangular from buccal view but rectangular from occlusal view. In specimens without considerable wear there is a strong crista down the center of the anterior surface of the tooth. P2 is broader than P1 and has a considerably wider posterolingual surface. There is a strong anterolingual crest on unworn teeth. A second crest starts at the tip of the cone then curves down and anterior to form a tear-drop connection. P3 is considerably more robust; the posterior portion of the tooth is more labiolingually expanded in some specimens, giving it a square rather than rectangular shape. There is a strong

lingual cingulum in unworn specimens. An anterolingual crista starts at the cingulum and terminates halfway up the tooth. A mesolingual crista starts at the cingulum and terminates at the tip of the cone. There is considerable variation in the relative strength of crests. P4 has a lingual and labial cone. The lingual surface of the labial cone of P4 may or may not have ridges, and the lingual cusp may or may not have a circle of enamel that creates an "enamel well" (Figure 4.1). The shape of the P4 varies from anteriorly thick to thin, and from triangular to rectangular in shape. There is often a cingulum along the P4 lingual cone.

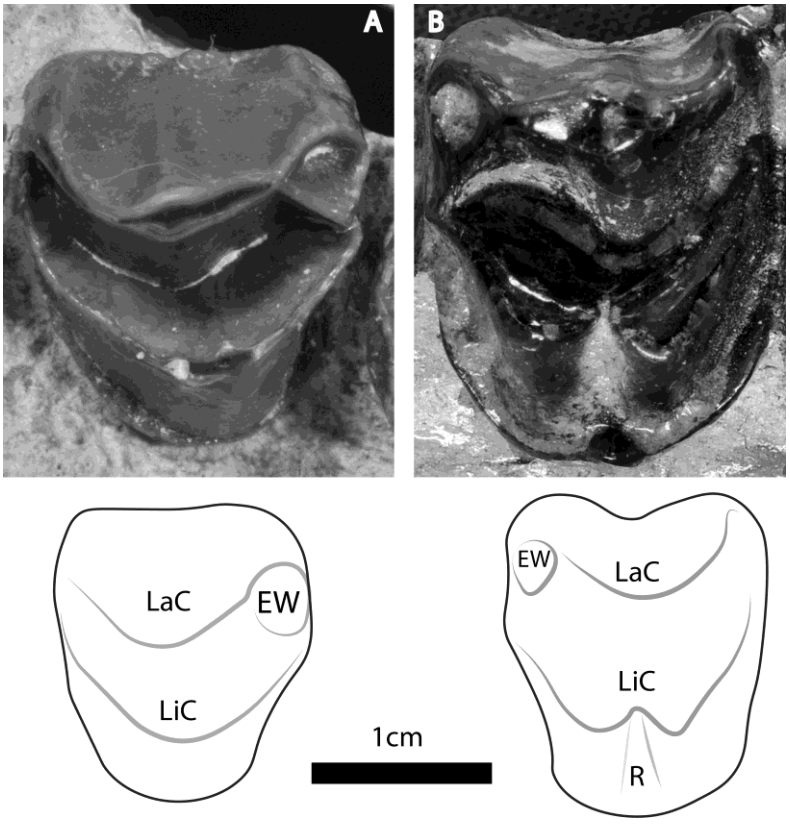

Figure 4.1 – Two specimens showing abnormalities of the P4. Part A shows an enamel well in the right portion of the labial cone in JODA 6315. Part B shows an enamel well in the left part of the lingual cone, and ripples in the lingual cone of UOMNCH F-76529. These ripples typically occur in the labial cone. Acronyms: ***LaC****, Labial Cone;* ***LiC****, Lingual Cone;* ***EW****: Enamel Well;* ***R****, Ripples.*

The molars are variable in size and shape, and change considerably through wear. The styles are prominent and taper vertically, which reveal larger and more bulbous style shapes as

the tooth wears. The molars may increase in size posteriorly, but this is variable and not diagnostic as has been suggested for other genera (Ludtke 2008). Typically the metaconules of the molars are displaced lingually, particularly in the M3. The metaconule and protocone are of comparable size in all the upper molars, unlike the upper deciduous P4. The cones of the molars jut occlusally from the toothrow at an approximately 45 degree angle, and wear of the fossettes causes dentine to emerge quickly in the shape of a large, gaping V. The lingual cones are more susceptible to intense wear than the labial, and very worn teeth will oven have completely smooth lingual cones while retaining remnants of the labial cones. There is always a prominent, shelf-like cingulum between the parastyle and mesostyle. Other cingula are not uncommon, and a cingulum between the anterior of protocone and anterior of the metaconule is the most common of these intermittent cingula. In some specimens (e.g. JODA 4851) the cingulum becomes a prominent entostyle. Connections between the postprotocrista (posterior arm of the protocone) and the premetaconulecrista (anterior arm of the metaconule) of the molars are highly variable: the postprotocrista and premetaconulecrista may meet equally in the loph, or one arm may overlap the other.

The upper deciduous teeth are present in many specimens and dP3 and dP4 were often misidentified as other smaller oreodont species in the collections at JODA. As per Bärmann and Rössner (2011), I follow the same terminology for deciduous dentition as in molars, and different nomenclature for premolars to reflect the homology between deciduous teeth and molariform teeth. The deciduous canine is small and looks like a thin incisor, and is replaced early in tooth development. P1 is mid-eruption in several specimens, but as in other oreodonts there is no evidence of a deciduous precursor (Miller and Wood 1963). dP2 is small with a single cone; the

anterior and posterior portions of the tooth are expanded labiolingually and have strong circular crista, giving the appearance of a bow-tie (Figure 4.2). Some dP2 possess strong styles. dP3 has a paracone, metacone and metaconule. The paracone is aligned with the metacone but the parastyle is shifted lingually and is much less distinct. The paracone is shifted labially and there are two strong crista that connect the paracone and the lingual cingulum. The metacone becomes more steeply angled with wear, and is more narrow anteroposteriorly than the metacone of the molars. The mesotyle and metastyle are very prominent. dP4 is very like a small M1, with four well-developed cones. There is a strong, shelf-like cingulum on the anterior edge of the protocone and the protocone is considerably wider than the metaconule; in all other regards, dP4 is easily confused for M1 (Figure 4.2).

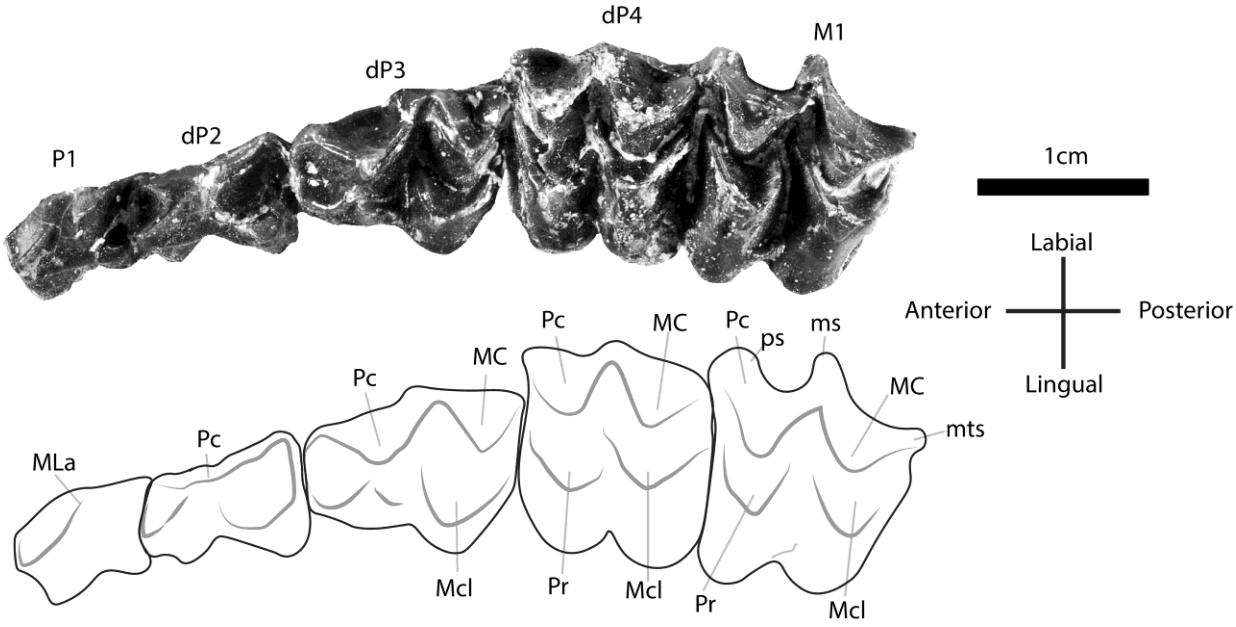

Figure 4.2 – Deciduous morphology of the upper teeth of UWBM 49498. Acronyms: ***MLA****, Mesolabial cone;* ***Pc****, Paracone;* ***MC****, metacone;* ***Mcl,*** *metaconule;* ***Pr,*** *protocone;* ***ps****, parastyle;* ***ms,*** *mesostyle;* ***mts,*** *metastyle;*

The lower incisors are spatulate, often with a small ridge on the posterior side that gives them the appearance of an oven mitt. The lower canine is incisiform but much larger than the

upper canine, and articulates with the anterior of the upper canine where it wears the anterolingual surface. p1 is caniniform and wears on the anterior side where it articulates with the upper canine. p2 is triangular and small, with a wider posterior than anterior. There are two cristids on the posterior surface of the tooth which link to form a teardrop-shaped posterior valley. p3 is similar but slightly larger and with stronger cristids. On unworn p3s there is an additional cristid that divides the posterior of the tooth into two posterior valleys between the two posterolingual cristids. p4 is partially molariform, with prominent anterolingual and anterolabial conids connected by a ridge. The posterior conulids of p4 are eradicated with minimal wear. Unworn p4s also display additional stalactites or buttresses of enamel: one between the two posterior conulids, and one off the ridge that connects the two anterior conids. The anterolabial cristid of p4 extends forward and lingually, forming a partial crescent shape. Rotation of p2 and p3 out of line with the toothrow (Colyer's variation) is fairly common, as it is in modern artiodactyls (Miles and Grigson 2003). Labial cingulids on the premolars are variably present. Lower premolars do not have stylids.

Prominent stylids are typically present in the lower molars of *Eporeodon bullatus*, and the metastylid overlaps the anterior edge of the entoconid. The morphology of the stylids and the displacement of the hypoconid in relation to the protoconid are the clearest ways to identify molar placement in the toothrow. In m1, the stylids of the metaconid are curled strongly towards one another, while the entostylid does not curl and subsequently the entoconid looks straight in comparison to the metaconid. The stylids of the m2 metaconid are comparatively much less curled and prominent, and are equally as curled on the entoconid so that both halves of the lingual edge of the tooth appear only slightly and equally curved. The m3 stylids are present but the lingual surfaces of the conids are almost flat in comparison to the preceeding teeth. On the

labial surface, the hypoconid of m1 is only slightly shifted labially, while it is dramatically shifted on the m2 and is shifted either not at all or is shifted lingually in the m3. Cingulids between the protoconid and hypoconid are common in all three molars. The posthypoconid cristid does not meet up with the postentostylid cristid in the M3, but encircles the hypoconulid.

All of the deciduous p2 in this sample were heavily worn, but were shorter than the adult p2. dp3 is superficially similar to p4, but lacks a separated lingual conid. dp3 has a strong, lingually curved anterolabial cristid as in p4. Instead of a separated lingual conid, dp3 has a strong mesolingual cristid which curves posteriorly to form a large tear-drop shape with the posterolabial cristid. dp3 is also smaller labiolingually and therefore appears more compressed than adult dp4. dp4 has six conids, typical of artidactyl dp4s (Miller and Wood 1963, Loring and Wood 1969). The lingual conids are interconnected by strong cingulids which do not extend more lingually than the boundary of the teeth themselves. The stylids are present but not particularly prominent. The tooth is wider at the posterior end than at the anterior, but not so dramatically as in *Oreodontoides*.

The symphysis of the jaw juts at a 40 degree angle from the toothrow and fuses together into a small but discernable ventral lump. There are typically two to three mental foramina: one is large and posterior to p1, a second more posterior and variably present one is posterior to p3, while the third and again larger foramen sits posterior to p4. The horizontal ramus is shallow and parallel with the toothrow until the posterior of m3, where it becomes a well-rounded mandibular angle. There is a large fossa on the lingual side of the mandibular angle. The posterior edge of the mandibular angle is rugose and nearly crenulated with muscle attachments. The mandibular condyle is perpendicular to the toothrow, and sits only slightly above the vertical extent of the

unworn teeth. The ascending ramus curves labially and terminates in a process that is only marginally higher than the condyle. The fossa of the ascending ramus is deep, the bone is thin and often fractures, and the fossa terminates just below the extent of the line of the toothrow.

Skull length (19.67 +/- 1.45 cm, Mean +/- Stdev from incisors to occipital condyles) is midrange for oreodonts (Lander 1998, Stevens and Stevens 2007). The overall arch of the skull is either flat on top or slightly domed with a midpoint just behind the orbits. Fracture of the sagittal crest or occipital fan lends a more rounded shape to the skull. The nasals are not retracted, with the tip of the nasals reaching or almost reaching the tip of the premaxillas and the maxillary notch no further posterior than P2. The premaxillae are not fused, and they are not as robust as in *Merycoides* or *Promerycochoerus.* The muzzle itself is rectangular and separate from the overall triangular outline of the skull, unlike in *Merycoides.* The orbits are relatively large in relationship to the skull, and face outward and forwards. There are two supraorbital foramina which sometimes have anterior grooves. There is no obvious maxillary fossa. There is considerable rugosity labial to P4-M3 where the buccinators would have attached. The malar is shallow, unlike in *Merycochoerus* or *Promerycochoerus.*

The postorbital constriction is considerably smaller than the braincase. The orbital width is about the size of the braincase and in some cases slightly wider. The frontal crests meet either at the end of the postorbital constriction or after it; their prominence varies but they are always present in adult specimens. The sagittal crest is ridge-like and thin when it is not broken off, and meets posteriorly with a fan-shaped occipital bone. There is a ridge where the temporals and parietals are fused, and there are one to four foramina which may be variably expressed between the two sides of the same individual, as is typical for oreodonts. The infraorbital foramen is

variable in placement but typically in line with the bottom of the malar and near P3. The pre-orbital fossa (lacrimal fossa of Schultz and Falkenbach 1968, Lander 1998, Stevens and Stevens 2007) is variable, but clearly visible and either circular or oval.

The anterior of the orbit is aligned with the second or third upper molar, and the zygomatic arch typically roots at the M1 or M2 (though rarely, M3). The breadth of the zygomatic arches is variable (Figure 4.3), and may be sexually dimorphic as it is in some species of fossil peccary (Herring 1972). In extreme cases the arches are spread so wide as to give the skull a very triangular appearance (as in AMNH FM 7505 and UCMP 1911).

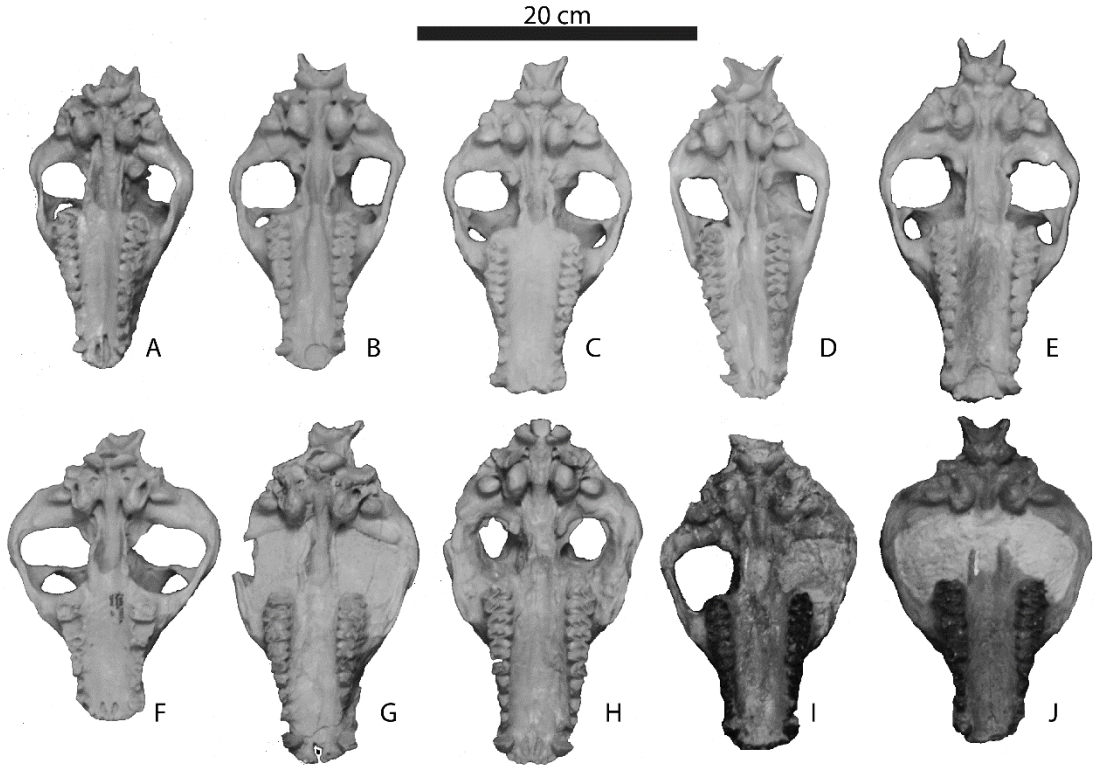

Figure 4.3 – Dorsal views of specimens of Eporeodon bullatus. ***A**, AMNH FM 7498; **B**, AMNH FM 7509 HT of* Pseudogenetochoerus covensis*; **C**, AMNH FM 7499; **D**, AMNH FM 7695 holotype of* Eporeodon leptacanthus*; **E**, AMNH FM 7496; **F**, AMNH FM 7505 holotype of* Dayohyus trigonocephalus*; **G**, JODA 10824A; **H**, JODA 4206; **I**, JODA 4200; **J**, UCMP 1911.*

The posterior extent of the zygomatic arch is partially curved and forms a large, curled shield where it meets with the braincase. The dorsal edge of the zygomatic arch is always sharp and nearly fin-like, unlike the rounded zygomatic arch edges more typical of *Promerycochoerus.* The jugal and squamosal sections of zygomatic arches are poorly fused as is typical for oreodonts. The anteriormost extension of the squamosal section of the zygomatic arch terminates beneath the posterior extent of the orbit (just ahead of the postorbital bar), often overlapping visibly underneath the post-orbital bar. There is not a complete lamboidal crest as there sometimes is in *Agriochoerus;* instead the posterior edge of the zygomatic arch terminates in a laterally-directed tuberosity near the posterior edge of the paroccipital process. No subsquamosal foramina are present.

Though the palate is prone to crumpling in deformed specimens, it naturally lies flat (as in UCMP 1911). The palate posteriorly increases in width, but much less so than in *Agriochoerus.* There is a small palatine foramen aligned with the middle or anterior of M1. The palate ends after the third upper molar, often very far behind the third upper molar, and is typically V or U-shaped where it meets with the pterygoid processes. Occasionally, the suture of the palate will extend posteriorly and create a W-shaped terminus; extension of the suture is short and fragile if present. The foramen orbito-rotundum is large and sits mesial to a small tuberosity of the sphenoid bone. Foramen ovale is bordered posteriorly by the temporal bone and mesially by the temporal bone, rather by the pterygoid process as in *Promerycochoerus* or *Agriochoerus.* The foramen lacerum is small, posterior to the foramen ovale and labial to the carotid foramen. The carotid foramen is larger than the foramen lacerum and is centered on or very near the confluence between the basioccipital and basisphenoid.

The post-glenoid process is a robust ridge rather than the peg-like morphology seen in *Agriochoerus*. There is a small post-glenoid foramen near the posterolateral side of the post-glenoid process; it is not rimmed by a process of the auditory meatus as in *Agriochoerus.* The auditory bullae are rounded and inflated, and may be laterally compressed, spherical, or tall and conical. Rarely there are anterior projections of the bullae as in *Agriochoerus*. The structure of the auditory meatus and how it interacts with the tympanohyal fossa has previously been used to diagnose *Eucrotaphus* versus *Eporeodon* (Lander 1998). The tympanohyal fossa is the groove between the lateral edge of the paroccipital process and the posterior boundary of the post-glenoid process – the two morphologies described by Lander (1998) are partial or complete closure of the tympanohyal fossa by the auditory meatus but this morphology proved to be continuous in my sample.

The stylomastoid foramen is often encircled by the posterior edge of the auditory meatus, but the laminae are so thin that it is likely lost without careful attention during preparation. The auditory bullae either connect directly to the paroccipital process, or there is a fine-scale, less than millimeter groove that separates the two partway up the process. Viewed posteriorly, the paroccipital process is tear-drop shaped and not spread laterally enough to obscure the post-glenoid process. Some specimens have ridges along the posterior of the paroccipital. The lateral edge of the paroccipital process may project perpendicular to the axis of the skull, or fold anteriorly in larger specimens (Figure 4). The mastoid foramen sits where the paroccipital process merges with the ridge of the occipital bone.

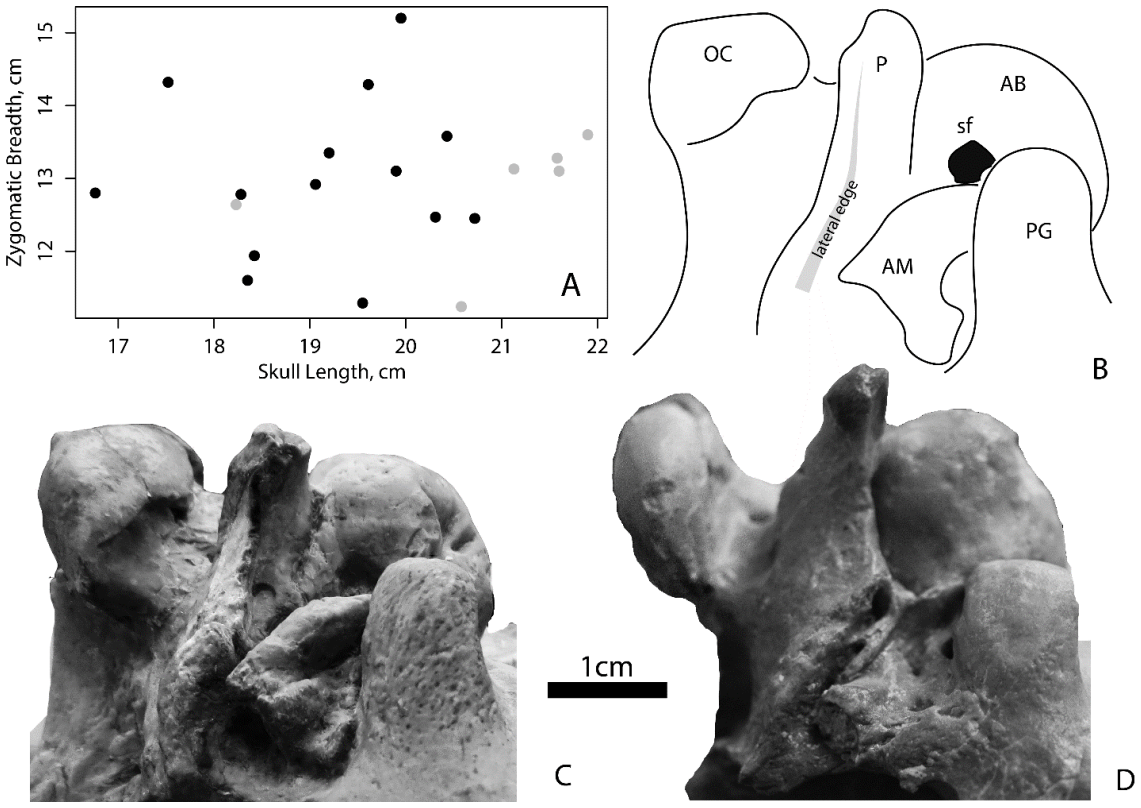

Figure 4.4 – Biplot of skull length and width, with lateral views of the paroccipital process and auditory bullae of Eporeodon bullatus*. Colors correspond to morphology of the paroccipital process. Gray corresponds to morphology C, where the lateral edge migrates anteriorly; black corresponds to morphology D, where the lateral edge is perpendicular to the axis of the skull. Acronyms for part B:* ***OC****, occipital condyles;* ***P****, paroccipital condyles;* ***lateral edge****, the morphology that moves anterior in part D, and is perpendicular to the skull in part C;* ***sf****, stylomastoid foramen;* ***AB****, auditory bullae;* ***AM,*** *auditory meatus;* ***PG****, postglenoid process.*

The basioccipital bone is either smooth or has a fine, pinched ridge that merges smoothly into the raised taper of the basisphenoid. There are no obvious tuberosities on the basioccipital bone. Cranial flexion (or the angle between the basioccipital region and the palate) is obtuse (153.64 +/ 5.83 degrees, mean +/standard deviation) and overall less flexed than in *Promerycochoerus*. The hypoglossal foramen is not encircled by a distinct rim of bone, but is well-separated from the jugular foramen. The jugular foramen is moved labially, out of line with the hypoglossal and carotid foramina. The occipital condyles lack the additional anterior articulation surface of

Agriochoerus, with the exception of AMNH FM 7496. The supraoccipital bone forms a narrow fan shape that does not spread onto the other bones of the skull as it does in *Merycochoerus*. The width of the fan is slightly greater than the occipital condyles but never wider than the postorbital processes. There is usually a thin ridge up the center of the underside of the occipital fan. The relative height of the fan above the occipital condyles is greater than in *Agriochoerus,* but shorter than in *Promerycochoerus.* The posterior and ventral portion of the occiput sometimes tapers downwards to a point just above the occipital condyles, but may also remain thick at the base.

Materials — AMNH FM 7496, Skull with C-M3 on both sides, missing incisors but otherwise complete; AMNH FM 7498, Skull with RC-M3, LP3-M3 and LI2-I3. Other alveoli present for incisors. Anterior nasals reconstructed; AMNH FM 7500, Skull with C1-M3, incisor alveoli. Zygomatic arches and postorbital bar reconstructed on both sides; AMNH FM 7502, Skull with RC1-M3, LP3-M3. Incisor alveoli present; AMNH FM 7504, Skull with signs of compression. Zygomatic arches reconstructed. C1-M3 present on both sides; AMNH FM 7505, Skull missing all teeth except fragments of heavily worn molars; AMNH FM 7509, Complete skull, missing right incisors; AMNH FM 7514, Skull and jaw fused, nasals missing, broken anterior to canine. Juvenile; AMNH FM 7564, Juvenile skull with dp2-M3 and alveoli for other teeth. Zygomatic arches broken and reconstructed. Auditory bullae missing; AMNH FM 7567, Skull with complete dentition, broken and reconstructed zygomatic arches; AMNH FM 7621, Juvenile skull with complete post-C1 dentition, M3 is erupting. Premaxilla missing anterior to canine. Zygomatic arches broken and reconstructed.; AMNH FM 7632, Complete skull; AMNH FM 7637, Complete skull; AMNH FM 7654, Skull with reconstructed zygomatic arches, missing occipital crest and fan. All teeth present except left incisors; AMNH FM 7672, Skull broken anterior to P1, zygomatic arches and occipital fan missing; AMNH FM 7695, Complete skull with broken canines. Skull is deformed and laterally compressed; AMNH FM 7725,

zygomatic arch and orbit reconstructed. Teeth present and very worn; CM 1584, Adult skull with P1-M3 preserved on both sides. Alveoli of incisors and canines preserved. Zygomatic arches reconstructed; CM 725, Juvenile skull missing anterior to DP3, zygomatic arches reconstructed, palate crushed and deformed; FMNH 12725, Right zygomatic arch broken, premaxilla broken anterior to P1. Only LM1-M3 preserved; FMNH P 26401, Right zygomatic arch broken, left is reconstructed, occipital fan reconstructed, Canines and incisors reconstructed; JODA 250, Right zygomatic arch missing. Left C1 and P1 and premaxilla not prepped out of matrix. Occipital fam missing; UCMP 1911, Missing P1-M2 and incisors, otherwise complete; UCMP 75280, Missing left zygomatic arch and I3 on both sides, otherwise complete skull; UCMP 76529, Mostly complete skull, with matrix supporting zygomatic arches. Occipital ridge and fan is missing; UOMNCH F-29689, partial skull with RP4-M1; UWBMN 49498, juvenile skull missing auditory bullae and zygomatic arches L P1-M1, R DP2-M1; UWBM 51725, Skull missing anterior to C1 but otherwise complete; UWBM 58118, Mostly complete skull with broken right zygomatic arch and missing incisors; YPM 10142, Skull with RP4-M3, LM3. Broken anterior to P3 alveolus. Zygomatic arches are missing; YPM 11016, Skull missing incisors, with some reconstruction of the palate, zygomatic arch and sagittal crest. Anterior nasals missing; YPM 13118, Laterally compressed skull. Right zygomatic arch broken. RI3-M3 and LP4-m3 preserved. Anterior section of palate missing; YPM 13119, Zygomatic arches missing, right C1-M3 and left P1-M3 preserved. I2 preserved on both sides, other alveoli missing. Anterior of nasals missing; YPM 13948, Complete skull. *Isolated* d*ental material described in Table S3.4.*

Methods

Measurements

I used two measurement methods: digital calipers (Mitutoyo CD-s6”C and CD-12”C) for dental characters, and the measurement function in Agisoft Photoscan on digital models of skulls (Agisoft 2013). Measurements in Agisoft Photoscan must be taken on the surface of the specimen but otherwise these two methods are comparable without significant differences (See Chapter II).

Several characters of the skull (pre-orbital fossa depth, and height of the muzzle) had to be calculated using trigonometry. For pre-orbital fossa depth, I measured length across the fossa, then length from the deepest part of the fossa to the anterior border of the orbit. I then used the Law of Cosines to find the depth (Hazewinkel 2013). For cranial flexion (also called basicranial tilt), I measured from the end of the palate to the anterior edge of the occipital condyles, from the palate to the midpoint of the foramen ovale, and from that midpoint to the occipital condyles to create a scalene triangle then used the Law of Cosines to calculate the cranial flexion (Hazewinkel 2013). Selecting foramen ovale as the midpoint reduced the extent of cranial flexion measured, but maximized the available sample as many specimens were not prepared between the pterygoid processes and would have been excluded if the midpoint for the flexion measurement had been any further anterior. Finally, I calculated muzzle height by measuring the palate width at P2 on the ventral model of the skull, and from P2 to the height of the muzzle on the dorsal model of the skull, then used Pythagorean theorem to solve for the true height (Hazewinkel 2013). Simply measuring from P2 to the height of the muzzle would have included lateral variation and not been representative of the character as reported in the literature.

Characters

I measured a variety of characters suggested from the literature, both discrete and continuous. Some characters from older literature had been subsequently proven inadequate by other workers: prominently, the "dolichocephaly" and "mesocephaly" reported in several species by Schultz and Falkenbach (1968) was related to deformation of the skulls during fossilization (Stevens and Stevens 2007). In the course of character scoring, I noticed that the high variation in overall skull profile reported by Cope (1884) directly relates to whether or not the sagittal and occipital crests are present: if absent, the skull appears convex rather than flat. For the purposes of this study, I have removed the overall outline of the skull as a character. Though skull silhouette may be valid for differentiating other species, in this sample it was a byproduct of preservation. Similarly, the thin (<1mm) lamina of bone separating the stylomastoid foramen from the tympanohyal canal (Cope 1884, Douglass 1906) is easily broken off and removed during preparation, and its presence or absence was therefore not a reliable generic character. Finally, the lachrymal tubercle was mentioned by Thorpe (1937) in a species description, but the role of the lachrymal tubercle as an attachment point for the muscles of the eyelid means it was likely present in all oreodonts (as in all mammals); additionally, the lachrymal tubercle is known to grow larger through ontogeny of domestic animals (Silver 1963).

With those three characters eliminated, the character set consisted of 21 continuous characters (Table 4.S1, 4.S2) and 13 discrete characters (Table 4.S1 – 4.S3), as well as three characters coded that differentiated the outgroup taxon (*Agriochoerus*). I also measured the respective lengths and widths of the molars and premolars of specimens at the John Day Fossil Beds using digital calipers, to determine whether lengths of different teeth were capable of discerning multiple populations (Table 4.S4).

Phylogenetic Analysis

The different systematic literatures of the John Day oreodonts suggested numerous discrete characters for diagnosis. To determine whether these traditional characters were unique morphologies indicative of more than one species or simply intraspecies variation, I conducted phylogenetic analysis of individual specimens in the freeware program TNT (Goloboff et al. 2008). I included a specimen of *Agriochoerus antiquus* (AMNH FM 7402) as an outgroup taxon. I then subsampled the character matrix to see if removing characters suggestive of intraspecific variation improved resolution, and compared synapomorphies in the final trees to each other to see which characters diagnosed large groups.

Distribution Analysis

Ostensibly, single-species samples should have normal distributions of continuous characters, with variation of about 10% (Simpson and Roe 1939, Cope and Lacy 1992). Samples that deviate from either of these two patterns may contain multiple species or high dimorphism (though, as I concluded in Chapter III, even samples that *do not* deviate may also contain multiple species). I evaluated these continuous character data for normal univariate and multivariate distributions using the 'mixtools' and 'dip.test' package in R (Hartigan and Hartigan 1985, Maechler 2015, Young et al. 2015). I subsampled the data for finite mixture analysis, conducting tests on the complete dataset as well as smaller groups of related characters to see whether the diagnostic power of different skull regions was overwhelmed by the overall correlation of the dataset.

Normal distributions in univariate and multivariate space can be mimicked by several closely overlapping species, and therefore I also evaluated these distributions for unusually large variation by measuring the coefficient of variation (Cope and Lacy 1992, Plavcan and Cope

2001). Coefficients of variation (CV) in modern populations do sometimes exceed a 10% rule of thumb (e.g. Roth 1992), so to ensure the fossil sample's CVs were similar to expected single-species distributions I compared large CVs in the oreodont sample to similar measurements on modern artiodactyls.

Correlation Analysis

Several characters were described as a ratio between two characters, e.g. the length in comparison to the width of the skull (Schultz and Falkenbach 1968, Stevens and Stevens 2007). Though these are traditionally described as ratio characters, ratio data has a non-normal distribution so I tested instead for correlation between characters using the 'stats' package in R (R Core Team 2016). If these characters are strongly correlated, show normal variation, and have no statistical support for multiple subgroupings, then it is likely that these linked characters are multivariate normal distributions that cannot be used to reject a single-species hypothesis. Low variation is not conclusive evidence of a single-species sample, but cannot be used to reject that null hypothesis. All our reported R^2 values are adjusted R^2, which can be negative in ordinary least squares regression if the correlation is poor enough and the parameters included don't improve it (Zar 1999).

Results and Discussion

Phylogenetic Analyses

No clear, consistent separation was found in the complete phylogenetic analyses. The two best-resolved phylogenies with the total character set were highly mismatched with almost no overlap (Figure 4.5). Furthermore, no separation was present between John Day oreodonts and oreodonts from the White River group - these characters do not divide species by geographic regions. The characters that were responsible for larger divisions in these trees were the shape of

the paroccipital process, the shape of the auditory meatus, and the placement of the maxillary notch but as I will discuss, these characters all may represent intraspecific variation.

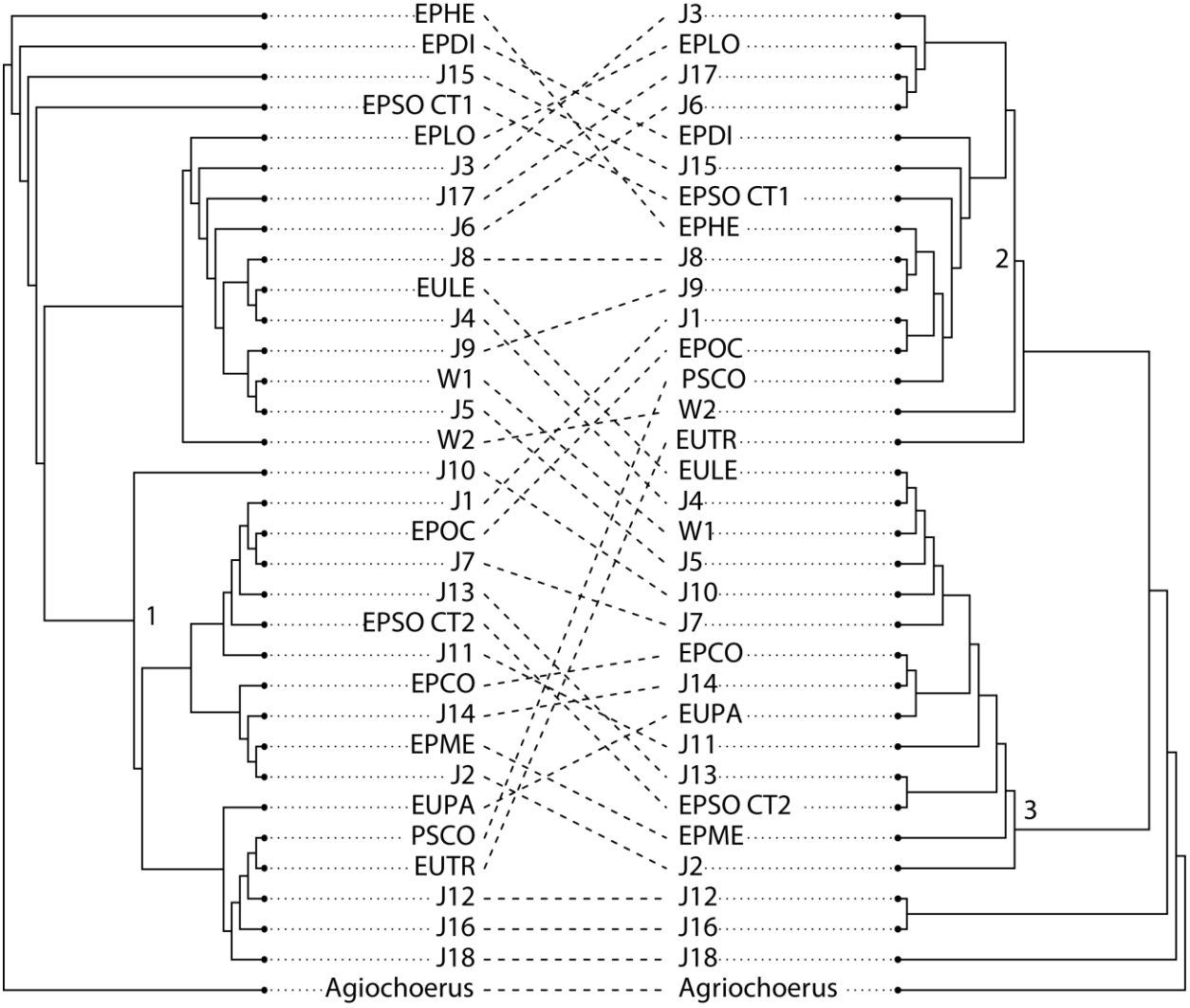

Figure 4.5 – Phylogenetic coplot, showing the two most resolved (of 3) trees of discrete characters. Specimens from the John Day formation are labeled with J and a number corresponding to their full name (Table 4.S1). Specimens labeled 'W' are from the White River group. Node 1 relates to shape of the auditory meatuses, Holotypes are designated with the first two letters of their genus and species (including the two Eporeodon socialis *cotypes): EUHE* – Eucrotaphus helenae, *EUDI* - Eucrotaphus dickinsonensis, *EPSO* - Eporeodon socialis, *EPLO* - Eporeodon longifrons, *EULE* - Eucrotaphus leptacanthus, *EPOC* - Eporeodon occidentalis, *EPCO* - Eporeodon condoni, *EPME* - Eporeodon meagherensis, *EUPA* - Eucrotaphus pacificus, *EUTR* - Eucrotaphus trigonocephalis. *Node 2 is designated by the palate shape, and Node 3 is designated by the paroccipital processes.*

When all characters that may represent intraspecific variation were removed, only characters that diagnosed *Agriochoerus* from *Eporeodon* and a single other character were left: the placement of the root of the zygomatic arch. In this oreodont sample the anterior zygomatic arch connected to the skull anywhere between M1 and M3, and though M2 was the most common placement (17 of 30 specimens), the placement of connection was not entirely discrete: the attachment point of the zygomatic root was often between two teeth, rather than specifically above one tooth or another. Ultimately, displacement of the teeth in the toothrow even by half a centimeter (or half the length of M2) can cause the zygomatic connection to be associated with a different tooth, and so the attachment point of the zygomatic arch in comparison to teeth may not be a reliably discrete character.

Distribution Analyses

Mixture analysis showed that no continuous characters were significantly likely ($p < .05$) to have more than one component, and dip tests showed no univariate measurement was significantly likely to be multimodal. Though distributions were unimodal, several measurements had greater CVs than might be expected for a single-species sample: in particular, the length and depth of the pre-orbital fossa (Table 4.1). CV of the pre-orbital fossa far exceeds that of modern muntjaks and duikers. Other CVs were well within single-species distributions, including those of the teeth (Figure 4.6). CVs of auditory bullae height were also high, but were much smaller than samples of modern *Vicugna vicugna* (Table 4.1).

Table 4.1 – Coefficients of variation of modern taxa and samples of Eporeodon bullatus *for the auditory bullae and measurements of the pre-orbital fossa.*

Species	n	Auditory Bullae	Pre-orbital Fossa Length	Pre-Orbital Fossa Depth
Hylochoerus meinertzhagheni	11	10.09		
Cephalophus leucogaster	20		5.53	12.85
Cephalophus weynsi	13		7.38	9.17
Muntiacus muntjak	12		11.36	13.57
Muntiacus reevesi (No Juvs)	7		9.94	12.19
Muntiacus reevesi (With Juvs)	9		15.13	16.66
All *Muntiacus*	21		15.28	16.26
Vicugna vicugna (No Juvs)	13	22.9		
Vicugna vicugna (With Juvs)	21	20.15		
All *Eporeodon*	32	15.33	15.876	36.36
John Day *Eporeodon*	25	12.58	18.031	34.52

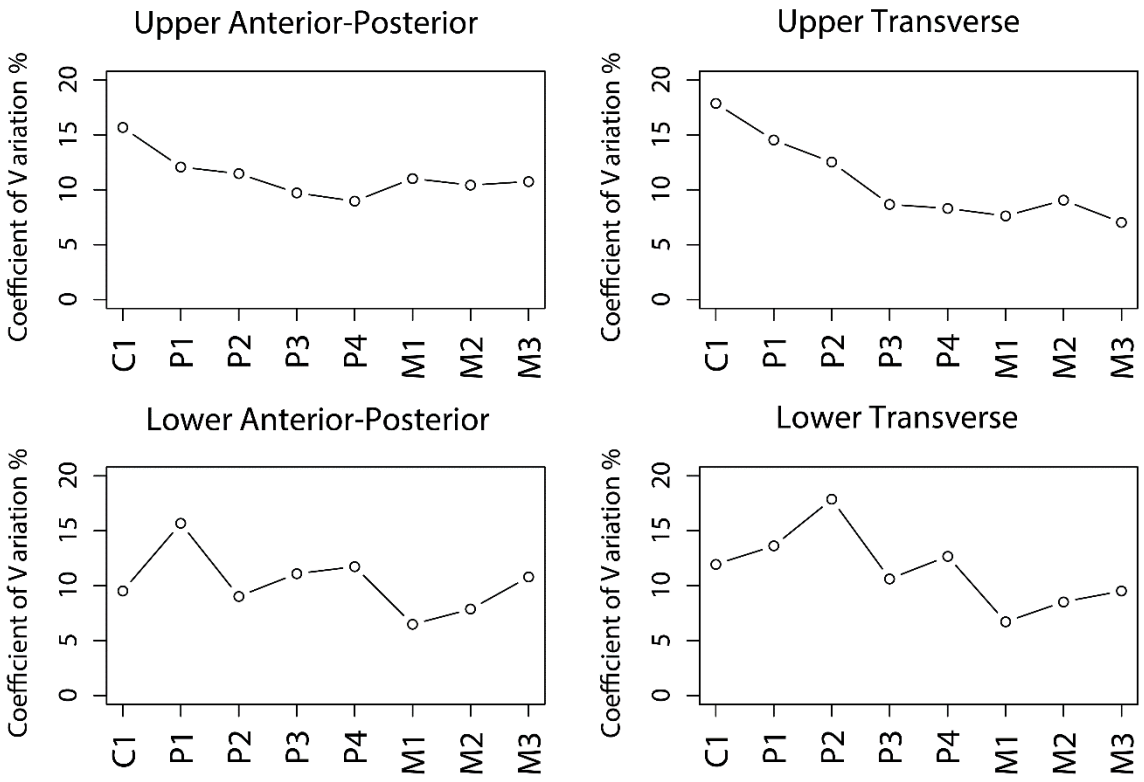

Figure 4.6 – Coefficient of variation of upper and lower teeth dimensions of Eporeodon.

Though skull dimensions of oreodonts have been used to divide the John Day oreodont sample into many different species (Schultz and Falkenbach 1968), I found that the distributions of skull characters in the sample were within range of the normal CV for a single species and had normal distributions (Figure 4.7). There was no evidence for dolichocephalic or brachycephalic groupings, as the anteriormost part of the skull and the rest of the skull was strongly correlated with minimal variation. In other words, skull morphology was too tightly correlated and not variable enough to be indicative of multiple populations (Figure 4.7). In most cases, holotypes that had been described as dolicocephalic ("long-faced") had been laterally compressed, and those that had been described as brachycephalic ("short-faced") were missing tips of the nasals or occipital fan (posteriormost projection of occipital ridge). The lack of subsets of facial proportions confirms the conclusion of Stevens and Stevens (2007) that subgroupings of skull dimensions were likely related to taphonomic factors rather than biology. The shape of the orbit (circular vs oval) has also been used as a character (Schultz and Falkenbach 1968); again, there was no evidence for multivariate multimodality, and there was strong correlation alongside minimal variation, suggestive of a single distribution. (Figure 4.7) In the *Eporeodon bullatus* from John Day, at least, orbital shape and overall skull length and width are inadequate characters for species diagnosis.

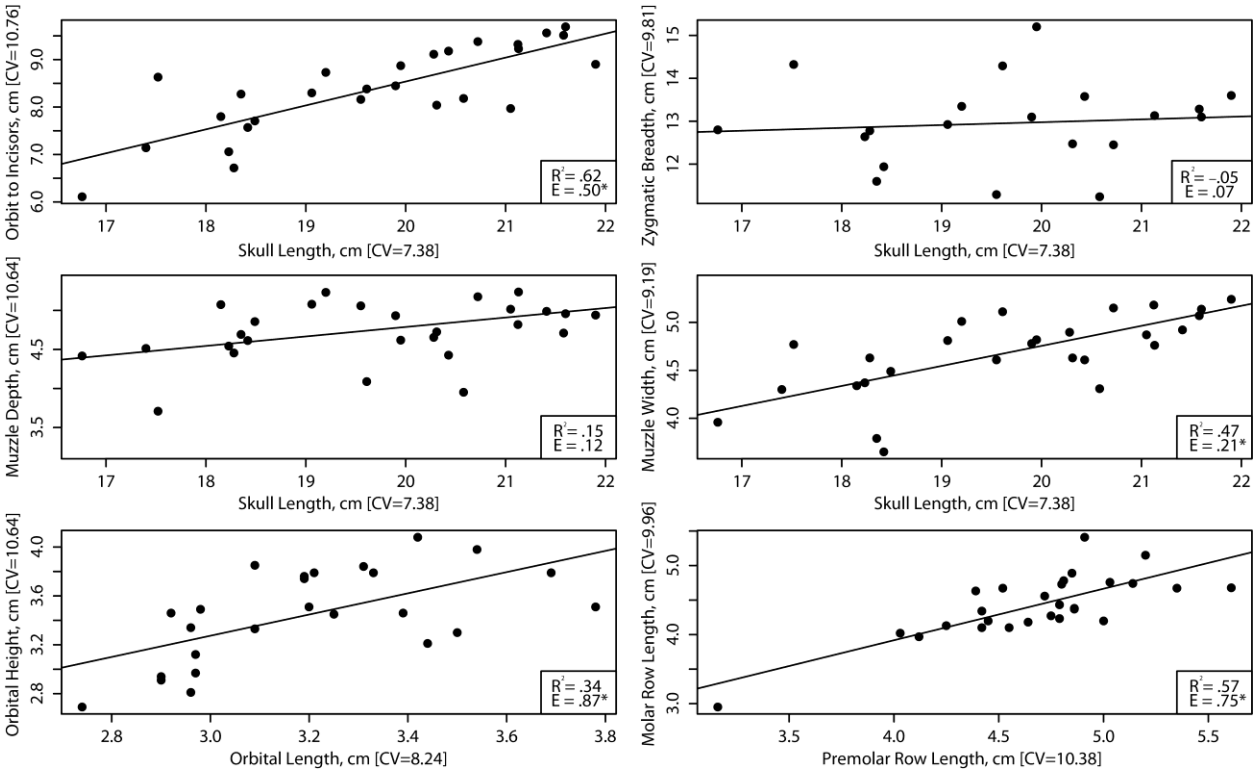

Figure 4.7 – Correlations of the different dimensions of the skull. Adjusted R^2 values and slope (E for Estimate) are reported for each plot. Asterisks indicate a slope significantly different from 0.

Conversely, the length of the skull and breadth of the zygomatic arch were not correlated (adjusted R^2 = -0.05, slope not significantly different from 0) (Figure 4.7). Neither character independently had unusually high variation, but the relationship between skull and zygomatic breadth was not purely related to size: larger individuals did not necessarily have wider zygomatic arches (Figures 4.3, 4.7). Similarly, skull length and muzzle depth did not have a significant relationship. Neither character displays significant groupings in multivariate or univariate space according to the finite mixture analysis and dip test results. The low variation of these characters and absence of statistical grouping make them not diagnostic of multiple species, but the absence of correlation in broad facial dimensions is unusual. A possible reason for the poor correlation is sexual dimorphism: in many fossil peccaries and pigs the males had comparatively wider faces (Herring 1972). If oreodonts followed a similar pattern, but males

were not also comparatively larger in size, that could explain the lack of correlation between zygomatic arch breadth and skull length. Post-adulthood ontogenetic change has been measured in modern pigs (Herring 1974), and post-adulthood growth of the zygomatic arches could also contribute to a non-significant relationship between width and length.

Auditory Bullae and Auditory Meatus

The shape and size of the auditory bulla and auditory meatus has historically been a prominent generic and species character in oreodonts (Schultz and Falkenbach 1968, Lander 1998). Bulla height in this sample was not more variable than in modern examples (Table 4.1), and the extent of shape variation was not greater than what can be seen in modern duikers (Figure 4.8). The auditory meatus was highly variable in the fossil sample, but that variation was matched by the extant sample - *Cephalophus weynsi* showed all of the possible morphologies of the auditory meatus described in oreodont literature (Figure 4.8, Table 4.1). This high variability in artiodactyls suggests that the precise shape of the auditory meatus is not highly constrained by natural selection at this scale. In fact, the presence or absence of the auditory meatus is not fundamental for hearing: after bilateral removal of the auditory meatus and the auditory bullae, 50% of dogs can still hear (Krahwinkel et al. 1993). Variation in the shape and size of the auditory meatus and auditory bullae of this sample may therefore be intraspecific, and does not contribute to rejection of the null hypothesis of a single-species sample.

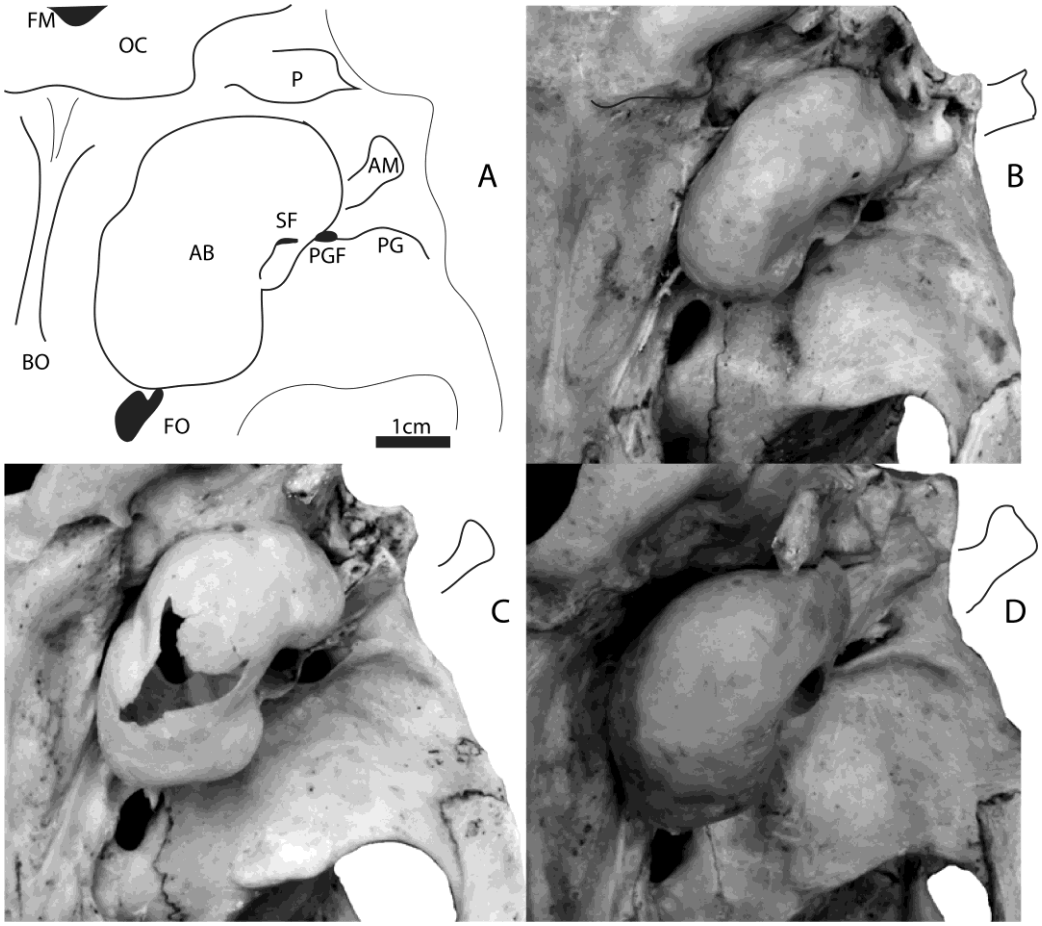

Figure 4.8 – Structure of the auditory meatus and bullae of modern specimens of Cephalophus weynsi. *Outlines on B-D show general shape of meatus. Abbreviations as follows: AM, auditory meatus; AB, auditory bullae; PGF, post-glenoid foramen;, PG, post-glenoid process; FO, foramen ovale;, BO, basioccipital; OC, occipital condyle; P, paroccipital process; SF, stylomastoid foramen; FM, foramen magnum. B is AMNH 53066, C is AMNH 53055, D is AMNH 53037.*

Paroccipital Processes

The shape of the paroccipital process was one of the characters that created partitioning in the phylogenetic analysis. The two primary morphotypes of paroccipital process in this sample reflect changes in the external edge of the process near the auditory meatus: in some, the external edge points perpendicular to the line of the skull with little to no curvature, and in others the external edge is folded anteriorly, becoming parallel with the skull (Figure 4.4). The paroccipital

process serves as the posterior attachment point for the digastric muscle, which attaches to the bottom of the anterior of the mandible and helps open the jaw (Cuccia et al. 2014). The lateral edge of the paroccipital process varies in modern artiodactyls (Figure 4.8), yet I found no example in modern taxa where the lateral edge of the paroccipital process was as variable as it was in the oreodont sample.

The shape of the lateral edge of the paroccipital process may relate to bone remodelling. The angle of the muscular force on the paroccipital process is reliant on the length and width of the face; changes in the angle could cause reworking of the lateral edge of the paroccipital process, potentially resulting in the two morphological states. I conducted an ANOVA in R, and found that skulls with anteriorly-warped paroccipital processes were significantly larger than those with perpendicular processes (p =.007, Figure 4.4). A significant relationship was not observed for zygomatic width (p =.74), but zygomatic width and skull length are uncorrelated in the oreodont sample (Figure 4.7). By increasing the length of the skull without a corresponding change in skull width, the force on the paraoccipital process would change, possibly leading to reworking of the lateral edge. Finally, a juvenile *Eporeodon bullatus* specimen had paroccipital processes with lateral edges that were posteriorly-facing, rather than the perpendicular or anteriorly facing morphology of adult specimens. Given that paroccipital process morphology was not linked in the phylogenetic analyses with any other character, I conclude that the anteriorly-folded morphology is driven by muscular reworking rather than species division.

Maxillary Notch and Infraorbital Foramen

Nasal retraction is an important evolutionary process in Merycoidodontidae, which may have occurred in several genera independently and for different functions (Schultz and

Falkenbach 1940, Lander 1998, Stevens and Stevens 2007). The length of the nasals and the position of the sutures between the nasals and the premaxilla (maxillary notch) are important phylogenetic characters, and are typically described by their relation to teeth. The maxillary notch was predominantly anterior to P1 but in four specimens the notch was posterior to P1. In artiodactyls, variation typically decreases posteriorly in the toothrow, with the canines and first premolars being the most variable (Chapter II). Additionally, oreodonts have a diastema between the canine and the first premolar, which is also highly variable in this sample (CV = 30.23%). While I found no evidence that maxillary notch placement was directly related to diastema length or premolar row length (Figure 4.9), the high variation in the anterior muzzle likely contributes to variation in the precise placement of the maxillary notch. Though an important character for generic distinctions (Douglass 1906), the variation in the maxillary notch in *Eporeodon bullatus* should be perceived as a result of high variation in the toothrow, which is normal for a single-species sample of artiodactyls (See Chapter II).

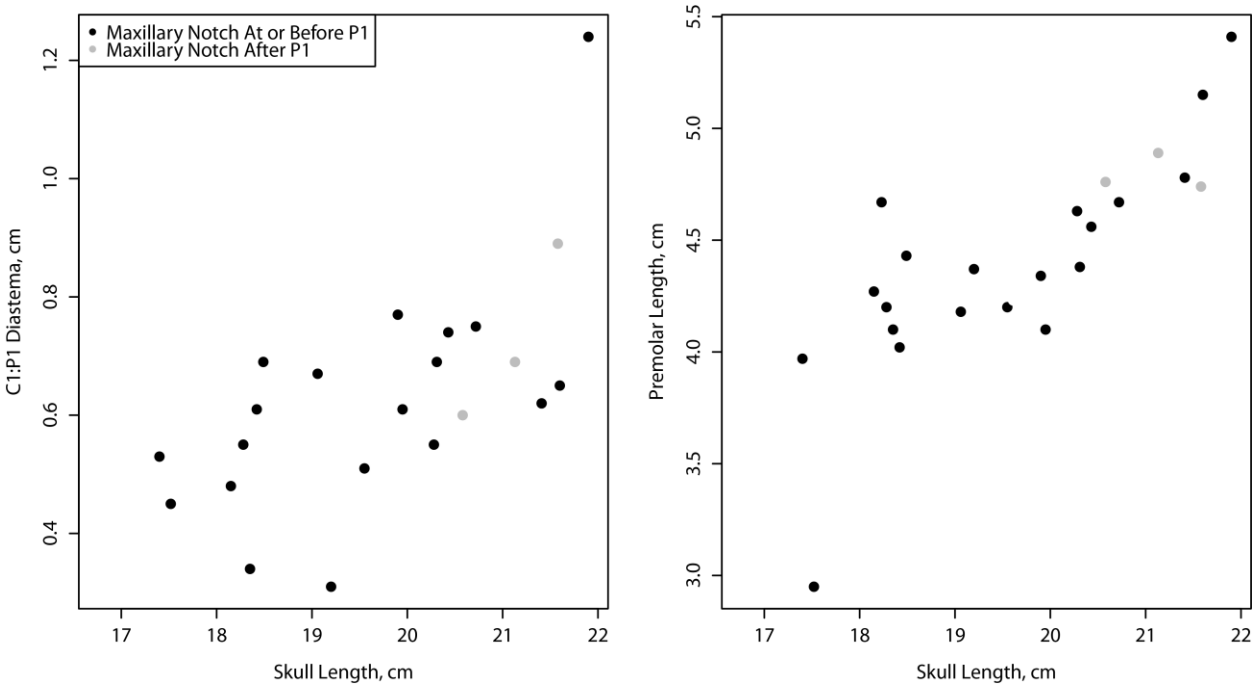

Figure 4.9 – Placement of the maxillary notch in comparison to skull length, premolar length, and diastema length. Gray indicates a maxillary notch posterior to P1.

Similarly, the infraorbital foramen varied between P3 and P4, with placement continuous between the two teeth. Foramina form when bone tissue ossifies around nerves; the placement of the nerve itself dictates the formation of the foramen (Canan et al. 1999). Anatomical variation in foramina placement humans is well-studied and recognized (Leo et al. 1995, Canan et al. 1999, Agthong et al. 2005, Macedo et al. 2009), and given the variation inherent in tooth placement as well as the known variation in nerve placement, there is some suggestion the variation of infraorbital foramen placement in this sample is intraspecific rather than interspecific variation.

Palate Shape

The terminus of the palate where it meets the pterygoid processes in this oreodont sample was either rounded (U-shaped), pointed (V-shaped), or had a small extension of the suture of the palate (W-shaped). Both W and U morphologies were present in *Hylochoerus meinertzhagheni* - 7 of 11 specimens had W shapes with posterior extension of the suture, while the rest were U-shaped. Nine of 20 specimens of *Cephalophus leucogaster* were V-shaped rather than U-shaped in the palatal terminus. Given the high rate of intraspecific variation in the shape of the palate in modern animals, I have disregarded palate shape as an appropriate diagnostic character. The exact placement of the terminus of the palate is also variable – in *Cephalophus leucogaster*, the palate terminates at M1, M2, or M3, and so the placement of the palate terminus is also unlikely to diagnose taxa rather than individuals.

Basioccipital Ridge

The presence or absence of a ridge on the occipital bone was variable in both the modern and fossil sample – 4 of 12 specimens of *Muntiacus muntjak* had a ridge. The basioccipital ridge occurs at the meeting point of the two sides of longus capitis, a weak head flexor (Ramirez et al. 1998). In modern *Canis familiaris*, basioccipital ridge shape is sexually dimorphic (Trouth et al. 1977) . The variability of the basioccipital ridge in modern artiodactyls and *Canis familiaris* suggests it had a similarly high level of intraspecific variability in oreodonts, and should not be considered a diagnostic character.

Enamel Irregularities

Size, shape, and crest pattern of premolars have all been used as characters in oreodont systematics (Douglass 1906, Schultz and Falkenbach 1968, Lander 1998). In Chapter II, I discuss the extent of variation that is present in premolars, and also the limitation of Photoscan technology: the smaller a character, the higher the variation because of measurement error. As a result, I decided to exclude measurements of individual premolar cones from this analysis; they were unlikely to be reliably measured by this system, and the high variation inherent in premolars makes using premolars as diagnostic characters potentially more difficult. Two characters that I did record were enamel irregularities. An enamel well (an additional crest that surrounds a small circle of dentine on the lingual cone) and enamel ridges on the labial cone of the P4 were both present in this sample (Figure 4.1). Enamel wells diagnose *Mesoreodon* (Douglass 1906) from *Eporeodon,* and enamel ridges on the P4 diagnose *Eucrotaphus* from *Eporeodon* (Lander 1998). However, two specimens had both P4 ridges and enamel wells (UCMP 76529, UO F-29689), and two specimens with ridges on one side of the palate and not on the other (UWBM 51725, AMNH FM 7567). In AMNH FM 7695, both sides had enamel

wells and the right side had a prominent, unusual labial style on the P4 that almost acted as an additional cusp. The presence of common intra-specimen variation in this character makes it unlikely to diagnose at a species level.

Pre-Orbital Fossa

The pre-orbital fossa was the one character with variation far higher than predicted by any of the modern species (Table 4.1, Figure 4.10). Possible causes of high pre-orbital fossa variation include postmortem deformation, sexual dimorphism, ontogenetic change, time-averaging, geographic variation and multiple species in this sample. The bone of the pre-orbital fossa is very thin in modern and fossil artiodactyls; it creates accommodation space for a gland or sac (Rehorek et al. 2005) and in many modern specimens, the bone was either transparent or broken. I excluded fossil specimens that had broken bases, so post-mortem deformation is unlikely to be a source of variation. The depth of the pre-orbital fossa is sexually dimorphic in modern artiodactyls as male muntjacs and duikers are more likely to scent-mark than females are, and so have correspondingly larger glands and fossa (Barrette 1976, 1977, Chapman and Chapman 1982). However, the modern sample contains males and females of all included species, and still the variation of the oreodont sample is more than double that of any of included modern groups. Ontogenetic variation likely affects the size of the pre-orbital fossa, but the observed variation remains high even when juvenile specimens are excluded. Post-adulthood ontogenetic growth could potentially explain some variation in this character, but the modern sample may also have contained such a variation source without subsequently increased variation.

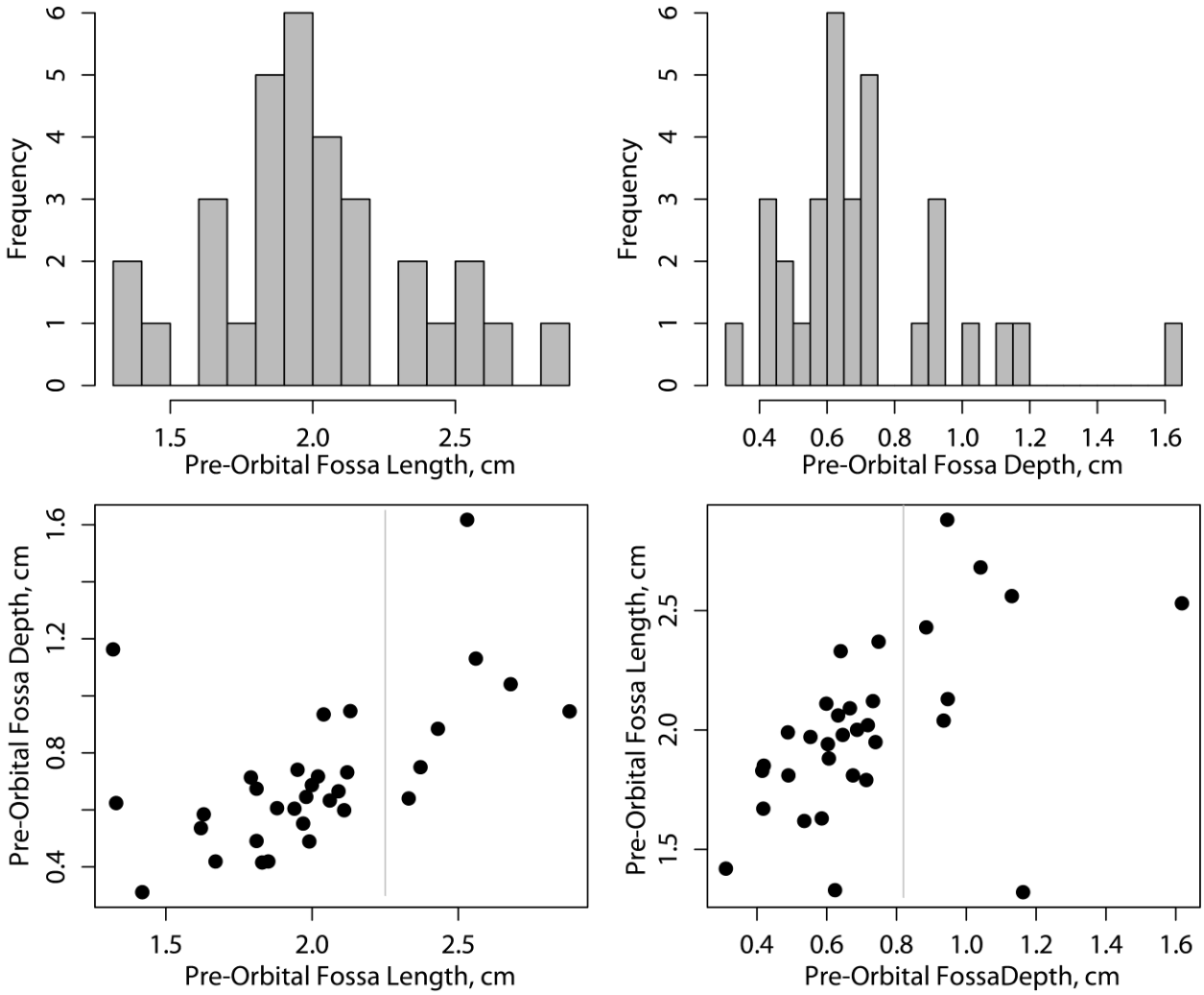

Figure 4.10 – Histograms and biplots of length and depth measurements of the pre-orbital fossa in Eporeodon bullatus*. Lines on each plot correspond to breaks in histogram distribution*

Therefore, the high variation of the pre-orbital fossa suggests more than one species in this sample. The high variation was not accompanied by discernable overlapping distributions: though there were visibly clear breaks in histograms of this sample, these were not statistically likely to have more than one component or mode according to the diptests or finite mixture analyses ($p>.05$). Furthermore, biplots of the muntjak and duiker samples show that even though the length and depth of the pre-orbital fossa may be diagnostically different, those differences are very difficult to correctly group according to species or sex (Figures 4.11-4.12).

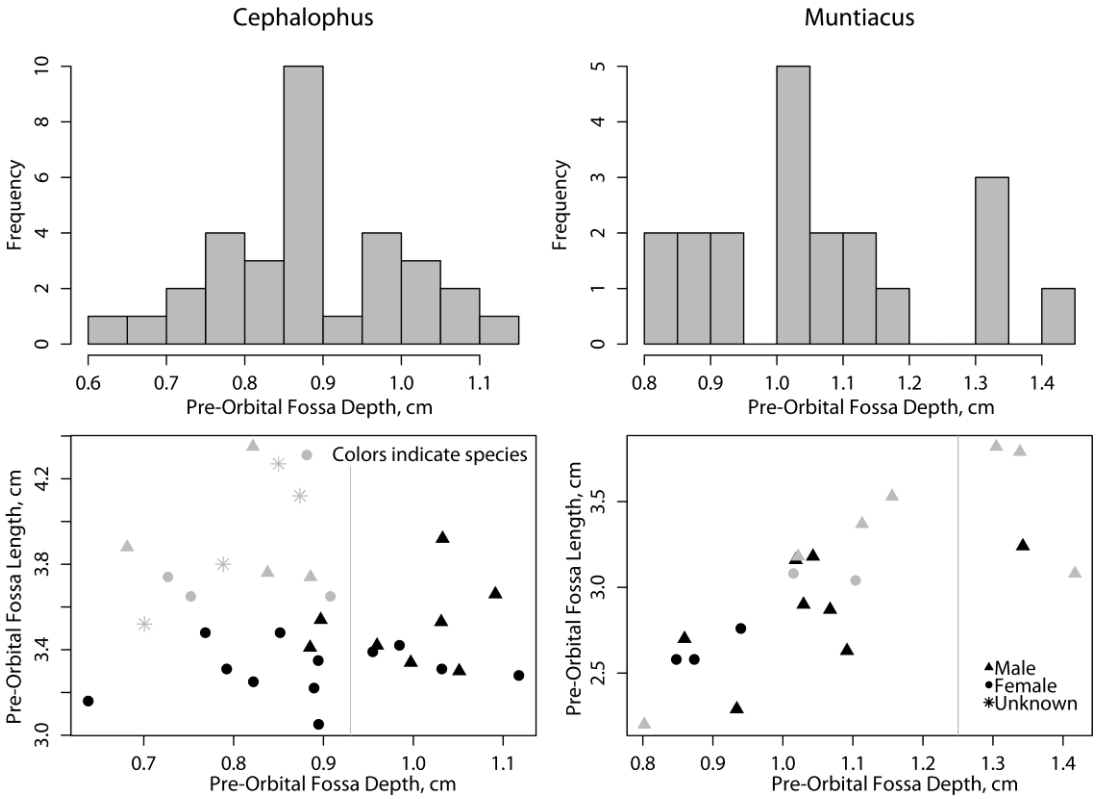

Figure 4.11 – Histograms and biplots of depth of pre-orbital fossa in Cephalophus and Muntiacus. Triangles represent male specimens, circles represent females, and asterisks have unknown sex. Colors correspond to species – black is Cephalophus leucogaster *and* Muntiacus muntjak*, while gray is* Cephalophus weynsi *and* Muntiacus reevesi*. Lines on each plot correspond to breaks in histogram distribution.*

By attempting to divide the sample along any distribution break or axes, I would undoubtedly be mixing up samples from different species – there was no reasonable species delineation line, and the length and depth of the pre-orbital fossa cannot currently be considered diagnostic for species of *Eporeodon* even though it is a clear indication of multiple species in this sample.

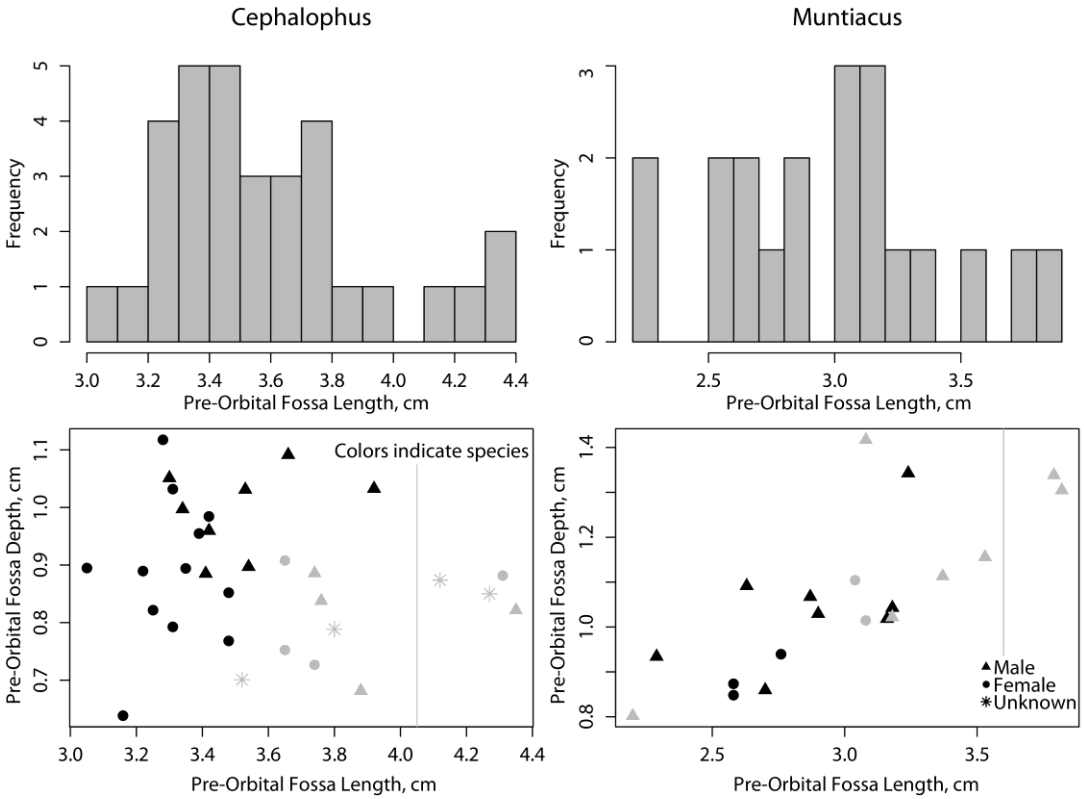

Figure 4.12 – Histograms and biplots of length of pre-orbital fossa in Cephalophus *and* Muntiacus*. Triangles represent male specimens, circles represent females, and asterisks have unknown sex. Colors correspond to species – black is* Cephalophus leucogaster *and* Muntiacus muntjak*, while gray is* Cephalophus weynsi *and* Muntiacus reevesi*. Lines on each plot correspond to breaks in histogram distribution.*

It is possible that the lack of diagnostic power of the length and depth of the pre-orbital fossa is a reflection of the geographic or temporal spread of these data. The oreodonts of this sample cover 7 million years in the John Day area (Albright III et al. 2008) and include specimens from the White River group. Including disparate geographic and temporal populations increases the chance of magnifying variation from evolution. Unfortunately, almost all of the skulls with pre-orbital fossae in this sample were collected before the importance of precise locality information was understood: there is currently no way to determine whether the size of the pre-orbital fossa has changed through time in the John Day Formation because I cannot place most of these specimens in clear stratigraphic context. For now, I can only recognize that the

high variation may result from the large time span captured in this sample, but not delineate it in any meaningful way.

Conclusion

Most of the characters previously used to diagnose the mid-sized oreodonts of John Day are no more variable than those of single-species samples of extant artiodactyls. The height and shape of the auditory bullae and auditory meatus, overall dimensions of the skull, and the size and shape of the orbit do not reject a single-species sample of the mid-size John Day oreodont, nor do they diagnose the mid-sized John Day oreodont sample as being significantly different from those of the White River Group. Several characters were variable, yet not diagnostic: the placement of the maxillary notch, placement of the infraorbital foramen, attachment of the zygomatic arch, and enamel abnormalities of P4 are more likely representative of intraspecific variation. These characters were also not diagnostic when used in phylogenetic analysis: the clades diagnosed by discrete characters were different between each tree, and supported by characters whose diagnostic capacity was unlikely.

One character which was unusually variable was the length and depth of the pre-orbital fossa. The pre-orbital fossa is a depression anterior to the orbit where a large gland or sac sits in life. The pre-orbital gland or sac is used by artiodactyls to scent-mark both territories and other individuals, and is sexually dimorphic and species-diagnostic in modern artiodactyls (Chapman and Chapman 1982, Rehorek et al. 2005). The fossa is particularly prominent in oreodonts, as it is in duikers and muntjacs, but is nearly three times as variable in this oreodont sample. The high variation in the oreodont sample was not caused by breakage and distortion of the fragile bone of the pre-orbital fossa, as I only measured individuals without crushing. Similarly, the high variation is unlikely to relate to sexual dimorphism, as the modern comparative samples had both

males and females of dimorphic species yet the fossil variation far exceeded that of the modern sample.

Because of the complicated interplay of sex and species in the length and depth of the pre-orbital fossa, I have chosen not to divide this sample into two or more species; such a division would be unlikely to capture the true species division (Figures 4.10-4.12), but rather create an artificial divide that would not be easily replicated between users or regions. Though the John Day eporeodontine oreodonts could simply be a single, highly variable species, the inordinately high variation of the pre-orbital fossa suggests more than one species were likely present in the John Day region, but I was unable to find a character that was capable of diagnosing these species from each other.

In the interest of replicability, I am calling *Eporeodon bullatus* a species complex: more than one species present, yet too closely overlapped to be diagnosed from one another. In modern duikers, the species resolution of cranial characters is approximately a third of what is defined by coat pattern and DNA (Chapter III). While one cannot reliably diagnose the varied taxa of John Day *Eporeodon bullatus* beyond a single morphological complex using the characters we have tested here, the morphology of *Eporeodon bullatus* is highly suggestive of sympatric species indiscernible by osteology alone.

Yet even without species-level resolution, the artiodactyls of John Day are unusually diverse: six other oreodont genera (*Promerycochoerus, Paroreodon, Merychyus, Oreodontoides, Merycochoerus, Agriochoerus)* and 19 other non-oreodont artiodactyl genera are present, a level of generic diversity that matches the species-level diversity of modern lowland African forests (Andrews et al. 1979, Albright III et al. 2008, IUCN 2016). If the cryptic diversity of the *Eporeodon bullatus* species complex is reflected in other John Day artiodactyls, then the species-

level diversity of the John Day formation far exceeds that of modern Oregon and many other ecosystems.

Ongoing collection and better temporal resolution may show that the atypical diversity of John Day artiodactyls is a feature of temporal averaging, but without taxonomic revisions that lead to replicable and reliable identifications, it will remain unclear how John Day compares to other regions and time periods. In particular, the other oreodont species of John Day are diagnosed at a scale reminiscent of the treatment of mid-sized oreodonts, which may lead to an over-inflation of their diversity. In this study I have taken a sample previously diagnosed as 2 subfamilies, 4 genera, and 10 species (Schultz and Falkenbach 1968) and diagnosed only a single species complex. If other artiodactyl taxa are similarly reducible, then part of the specific and generic diversity of the John Day formation may not be a result of incredible biological diversity or even high temporal averaging, but simply inconsistent systematics.

Supplementary Table Captions

Table S3.1 – Discrete and continuous measurements of *Eporeodon bullatus*.

Table S3.2 – Discrete and continuous measurements of extant artiodactyls.

Table S3.3 – Descriptions of discrete character states.

Table S3.4 – Teeth measurements data.

Table S3.5 – CV data for teeth measurements, for use in R script.

Additional Supplementary Data: tree.nex is a nexus file of *Eporeodon* phylogenies from TNT.

CHAPTER V

DISSERTATION CONCLUSION

The increased use of fossil data to evaluate evolutionary and ecological processes has necessitated the assumption that fossil taxa are comparable to modern taxa. Because fossil taxa can only generally be diagnosed using osteological characters, while modern taxa are typically diagnosed using soft-tissue characters, fossil species may not necessarily match extant species. For fossil species diversity to accurately be compared to modern diversity, any differences in species concept should be recognized and be related to a matter of scale (Figure 5.1).

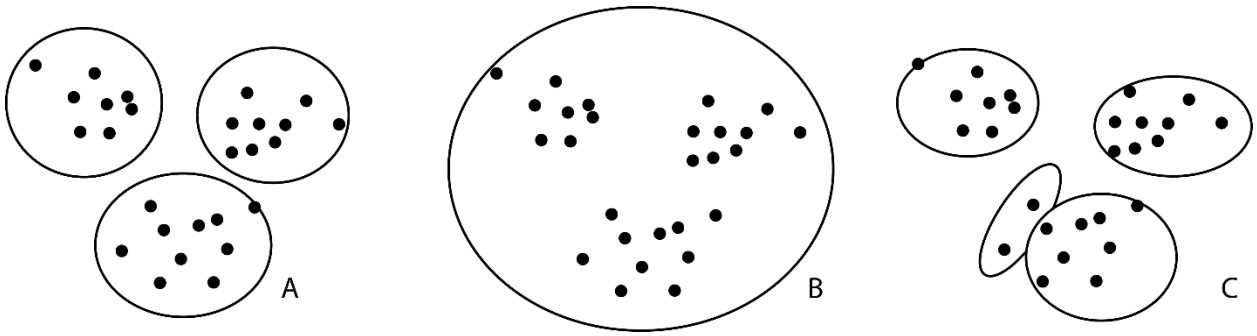

Figure 5.1: A) biological species concept. B) Lumped osteological species concept, showing similar divisions at different scale. C) Inaccurate and over-split osteological species concept, not comparible to biological species.

In this dissertation, I have concentrated my studies on artiodactyls, with particular focus on the extinct group Merycoidodontoidea. I have tested the utility of dental and cranial measurements to diagnose related modern taxa, and measured the resolution at which osteological characters reflect biological division. In Chapter I, I summarized dental variation in a sample of modern artiodactyls. Dental variation in artiodactyls follows a different pattern than in primates – the length of M1 is the most variable in artiodactyls and the least variable in primates. This difference arises from the different structure and function of the dentition: selenodont artiodactyls often have styles that spread the tooth surface anteroposteriorly, and the

tooth surface area decreases as the styles wear. Because the tooth surface of selenodont artiodactyls shrinks through ontogeny, they have higher variation than primates or carnivores. I also found that the coefficient of variation did not adequately remove the influence of size in my measurements: bigger animals were more variable than predicted by the relationship between size and variation of smaller animals. Future work should be conducted to conclude whether this trend was driven by phylogenetics or a true size relationship, but in the meantime it is clear that any systematicist should choose a model organism of similar size and morphology if they hope to compare the variation of a fossil to the variation in a modern sample.

In Chapter II I evaluated how well cranial characters diagnosed extant artiodactyl species. I used the skulls of 10 different species of duiker antelope, up to 8 of which share ranges in the lowland forests of Africa. Duiker antelope are sympatric and share nearly identical dietary niche spaces, primarily eating figs and other fruit (Bowland and Perrin 1995). The predominant niche partitions are behavioral rather than dietary: certain species have larger ranges, or are nocturnal, or eat slightly larger fruit and in this way duikers have successfully negotiated space in their overlapping ecosystems (Newing 1994). The minimal dietary divergence has resulted in very similar morphologies between species, leading to crania that are more likely to reflect geography than phylogeny. I found that species that shared range space were confused as one another by discriminant function analysis of cranial landmarks, more often than species were confused for their closest sister species. Additionally, I found that cranial landmarks were not effective at identifying species (only accurate 70% of the time). Distributions of cranial characters were only successful at identifying the three main size classes, rather than the 10 species present.

For fossil taxa, the limited effectiveness of osteological materials for identifying duiker species means that worst-case scenario sympatric species complexes are unlikely to be identified

in the fossil record. This is a scaling issue: three clades of duiker were identifiable using measurements in both teeth and crania, and though this does not adequately capture the full species diversity it does accurately capture some of the relationships within duikers (Figure 3.4).

A dominant character of duiker crania is the presence of a large pre-orbital fossa, a feature they share in common with oreodonts. This fossa houses a gland or sac used to scent-mark territory, and modern artiodactyls with large fossae have species-unique chemical compounds used to identify one another (Burger et al. 1988). Reliance on scent-marking with a facial gland may also further reduce the necessity of cranial differentiation between sympatric species, as they are no longer using visual cues for species discrimination.

The pre-orbital fossa was the only character that was unusually variable in the mid-sized oreodonts of John Day. In Chapter III, I used distribution tests and phylogenetic analyses to reassess the mid-sized oreodonts of John Day. Ultimately, almost every character proved continuous without diagnostic potential, but while most characters also lacked inflated variation statistics, the length and particularly the depth of the pre-orbital fossa were too variable to have come from one species. In modern muntjacs and duikers, the length of the pre-orbital fossa is statistically different between species and sexes (Chapman and Chapman 1982). However, this statistical difference is only visible with *a priori* knowledge of species and sex – information sadly unavailable in paleontological samples. Though there were several natural divisions in the distributions of length and depth of my oreodont sample, these were A) not statistically significant, and B) were similar to natural divisions in my sample of muntjacs and duikers, neither of which were biologically meaningful (Figures 4.7-4.9). The variation of the pre-orbital fossa in *Eporeodon bullatus* was enough to tell there was more than one species, but the overlap between these species was so extensive that I could not accurately discern how many species

were present, and which taxa belonged to which group. As a result, Chapter III describes *Eporeodon bullatus* as a species complex – an ostologically overlapping group of more than one species that cannot be diagnosed from one another.

In Chapter III, I took a group of oreodonts previously described as 4 genera and redescribed them as a single genus with an unknown number of species. *Eporeodon bullatus* is unlikely to be the only oreodont where intraspecific osteological variation is used to dramatically oversplit a group – in fact, the large species of John Day are described as a very similar 11 species, 4 genera and 2 subfamilies (Schultz and Falkenbach 1949, 1954). Additionally, the characters I found captured intraspecific variation in Chapter III are used for most all other oreodont taxa, suggesting that similar levels of over-splitting are common throughout the superfamily.

Ultimately, the goal of any systematist should be to create species divisions that make biological sense and are replicable between users. The goal of a paleosystematist should contain an additional step: to understand and describe any cryptic diversity present in their sample. In this dissertation, I have discussed how osteology is not always adequate for discerning different species. Sometimes, as in Chapter III, high variation can be a good clue that multiple taxa are present; other cases, as shown in Chapter II, certain morphologies can indicate the possibility of sympatric species complexes. Osteology of artiodactyls does not always capture as fine-scale species resolution as DNA, and the potential differences between fossil and extant species should be recognized and accounted for in diversity studies.

The burden of comparability should also fall on the shoulders of those ecologists and evolutionary biologists who wish to compare fossil and modern populations. In this dissertation I have shown how modern artiodactyls with similar sizes and ecologies are unlikely to be

accurately distinguished in the fossil record; including discrete sympatric modern species when comparing to a fossil system will lead to unfair inflation of the modern system. Paleosystematists should make every effort to incorporate and discuss cryptic diversity into their systematics, but broad-scale studies should also take care that their modern system is scaled for better comparison to fossil systems. Modern workers should work toward further understanding of the osteological species resolution in modern ecosystems, possibly down-scaling minimaly osteologically diverse taxa like duikers, muntjaks, and dik-diks to obtain meaningful comparisons between time periods. Paleontologists should make all efforts to identify and describe the possibility of cryptic diversity in their sample, but also ensure that modern biological species are not unreasonably weighted by the greater availability of modern characters with which to divide them.

APPENDIX A

R SCRIPT FOR CHAPTER I

```
##############################
########DATA ANALYSIS######
##############################
library(dplyr)
camel <- read.csv("TS1.csv") %>%
filter(Species=="Camelus dromedarius" | Species=="Camelus bactrianus")
ovis <- read.csv("TS1.csv") %>%
filter(Species=="Ovis dalli")
muntiacus <- read.csv("TS1.csv") %>%
filter(Species=="Muntiacus muntjak" | Species=="Muntiacus reevesi")
ceph <- read.csv("TS1.csv") %>%
filter(Species=="Cephalophus leucogaster" | Species=="Cephalophus weynsi" | Species=="Cephalophus dorsalis" |
Species=="Cephalophus nigifirons" | Species=="Cephalophus silvicultor" | Species=="Philantomba monticola")
vicu <- read.csv("TS1.csv") %>%
filter(Species=="Vicugna vicugna")
guan <- read.csv("TS1.csv")%>%
filter(Species=="Lama guanaco")
hyme <- read.csv("TS1.csv")%>%
filter(Species=="Hylochoerus meinertzhagheni")
hylo <- hyme
ceph2 <- read.csv("TS1.csv")%>% #without silvicultor
filter(Species=="Cephalophus leucogaster" | Species=="Cephalophus weynsi" | Species=="Cephalophus dorsalis" |
Species=="Cephalophus nigifirons" | Species=="Philantomba monticola")
```

```
CVtest <- read.csv("CVtest.csv")



#Species Subsets
bact <- subset(camel, Species == "Camelus bactrianus", select=c(adult, male, zoo, X., Age.Class, L.Muzzle, L.C1,
H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.C1, W.P2, W.P3, W.P4, L.Premolars,
L.Molars, L.Toothrow))
drom <- subset(camel, Species == "Camelus dromedarius", select=c(adult, male, zoo, X., Age.Class, L.Muzzle,
L.C1, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.C1, W.P2, W.P3, W.P4, L.Premolars,
L.Molars, L.Toothrow))
munt <- subset(muntiacus, Species == "Muntiacus muntjak", select=c(adult, male, zoo, X., Age.Class, L.Muzzle,
L.C1, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars,
L.Molars, L.Toothrow))
reev <- subset(muntiacus, Species == "Muntiacus reevesi", select=c(adult, male, zoo, X., Age.Class, L.Muzzle,
L.C1, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars,
L.Molars, L.Toothrow))
mont <- subset(ceph, Species == "Philantomba monticola", select=c(adult, male, X., Age.Class, L.Muzzle, H.M1,
L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars, L.Molars,
L.Toothrow))
leuc <- subset(ceph, Species == "Cephalophus leucogaster", select=c(adult, male, X., Age.Class, L.Muzzle, H.M1,
L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars, L.Molars,
L.Toothrow))
dors <- subset(ceph, Species == "Cephalophus dorsalis", select=c(adult, male, X., Age.Class, L.Muzzle, H.M1,
L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars, L.Molars,
L.Toothrow))
weyn <- subset(ceph, Species == "Cephalophus weynsi", select=c(adult, male, X., Age.Class, L.Muzzle, H.M1,
L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars, L.Molars,
L.Toothrow))
```

```
silv <- subset(ceph, Species == "Cephalophus silvicultor", select=c(adult, male, X., Age.Class, L.Muzzle, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars, L.Molars, L.Toothrow))
nigi <- subset(ceph, Species == "Cephalophus nigifirons", select=c(adult, male, X., Age.Class, L.Muzzle, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars, L.Molars, L.Toothrow))


#Discriminant Function Analysis Linear
library(MASS)
subsetCeph <- subset(ceph, select=c(Species, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4))
subsetCeph2 <- na.omit(subsetCeph)
camelz <- subset(camel, select=c(Species, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P3, L.P4, W.P3, W.P4))
lamaz <- subset(guan, select=c(Species, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P3, L.P4, W.P3, W.P4))
vicugnaz <- subset(vicu, select=c(Species, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P3, L.P4, W.P3, W.P4))
camelids <- rbind(camelz, lamaz, vicugnaz)
camelids.na <- na.omit (camelids)
muntjaks <- subset(muntiacus, select=c(Species, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P3, L.P4, W.P3, W.P4))
muntjaks.na <- na.omit(muntjaks)

cephfit <- lda(Species ~ L.M1 + L.M2 + L.M3 + L.P2 +L.P3 + L.P4 + W.M1 + W.M2 + W.M3 + W.P2 + W.P3 + W.P4, data=subsetCeph2, na.action="na.omit", priors=c(1,1,1,1,1,1)/6, CV=TRUE)
ct1 <- table(subsetCeph2$Species, cephfit$class)
ceph_lda <- diag(prop.table(ct1, 1))# percent correct for each species
sum(diag(prop.table(ct1))) # total percent correct
```

```
camelfit <- lda(Species ~ L.M1 + L.M2 + L.M3 + L.P3 + L.P4 + W.M1 + W.M2 + W.M3 + W.P3 + W.P4,
data=camelids.na, na.action="na.omit", priors=c(1,1,1,1)/4, CV=TRUE)
ct2 <- table(camelids.na$Species, camelfit$class)
camel_lda <- diag(prop.table(ct2, 1))# percent correct for each species
sum(diag(prop.table(ct2))) # total percent correct

muntjakfit <- lda(Species ~ L.M1 + L.M2 + L.M3 + L.P3 + L.P4 + W.M1 + W.M2 + W.M3 + W.P3 + W.P4,
data=muntjaks.na, na.action="na.omit", priors=c(1,1)/2, CV=TRUE)
ct3 <- table(muntjaks.na$Species, muntjakfit$class)
munt_lda <- diag(prop.table(ct3, 1))# percent correct for each species
sum(diag(prop.table(ct3))) # total percent correct


###Quadratic discriminant function analysis with jackknifing.
ceph_Q <- qda(Species ~ L.M1 + L.M2 + L.M3 + L.P2 +L.P3 + L.P4, data=subsetCeph2, na.action="na.omit",
priors=c(1,1,1,1,1,1)/6, CV=TRUE)
qct <- table(subsetCeph2$Species, ceph_Q$class)
ceph_qda_l <- diag(prop.table(qct, 1))# percent correct for each species
sum(diag(prop.table(qct))) # total percent correct

ceph_Q_w <- qda(Species ~ W.M1 + W.M2 + W.M3 + W.P2 +W.P3 + W.P4, data=subsetCeph2,
na.action="na.omit", priors=c(1,1,1,1,1,1)/6, CV=TRUE)
qct_w <- table(subsetCeph2$Species, ceph_Q_w$class)
ceph_qda_w <- diag(prop.table(qct_w, 1))# percent correct for each species
sum(diag(prop.table(qct_w))) # total percent correct

camel_Q <- qda(Species ~ L.M1 + L.M2 + L.M3 + L.P3 + L.P4, data=camelids.na, na.action="na.omit",
priors=c(1,1,1,1)/4, CV=TRUE)
```

```
qct2 <- table(camelids.na$Species, camel_Q$class)
camel_qda_l <- diag(prop.table(qct2, 1))# percent correct for each species
sum(diag(prop.table(qct2))) # total percent correct

camel_Q_w <- qda(Species ~ W.M1 + W.M2 + W.M3 + W.P3 + W.P4, data=camelids.na, na.action="na.omit",
priors=c(1,1,1,1)/4, CV=TRUE) #widths
qct2_w <- table(camelids.na$Species, camel_Q_w$class)
camel_qda_w <- diag(prop.table(qct2_w, 1))# percent correct for each species
sum(diag(prop.table(qct2_w))) # total percent correct

muntjak_Q <- qda(Species ~ L.M1 + L.M2 + L.M3 + L.P3 + L.P4, data=muntjaks.na, na.action="na.omit",
CV=TRUE, priors=c(1,1)/2)
qct3 <- table(muntjaks.na$Species, muntjak_Q$class)
munt_qda_l <- diag(prop.table(qct3, 1))# percent correct for each species
sum(diag(prop.table(qct3))) # total percent correct

muntjak_Q_w <- qda(Species ~ W.M1 + W.M2 + W.M3 + W.P3 + W.P4, data=muntjaks.na, na.action="na.omit",
CV=TRUE, priors=c(1,1)/2)
qct3_w <- table(muntjaks.na$Species, muntjak_Q_w$class)
munt_qda_w <- diag(prop.table(qct3_w, 1))# percent correct for each species
sum(diag(prop.table(qct3_w))) # total percent correct

munt4 <- data.frame(munt_qda_l, munt_qda_w, munt_lda)
names(munt4)[c(1,2,3)] <- c("QDA Length", "QDA Width", "LDA")
ceph_results <- data.frame(ceph_qda_l, ceph_qda_w, ceph_lda)
names(ceph_results)[c(1,2,3)] <- c("QDA Length", "QDA Width", "LDA")
camel_results <- data.frame(camel_qda_w, camel_qda_l, camel_lda)
names(camel_results)[c(1,2,3)] <- c("QDA Length", "QDA Width", "LDA")
```

```
total <- rbind(camel_results, munt4, ceph_results)
write.csv(total, "C:/discriminant.csv")

#RandomForest with Duikers
library(randomForest)
subsetCeph <- subset(ceph, select=c(Species, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2,
W.P3, W.P4))
subsetCeph2 <- na.omit(subsetCeph)
Species <- subsetCeph2$Species
teeth <- subset(subsetCeph2, select=c(L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3,
W.P4))
results <- randomForest(teeth, Species, data=subsetCeph2, na.action="na.omit", importance=TRUE)
data <- data.frame(results$importance)
rF <- table(results$classes, results$confusion)
ceph_g_rf <- diag(prop.table(results$confusion))
rf_G_sum <- sum(diag(prop.table(rF)))
sum(ceph_g_rf)

#Dimorphism Finite Mixtures of Canines
C1drom <- na.omit(drom$L.C1)
C1Tdrom <- na.omit(drom$W.C1)
P2drom <- na.omit(drom$L.P2)
P2Tdrom <- na.omit(drom$W.P2)
C1bact <- na.omit(bact$L.C1)
C1Tbact <- na.omit(bact$W.C1)
P2bact <- na.omit(bact$L.P2)
P2Tbact <- na.omit(bact$W.P2)
C1hylo <- na.omit(hylo$L.C1)
```

```
C1Thylo <- na.omit(hylo$W.C1)

C1Hhylo <- na.omit(hylo$L.HC1)


df <- data.frame(bact$L.C1, bact$L.P2, bact$W.C1, bact$W.P2)

nadf <- na.omit(df)

bactC1P2M <- data.matrix(nadf, rownames.force=NA)


df2 <- data.frame(drom$L.C1, drom$L.P2, drom$W.C1, drom$W.P2)

nadf2 <- na.omit(df2)

dromC1P2M <- data.matrix(nadf2, rownames.force=NA)


df3 <- data.frame(hylo$L.C1, hylo$L.HC1, hylo$W.C1)

nadf3 <- na.omit(df3)

hyloC1C1C1 <- data.matrix(nadf3, rownames.force=NA)


#Actually Bootstrap for Components

library(mixtools)

P2bactNM <- boot.comp(P2bact, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06, mix.type=c("normalmix"),

hist=TRUE)

P2TbactNM <- boot.comp(P2Tbact, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06,

mix.type=c("normalmix"), hist=TRUE)

C1bactNM <- boot.comp(C1bact, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06, mix.type=c("normalmix"),

hist=TRUE)

C1TbactNM <- boot.comp(C1Tbact, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06,

mix.type=c("normalmix"), hist=TRUE)

P2dromNM <- boot.comp(P2drom, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06, mix.type=c("normalmix"),

hist=TRUE)
```

```
P2TdromNM <- boot.comp(P2Tdrom, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06,
mix.type=c("normalmix"), hist=TRUE)
C1dromNM <- boot.comp(C1drom, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06,
mix.type=c("normalmix"), hist=TRUE)
C1TdromNM <- boot.comp(C1Tdrom, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06,
mix.type=c("normalmix"), hist=TRUE)
MultiBact <- boot.comp(bactC1P2M, x=NULL, N=NULL, max.comp=3, B=1000, sig=.06,
mix.type=c("mvnormalmix"), hist=TRUE)
MultiDrom <- boot.comp(dromC1P2M, x=NULL, N=NULL, max.comp=3, B=1000, sig=.06,
mix.type=c("mvnormalmix"), hist=TRUE)
C1ThyloNM <- boot.comp(C1Thylo, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06,
mix.type=c("normalmix"), hist=TRUE)
C1hyloNM <- boot.comp(C1hylo, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06, mix.type=c("normalmix"),
hist=TRUE)
C1HhyloNM <- boot.comp(C1Hhylo, x=NULL, N=NULL, max.comp=2, B=1000, sig=.06,
mix.type=c("normalmix"), hist=TRUE)
MultiHylo <- boot.comp(hyloC1C1C1, x=NULL, N=NULL, max.comp=3, B=1000, sig=.06,
mix.type=c("mvnormalmix"), hist=TRUE)

#Shapiro-Wilkes test for normality
library("mvShapiroTest")
C1dromST <- mvShapiro.Test(data.matrix(na.omit(drom$L.C1)))
C1TdromST <- mvShapiro.Test(data.matrix(na.omit(drom$W.C1)))
P2dromST <- mvShapiro.Test(data.matrix(na.omit(drom$L.P2)))
P2TdromST <- mvShapiro.Test(data.matrix(na.omit(drom$W.P2)))
C1bactST <- mvShapiro.Test(data.matrix(na.omit(bact$L.C1)))
C1TbactST <- mvShapiro.Test(data.matrix(na.omit(bact$W.C1)))
P2bactST <- mvShapiro.Test(data.matrix(na.omit(bact$L.P2)))
```

```
P2TbactST <- mvShapiro.Test(data.matrix(na.omit(bact$W.P2)))
C1hyloST <- mvShapiro.Test(data.matrix(na.omit(hylo$L.C1)))
C1ThyloST <- mvShapiro.Test(data.matrix(na.omit(hylo$W.C1)))
C1HhyloST <- mvShapiro.Test(data.matrix(na.omit(hylo$L.HC1)))

#Hartigan's dip test for multimodality
library("diptest")
C1dromDT <- dip.test(data.matrix(na.omit(drom$L.C1)))
C1TdromDT <- dip.test(data.matrix(na.omit(drom$W.C1)))
P2dromDT <- dip.test(data.matrix(na.omit(drom$L.P2)))
P2TdromDT <- dip.test(data.matrix(na.omit(drom$W.P2)))
C1bactDT <- dip.test(data.matrix(na.omit(bact$L.C1)))
C1TbactDT <- dip.test(data.matrix(na.omit(bact$W.C1)))
P2bactDT <- dip.test(data.matrix(na.omit(bact$L.P2)))
P2TbactDT <- dip.test(data.matrix(na.omit(bact$W.P2)))
C1hyloDT <- dip.test(data.matrix(na.omit(hylo$L.C1)))
C1ThyloDT <- dip.test(data.matrix(na.omit(hylo$W.C1)))
C1HhyloDT <- dip.test(data.matrix(na.omit(hylo$L.HC1)))

#Export distributional analysis results
names <- c("Drom AP C1", "Drom T C1", "Drom AP P2", "Drom T P3", "Bact AP C1", "Bact T C1", "Bact AP
P2", "Bact T P2", "MultiBact", "MultiDrom", "Hylo APC1", "Hylo TC1", "Hylo HC1", "Hylo Multi")
p.value1 <- c(C1dromNM$p.value[1], C1TdromNM$p.value[1], P2dromNM$p.value[1], P2TdromNM$p.value[1],
C1bactNM$p.value[1], C1TbactNM$p.value[1], P2bactNM$p.value[1], P2TbactNM$p.value[1],
MultiBact$p.value[1], MultiDrom$p.value[1], C1hyloNM$p.value[1], C1ThyloNM$p.value[1],
C1HhyloNM$p.value[1], MultiHylo$p.value[1])
p.value2 <- c(C1dromNM$p.value[2], C1TdromNM$p.value[2], P2dromNM$p.value[2], P2TdromNM$p.value[2],
C1bactNM$p.value[2], C1TbactNM$p.value[2], P2bactNM$p.value[2], P2TbactNM$p.value[2],
```

```
MultiBact$p.value[2], MultiDrom$p.value[2], C1hyloNM$p.value[2], C1ThyloNM$p.value[2],
C1HhyloNM$p.value[2], MultiHylo$p.value[2])
na <- 9999
shapiro <- c(C1dromST$p.value, C1TdromST$p.value, P2dromST$p.value, P2TdromST$p.value,
C1bactST$p.value, na, P2bactST$p.value, P2TbactST$p.value, na, na, C1hyloST$p.value, C1ThyloST$p.value,
C1HhyloST$p.value, na)
diptest <- c(C1dromDT$p.value, C1TdromDT$p.value, P2dromDT$p.value, P2TdromDT$p.value,
C1bactDT$p.value, C1TbactDT$p.value, P2bactDT$p.value, P2TbactDT$p.value, na, na, C1hyloDT$p.value,
C1ThyloDT$p.value, C1HhyloDT$p.value, na)

mixture <- data.frame(names, p.value1, p.value2, shapiro, diptest)
library("xlsx")
write.xlsx(mixture, "E:/mixture.xlsx")

######OVIS DIMORPHISM
sex <- read.csv("sex.csv")
sexUAPM1 <- as.matrix(na.omit(sex$L.M1, data=sex))
sexUAPM2 <- as.matrix(na.omit(sex$L.M2, data=sex))
sexUAPM3 <- as.matrix(na.omit(sex$L.M3, data=sex))
sexUTM1 <- as.matrix(na.omit(sex$W.M1, data=sex))
sexUTM2 <- as.matrix(na.omit(sex$W.M2, data=sex))
sexUTM3 <- as.matrix(na.omit(sex$W.M3, data=sex))

#Shapiro-Wilkes Test for Normality
library("mvShapiroTest")
shap.APM1 <- mvShapiro.Test(sexUAPM1)
shap.APM2 <- mvShapiro.Test(sexUAPM2)
shap.TM1 <- mvShapiro.Test(sexUTM1)
```

```
shap.TM2 <- mvShapiro.Test(sexUTM2)
na <- 9999 #APM3 and TM3 did not work, I do not have a sample size greater than 12.This NA fills in the blank.

#Hartigan's Diptest for multimodality
library("diptest")
dip.APM1 <- dip.test(sex$L.M1)
dip.APM2 <- dip.test(sex$L.M2)
dip.APM3 <- dip.test(sex$L.M3)
dip.TM1 <- dip.test(sex$W.M1)
dip.TM2 <- dip.test(sex$W.M2)
dip.TM3 <- dip.test(sex$W.M3)

#Export results for dimorphism test
names1 <- c("APM1", "APM2", "APM3", "TM1", "TM2", "TM3")
na <- 9999
shapiro1 <- c(shap.APM1$p.value, shap.APM2$p.value, na, shap.TM1$p.value, shap.TM2$p.value, na)
diptest1 <- c(dip.APM1$p.value, dip.APM2$p.value, dip.APM3$p.value, dip.TM1$p.value, dip.TM2$p.value,
dip.TM3$p.value)

Ovisdimorphismtests <- data.frame(names1, shapiro1, diptest1)
library("xlsx")
write.xlsx(Ovisdimorphismtests, "C:/Ovisdimorphismtests.xlsx")

#CV testing infracharacter
UAPM1 <- subset(CVtest, type== "UAM1", select=c(sp, stdev, avg, char))
UAPM2 <- subset(CVtest, type== "UAM2", select=c(sp, stdev, avg, char))
UAPM3 <- subset(CVtest, type== "UAM3", select=c(sp, stdev, avg, char))
UAPP2 <- subset(CVtest, type== "UAP2", select=c(sp, stdev, avg, char))
```

```
UAPP3 <- subset(CVtest, type== "UAP3", select=c(sp, stdev, avg, char))

UAPP4 <- subset(CVtest, type== "UAP4", select=c(sp, stdev, avg, char))

Molars <- subset(CVtest, type== "Umolars", select=c(sp, stdev, avg, char))

Premolars <- subset(CVtest, type== "Upremolars", select=c(sp, stdev, avg, char))

Toothrow <- subset(CVtest, type== "Utoothrow", select=c(sp, stdev, avg, char))

Muzzle <- subset(CVtest, type== "Muzzle", select=c(sp, stdev, avg, char))

Canine <- subset(CVtest, type== "Canine", select=c(sp, stdev, avg, char))

UTM1 <- subset(CVtest, type== "UTM1", select=c(sp, stdev, avg, char))

UTM2 <- subset(CVtest, type== "UTM2", select=c(sp, stdev, avg, char))

UTM3 <- subset(CVtest, type== "UTM3", select=c(sp, stdev, avg, char))

UTP2 <- subset(CVtest, type== "UTP2", select=c(sp, stdev, avg, char))

UTP3 <- subset(CVtest, type== "UTP3", select=c(sp, stdev, avg, char))

UTP4 <- subset(CVtest, type== "UTP4", select=c(sp, stdev, avg, char))


cvGroup <- summary(lm(CVtest$stdev~CVtest$avg))

cvUAPM1 <- summary(lm(UAPM1$stdev~UAPM1$avg))

cvUAPM2 <- summary(lm(UAPM2$stdev~UAPM2$avg))

cvUAPM3 <- summary(lm(UAPM3$stdev~UAPM3$avg))

cvUAPP2 <- summary(lm(UAPP2$stdev~UAPP2$avg))

cvUAPP3 <- summary(lm(UAPP3$stdev~UAPP3$avg))

cvUAPP4 <- summary(lm(UAPP4$stdev~UAPP4$avg))

cvUTM1 <- summary(lm(UTM1$stdev~UTM1$avg))

cvUTM2 <- summary(lm(UTM2$stdev~UTM2$avg))

cvUTM3 <- summary(lm(UTM3$stdev~UTM3$avg))

cvUTP2 <- summary(lm(UTP2$stdev~UTP2$avg))

cvUTP3 <- summary(lm(UTP3$stdev~UTP3$avg))

cvUTP4 <- summary(lm(UTP4$stdev~UTP4$avg))

cvMolars <- summary(lm(Molars$stdev~Molars$avg))
```

```
cvPremolars <- summary(lm(Premolars$stdev~Premolars$avg))
cvToothrow <- summary(lm(Toothrow$stdev~Toothrow$avg))
cvMuzzle <- summary(lm(Muzzle$stdev~Muzzle$avg))
cvCanine <- summary(lm(Canine$stdev~Canine$avg))


char <- c("All Characters", "UAPP2", "UAPP3", "UAPP4", "UAPM1", "UAPM2", "UAPM3", "UTP2", "UTP3",
"UTP4", "UTM1", "UTM2", "UTM3", "Premolars", "Molars", "Toothrow", "Caniform Teeth")
adjR2 <-  c(cvGroup$adj.r.squared, cvUAPP2$adj.r.squared, cvUAPP3$adj.r.squared, cvUAPP4$adj.r.squared,
cvUAPM1$adj.r.squared, cvUAPM2$adj.r.squared, cvUAPM3$adj.r.squared, cvUTP2$adj.r.squared,
cvUTP3$adj.r.squared, cvUTP4$adj.r.squared, cvUTM1$adj.r.squared, cvUTM2$adj.r.squared,
cvUTM3$adj.r.squared, cvPremolars$adj.r.squared, cvMolars$adj.r.squared, cvToothrow$adj.r.squared,
cvCanine$adj.r.squared)
B1 <- c(cvGroup$coef[2,1], cvUAPP2$coef[2,1], cvUAPP3$coef[2,1], cvUAPP4$coef[2,1], cvUAPM1$coef[2,1],
cvUAPM2$coef[2,1], cvUAPM3$coef[2,1], cvUTP2$coef[2,1], cvUTP3$coef[2,1], cvUTP4$coef[2,1],
cvUTM1$coef[2,1], cvUTM2$coef[2,1], cvUTM3$coef[2,1], cvPremolars$coef[2,1], cvMolars$coef[2,1],
cvToothrow$coef[2,1], cvCanine$coef[2,1])
Intercept <- c(cvGroup$coef[1,1], cvUAPP2$coef[1,1], cvUAPP3$coef[1,1], cvUAPP4$coef[1,1],
cvUAPM1$coef[1,1], cvUAPM2$coef[1,1], cvUAPM3$coef[1,1], cvUTP2$coef[1,1], cvUTP3$coef[1,1],
cvUTP4$coef[1,1], cvUTM1$coef[1,1], cvUTM2$coef[1,1], cvUTM3$coef[1,1], cvPremolars$coef[1,1],
cvMolars$coef[1,1], cvToothrow$coef[1,1], cvCanine$coef[1,1])
InterceptPvalue <- c(cvGroup$coef[1,4], cvUAPP2$coef[1,4], cvUAPP3$coef[1,4], cvUAPP4$coef[1,4],
cvUAPM1$coef[1,4], cvUAPM2$coef[1,4], cvUAPM3$coef[1,4], cvUTP2$coef[1,4], cvUTP3$coef[1,4],
cvUTP4$coef[1,4], cvUTM1$coef[1,4], cvUTM2$coef[1,4], cvUTM3$coef[1,4], cvPremolars$coef[1,4],
cvMolars$coef[1,4], cvToothrow$coef[1,4], cvCanine$coef[1,4])
pB1 <- c(cvGroup$coef[2,4], cvUAPP2$coef[2,4], cvUAPP3$coef[2,4], cvUAPP4$coef[2,4], cvUAPM1$coef[2,4],
cvUAPM2$coef[2,4], cvUAPM3$coef[2,4], cvUTP2$coef[2,4], cvUTP3$coef[2,4], cvUTP4$coef[2,4],
```

```
cvUTM1$coef[2,4], cvUTM2$coef[2,4], cvUTM3$coef[2,4], cvPremolars$coef[2,4], cvMolars$coef[2,4],
cvToothrow$coef[2,4], cvCanine$coef[2,4])
SE <- c(cvGroup$coef[2,2], cvUAPP2$coef[2,2], cvUAPP3$coef[2,2], cvUAPP4$coef[2,2], cvUAPM1$coef[2,2],
cvUAPM2$coef[2,2], cvUAPM3$coef[2,2], cvUTP2$coef[2,2], cvUTP3$coef[2,2], cvUTP4$coef[2,2],
cvUTM1$coef[2,2], cvUTM2$coef[2,2], cvUTM3$coef[2,2], cvPremolars$coef[2,2], cvMolars$coef[2,2],
cvToothrow$coef[2,2], cvCanine$coef[2,2])

CVcharRegressions <- data.frame(char, Intercept, InterceptPvalue, adjR2, B1, SE, pB1)
library("xlsx")
write.xlsx(CVcharRegressions, "C:/CVcharRegressions.xlsx")


###Regression on log transformed data
LcvGroup <- summary(lm(log(CVtest$stdev)~log(CVtest$avg)))
LcvUAPM1 <- summary(lm(log(UAPM1$stdev)~(log(UAPM1$avg))))
LcvUAPM2 <- summary(lm(log(UAPM2$stdev)~(log(UAPM2$avg))))
LcvUAPM3 <- summary(lm(log(UAPM3$stdev)~(log(UAPM3$avg))))
LcvUAPP2 <- summary(lm(log(UAPP2$stdev)~(log(UAPP2$avg))))
LcvUAPP3 <- summary(lm(log(UAPP3$stdev)~(log(UAPP3$avg))))
LcvUAPP4 <- summary(lm(log(UAPP4$stdev)~(log(UAPP4$avg))))
LcvUTM1 <- summary(lm(log(UTM1$stdev)~(log(UTM1$avg))))
LcvUTM2 <- summary(lm(log(UTM2$stdev)~(log(UTM2$avg))))
LcvUTM3 <- summary(lm(log(UTM3$stdev)~(log(UTM3$avg))))
LcvUTP2 <- summary(lm(log(UTP2$stdev)~(log(UTP2$avg))))
LcvUTP3 <- summary(lm(log(UTP3$stdev)~(log(UTP3$avg))))
LcvUTP4 <- summary(lm(log(UTP4$stdev)~(log(UTP4$avg))))
LcvMolars <- summary(lm(log(Molars$stdev)~(log(Molars$avg))))
LcvPremolars <- summary(lm(log(Premolars$stdev)~(log(Premolars$avg))))
```

```
LcvToothrow <- summary(lm(log(Toothrow$stdev)~(log(Toothrow$avg))))
LcvMuzzle <- summary(lm(log(Muzzle$stdev)~(log(Muzzle$avg))))
LcvCanine <- summary(lm(log(Canine$stdev)~(log(Canine$avg))))

Lchar <- c("Log of All Characters", "Log of UAPP2", "Log of UAPP3", "Log of UAPP4", "Log of UAPM1", "Log of UAPM2", "Log of UAPM3", "Log of UTP2", "Log of UTP3", "Log of UTP4", "Log of UTM1", "Log of UTM2", "Log of UTM3", "Log of Premolars", "Log of Molars", "Log of Toothrow", "Log of Caniform Teeth")
LadjR2 <-  c(LcvGroup$adj.r.squared, LcvUAPP2$adj.r.squared, LcvUAPP3$adj.r.squared, LcvUAPP4$adj.r.squared, LcvUAPM1$adj.r.squared, LcvUAPM2$adj.r.squared, LcvUAPM3$adj.r.squared, LcvUTP2$adj.r.squared, LcvUTP3$adj.r.squared, LcvUTP4$adj.r.squared, LcvUTM1$adj.r.squared, LcvUTM2$adj.r.squared, LcvUTM3$adj.r.squared, LcvPremolars$adj.r.squared, LcvMolars$adj.r.squared, LcvToothrow$adj.r.squared, LcvCanine$adj.r.squared)
LB1 <- c(LcvGroup$coef[2,1], LcvUAPP2$coef[2,1], LcvUAPP3$coef[2,1], LcvUAPP4$coef[2,1], LcvUAPM1$coef[2,1], LcvUAPM2$coef[2,1], LcvUAPM3$coef[2,1], LcvUTP2$coef[2,1], LcvUTP3$coef[2,1], LcvUTP4$coef[2,1], LcvUTM1$coef[2,1], LcvUTM2$coef[2,1], LcvUTM3$coef[2,1], LcvPremolars$coef[2,1], LcvMolars$coef[2,1], LcvToothrow$coef[2,1], LcvCanine$coef[2,1])
LIntercept <- c(LcvGroup$coef[1,1], LcvUAPP2$coef[1,1], LcvUAPP3$coef[1,1], LcvUAPP4$coef[1,1], LcvUAPM1$coef[1,1], LcvUAPM2$coef[1,1], LcvUAPM3$coef[1,1], LcvUTP2$coef[1,1], LcvUTP3$coef[1,1], LcvUTP4$coef[1,1], LcvUTM1$coef[1,1], LcvUTM2$coef[1,1], LcvUTM3$coef[1,1], LcvPremolars$coef[1,1], LcvMolars$coef[1,1], LcvToothrow$coef[1,1], LcvCanine$coef[1,1])
LInterceptPvalue <- c(LcvGroup$coef[1,4], LcvUAPP2$coef[1,4], LcvUAPP3$coef[1,4], LcvUAPP4$coef[1,4], LcvUAPM1$coef[1,4], LcvUAPM2$coef[1,4], LcvUAPM3$coef[1,4], LcvUTP2$coef[1,4], LcvUTP3$coef[1,4], LcvUTP4$coef[1,4], LcvUTM1$coef[1,4], LcvUTM2$coef[1,4], LcvUTM3$coef[1,4], LcvPremolars$coef[1,4], LcvMolars$coef[1,4], LcvToothrow$coef[1,4], LcvCanine$coef[1,4])
LpB1 <- c(LcvGroup$coef[2,4], LcvUAPP2$coef[2,4], LcvUAPP3$coef[2,4], LcvUAPP4$coef[2,4], LcvUAPM1$coef[2,4], LcvUAPM2$coef[2,4], LcvUAPM3$coef[2,4], LcvUTP2$coef[2,4], LcvUTP3$coef[2,4], LcvUTP4$coef[2,4], LcvUTM1$coef[2,4], LcvUTM2$coef[2,4], LcvUTM3$coef[2,4], LcvPremolars$coef[2,4], LcvMolars$coef[2,4], LcvToothrow$coef[2,4], LcvCanine$coef[2,4])
```

```
LSE <- c(LcvGroup$coef[2,2], LcvUAPP2$coef[2,2], LcvUAPP3$coef[2,2], LcvUAPP4$coef[2,2],
LcvUAPM1$coef[2,2], LcvUAPM2$coef[2,2], LcvUAPM3$coef[2,2], LcvUTP2$coef[2,2], LcvUTP3$coef[2,2],
LcvUTP4$coef[2,2], LcvUTM1$coef[2,2], LcvUTM2$coef[2,2], LcvUTM3$coef[2,2], LcvPremolars$coef[2,2],
LcvMolars$coef[2,2], LcvToothrow$coef[2,2], LcvCanine$coef[2,2])

LogCVcharRegressions <- data.frame(Lchar, LIntercept, LInterceptPvalue, LadjR2, LB1, LSE, LpB1)
library("xlsx")
write.xlsx(LogCVcharRegressions, "C:/LogCVcharRegressions.xlsx")


#COMPARING NONLINEAR REGRESSIONS
nlsGroup <- summary(nls(stdev~a*avg^b, data=CVtest, start = list(a=0.006734, b=0.974604)))
nlsUAPP2 <- summary(nls(stdev~a*avg^b, data=UAPP2, start = list(a=.003554, b=.96752)))
nlsUAPP3 <- summary(nls(stdev~a*avg^b, data=UAPP3, start = list(a=.005676, b=1.182205)))
nlsUAPP4 <- summary(nls(stdev~a*avg^b, data=UAPP4, start = list(a=.00411, b=1.049677)))
nlsUAPM1 <- summary(nls(stdev~a*avg^b, data=UAPM1, start = list(a=0.006882, b=1.318445)))
nlsUAPM2 <- summary(nls(stdev~a*avg^b, data=UAPM2, start = list(a=0.004, b=1.345411)))
nlsUAPM3 <- summary(nls(stdev~a*avg^b, data=UAPM3, start = list(a=0.00243, b=0.967543)))
nlsUTP2 <- summary(nls(stdev~a*avg^b, data=UTP2, start = list(a=0.003083, b=0.436334)))
nlsUTP3 <- summary(nls(stdev~a*avg^b, data=UTP3, start = list(a=0.003878, b=0.551232)))
nlsUTP4 <- summary(nls(stdev~a*avg^b, data=UTP4, start = list(a=0.003411, b=1.117034)))
nlsUTM1 <- summary(nls(stdev~a*avg^b, data=UTM1, start = list(a=0.003017, b=1.230286)))
nlsUTM2 <- summary(nls(stdev~a*avg^b, data=UTM2, start = list(a=0.002465, b=1.304321)))
nlsUTM3 <- summary(nls(stdev~a*avg^b, data=UTM3, start = list(a=0.001795, b=1.634642)))
nlsPremolars <- summary(nls(stdev~a*avg^b, data=Premolars, start = list(a=0.008164, b=0.656576)))
nlsMolars <- summary(nls(stdev~a*avg^b, data=Molars, start = list(a=0.000541, b=1.440005)))
nlsToothrow <- summary(nls(stdev~a*avg^b, data=Toothrow, start = list(a=.00047206304, b=1.2960)))
nlsCaniform <- summary(nls(stdev~a*avg^b, data=Canine, start = list(a=0.054876, b=1.077202)))
```

```
RSSGroup <- sum((nlsGroup$residuals-mean(nlsGroup$residuals))^2)
RSSUAPP2 <- sum((nlsUAPP2$residuals-mean(nlsUAPP2$residuals))^2)
RSSUAPP3 <- sum((nlsUAPP3$residuals-mean(nlsUAPP3$residuals))^2)
RSSUAPP4 <- sum((nlsUAPP4$residuals-mean(nlsUAPP4$residuals))^2)
RSSUAPM1 <- sum((nlsUAPM1$residuals-mean(nlsUAPM1$residuals))^2)
RSSUAPM2 <- sum((nlsUAPM2$residuals-mean(nlsUAPM2$residuals))^2)
RSSUAPM3 <- sum((nlsUAPM3$residuals-mean(nlsUAPM3$residuals))^2)
RSSUTP2 <- sum((nlsUTP2$residuals-mean(nlsUTP2$residuals))^2)
RSSUTP3 <- sum((nlsUTP3$residuals-mean(nlsUTP3$residuals))^2)
RSSUTP4 <- sum((nlsUTP4$residuals-mean(nlsUTP4$residuals))^2)
RSSUTM1 <- sum((nlsUTM1$residuals-mean(nlsUTM1$residuals))^2)
RSSUTM2 <- sum((nlsUTM2$residuals-mean(nlsUTM2$residuals))^2)
RSSUTM3 <- sum((nlsUTM3$residuals-mean(nlsUTM3$residuals))^2)
RSSPremolars <- sum((nlsPremolars$residuals-mean(nlsPremolars$residuals))^2)
RSSMolars <- sum((nlsMolars$residuals-mean(nlsMolars$residuals))^2)
RSSToothrow <- sum((nlsToothrow$residuals-mean(nlsToothrow$residuals))^2)
RSSCaniform <- sum((nlsCaniform$residuals-mean(nlsCaniform$residuals))^2)

RSSCVGroup <- sum((cvGroup$residuals-mean(cvGroup$residuals))^2)
RSSCVUAPP2 <- sum((cvUAPP2$residuals-mean(cvUAPP2$residuals))^2)
RSSCVUAPP3 <- sum((cvUAPP3$residuals-mean(cvUAPP3$residuals))^2)
RSSCVUAPP4 <- sum((cvUAPP4$residuals-mean(cvUAPP4$residuals))^2)
RSSCVUAPM1 <- sum((cvUAPM1$residuals-mean(cvUAPM1$residuals))^2)
RSSCVUAPM2 <- sum((cvUAPM2$residuals-mean(cvUAPM2$residuals))^2)
RSSCVUAPM3 <- sum((cvUAPM3$residuals-mean(cvUAPM3$residuals))^2)
RSSCVUTP2 <- sum((cvUTP2$residuals-mean(cvUTP2$residuals))^2)
```

```
RSSCVUTP3 <- sum((cvUTP3$residuals-mean(cvUTP3$residuals))^2)
RSSCVUTP4 <- sum((cvUTP4$residuals-mean(cvUTP4$residuals))^2)
RSSCVUTM1 <- sum((cvUTM1$residuals-mean(cvUTM1$residuals))^2)
RSSCVUTM2 <- sum((cvUTM2$residuals-mean(cvUTM2$residuals))^2)
RSSCVUTM3 <- sum((cvUTM3$residuals-mean(cvUTM3$residuals))^2)
RSSCVPremolars <- sum((cvPremolars$residuals-mean(cvPremolars$residuals))^2)
RSSCVMolars <- sum((cvMolars$residuals-mean(cvMolars$residuals))^2)
RSSCVToothrow <- sum((cvToothrow$residuals-mean(cvToothrow$residuals))^2)
RSSCVCaniform <- sum((cvCanine$residuals-mean(cvCanine$residuals))^2)

nlschar <- c("All Characters", "UAPP2", "UAPP3", "UAPP4", "UAPM1", "UAPM2", "UAPM3", "UTP2", "UTP3",
"UTP4", "UTM1", "UTM2", "UTM3", "Premolars", "Molars", "Toothrow", "Caniform Teeth")
nlsRSS <- c(RSSGroup, RSSUAPP2, RSSUAPP3, RSSUAPP4, RSSUAPM1, RSSUAPM2, RSSUAPM3,
RSSUTP2, RSSUTP3, RSSUTP4, RSSUTM1, RSSUTM2, RSSUTM3, RSSPremolars, RSSMolars, RSSToothrow,
RSSCaniform)
cvRSS <- c(RSSCVGroup, RSSCVUAPP2, RSSCVUAPP3, RSSCVUAPP4, RSSCVUAPM1, RSSCVUAPM2,
RSSCVUAPM3, RSSCVUTP2, RSSCVUTP3, RSSCVUTP4, RSSCVUTM1, RSSCVUTM2, RSSCVUTM3,
RSSCVPremolars, RSSCVMolars, RSSCVToothrow, RSSCVCaniform)

nlsB1 <- c(nlsGroup$coef[2,1], nlsUAPP2$coef[2,1], nlsUAPP3$coef[2,1], nlsUAPP4$coef[2,1],
nlsUAPM1$coef[2,1], nlsUAPM2$coef[2,1], nlsUAPM3$coef[2,1], nlsUTP2$coef[2,1], nlsUTP3$coef[2,1],
nlsUTP4$coef[2,1], nlsUTM1$coef[2,1], nlsUTM2$coef[2,1], nlsUTM3$coef[2,1], nlsPremolars$coef[2,1],
nlsMolars$coef[2,1], nlsToothrow$coef[2,1], nlsCaniform$coef[2,1])
nlsIntercept <- c(nlsGroup$coef[1,1], nlsUAPP2$coef[1,1], nlsUAPP3$coef[1,1], nlsUAPP4$coef[1,1],
nlsUAPM1$coef[1,1], nlsUAPM2$coef[1,1], nlsUAPM3$coef[1,1], nlsUTP2$coef[1,1], nlsUTP3$coef[1,1],
nlsUTP4$coef[1,1], nlsUTM1$coef[1,1], nlsUTM2$coef[1,1], nlsUTM3$coef[1,1], nlsPremolars$coef[1,1],
nlsMolars$coef[1,1], nlsToothrow$coef[1,1], nlsCaniform$coef[1,1])
```

```
nlsInterceptPvalue <- c(nlsGroup$coef[1,4], nlsUAPP2$coef[1,4], nlsUAPP3$coef[1,4], nlsUAPP4$coef[1,4],
nlsUAPM1$coef[1,4], nlsUAPM2$coef[1,4], nlsUAPM3$coef[1,4], nlsUTP2$coef[1,4], nlsUTP3$coef[1,4],
nlsUTP4$coef[1,4], nlsUTM1$coef[1,4], nlsUTM2$coef[1,4], nlsUTM3$coef[1,4], nlsPremolars$coef[1,4],
nlsMolars$coef[1,4], nlsToothrow$coef[1,4], nlsCaniform$coef[1,4])
nlspB1 <- c(nlsGroup$coef[2,4], nlsUAPP2$coef[2,4], nlsUAPP3$coef[2,4], nlsUAPP4$coef[2,4],
nlsUAPM1$coef[2,4], nlsUAPM2$coef[2,4], nlsUAPM3$coef[2,4], nlsUTP2$coef[2,4], nlsUTP3$coef[2,4],
nlsUTP4$coef[2,4], nlsUTM1$coef[2,4], nlsUTM2$coef[2,4], nlsUTM3$coef[2,4], nlsPremolars$coef[2,4],
nlsMolars$coef[2,4], nlsToothrow$coef[2,4], nlsCaniform$coef[2,4])
nlsSE <- c(nlsGroup$coef[2,2], nlsUAPP2$coef[2,2], nlsUAPP3$coef[2,2], nlsUAPP4$coef[2,2],
nlsUAPM1$coef[2,2], nlsUAPM2$coef[2,2], nlsUAPM3$coef[2,2], nlsUTP2$coef[2,2], nlsUTP3$coef[2,2],
nlsUTP4$coef[2,2], nlsUTM1$coef[2,2], nlsUTM2$coef[2,2], nlsUTM3$coef[2,2], nlsPremolars$coef[2,2],
nlsMolars$coef[2,2], nlsToothrow$coef[2,2], nlsCaniform$coef[2,2])

NLSRegressions <- data.frame(nlschar, nlsRSS, cvRSS, nlsIntercept, nlsInterceptPvalue, nlsB1, nlsSE, nlspB1)
library("xlsx")
write.xlsx(NLSRegressions, "C:/NLSRegressions.xlsx")

#### Nonlinear regression without camels
nocamels <- read.csv("nocamels.csv")
UAPM1nc <- subset(nocamels, type== "UAM1", select=c(sp, stdev, avg, char))
UAPM2nc <- subset(nocamels, type== "UAM2", select=c(sp, stdev, avg, char))
UAPM3nc <- subset(nocamels, type== "UAM3", select=c(sp, stdev, avg, char))
UAPP2nc <- subset(nocamels, type== "UAP2", select=c(sp, stdev, avg, char))
UAPP3nc <- subset(nocamels, type== "UAP3", select=c(sp, stdev, avg, char))
UAPP4nc <- subset(nocamels, type== "UAP4", select=c(sp, stdev, avg, char))
Molarsnc <- subset(nocamels, type== "Umolars", select=c(sp, stdev, avg, char))
Premolarsnc <- subset(nocamels, type== "Upremolars", select=c(sp, stdev, avg, char))
Toothrownc <- subset(nocamels, type== "Utoothrow", select=c(sp, stdev, avg, char))
```

```
Muzzlenc <- subset(nocamels, type== "Muzzle", select=c(sp, stdev, avg, char))

Caninenc <- subset(nocamels, type== "Canine", select=c(sp, stdev, avg, char))

UTM1nc <- subset(nocamels, type== "UTM1", select=c(sp, stdev, avg, char))

UTM2nc <- subset(nocamels, type== "UTM2", select=c(sp, stdev, avg, char))

UTM3nc <- subset(nocamels, type== "UTM3", select=c(sp, stdev, avg, char))

UTP2nc <- subset(nocamels, type== "UTP2", select=c(sp, stdev, avg, char))

UTP3nc <- subset(nocamels, type== "UTP3", select=c(sp, stdev, avg, char))

UTP4nc <- subset(nocamels, type== "UTP4", select=c(sp, stdev, avg, char))


cvGroupnc <- summary(lm(nocamels$stdev~nocamels$avg))

cvUAPM1nc <- summary(lm(UAPM1nc$stdev~UAPM1nc$avg))

cvUAPM2nc <- summary(lm(UAPM2nc$stdev~UAPM2nc$avg))

cvUAPM3nc <- summary(lm(UAPM3nc$stdev~UAPM3nc$avg))

cvUAPP2nc <- summary(lm(UAPP2nc$stdev~UAPP2nc$avg))

cvUAPP3nc <- summary(lm(UAPP3nc$stdev~UAPP3nc$avg))

cvUAPP4nc <- summary(lm(UAPP4nc$stdev~UAPP4nc$avg))

cvUTM1nc <- summary(lm(UTM1nc$stdev~UTM1nc$avg))

cvUTM2nc <- summary(lm(UTM2nc$stdev~UTM2nc$avg))

cvUTM3nc <- summary(lm(UTM3nc$stdev~UTM3nc$avg))

cvUTP2nc <- summary(lm(UTP2nc$stdev~UTP2nc$avg))

cvUTP3nc <- summary(lm(UTP3nc$stdev~UTP3nc$avg))

cvUTP4nc <- summary(lm(UTP4nc$stdev~UTP4nc$avg))

cvMolarsnc <- summary(lm(Molarsnc$stdev~Molarsnc$avg))

cvPremolarsnc <- summary(lm(Premolarsnc$stdev~Premolarsnc$avg))

cvToothrownc <- summary(lm(Toothrownc$stdev~Toothrownc$avg))

cvMuzzlenc <- summary(lm(Muzzlenc$stdev~Muzzlenc$avg))

cvCaninenc <- summary(lm(Caninenc$stdev~Caninenc$avg))
```

```
charnc <- c("All Characters", "UAPP2", "UAPP3", "UAPP4", "UAPM1", "UAPM2", "UAPM3", "UTP2", "UTP3",
"UTP4", "UTM1", "UTM2", "UTM3", "Premolars", "Molars", "Toothrow", "Caniform Teeth")
adjR2nc <-  c(cvGroupnc$adj.r.squared, cvUAPP2nc$adj.r.squared, cvUAPP3nc$adj.r.squared,
cvUAPP4nc$adj.r.squared, cvUAPM1nc$adj.r.squared, cvUAPM2nc$adj.r.squared, cvUAPM3nc$adj.r.squared,
cvUTP2nc$adj.r.squared, cvUTP3nc$adj.r.squared, cvUTP4nc$adj.r.squared, cvUTM1nc$adj.r.squared,
cvUTM2nc$adj.r.squared, cvUTM3nc$adj.r.squared, cvPremolarsnc$adj.r.squared, cvMolarsnc$adj.r.squared,
cvToothrownc$adj.r.squared, cvCaninenc$adj.r.squared)
B1nc <- c(cvGroupnc$coef[2,1], cvUAPP2nc$coef[2,1], cvUAPP3nc$coef[2,1], cvUAPP4nc$coef[2,1],
cvUAPM1nc$coef[2,1], cvUAPM2nc$coef[2,1], cvUAPM3nc$coef[2,1], cvUTP2nc$coef[2,1],
cvUTP3nc$coef[2,1], cvUTP4nc$coef[2,1], cvUTM1nc$coef[2,1], cvUTM2nc$coef[2,1], cvUTM3nc$coef[2,1],
cvPremolarsnc$coef[2,1], cvMolarsnc$coef[2,1], cvToothrownc$coef[2,1], cvCaninenc$coef[2,1])
Interceptnc <- c(cvGroupnc$coef[1,1], cvUAPP2nc$coef[1,1], cvUAPP3nc$coef[1,1], cvUAPP4nc$coef[1,1],
cvUAPM1nc$coef[1,1], cvUAPM2nc$coef[1,1], cvUAPM3nc$coef[1,1], cvUTP2nc$coef[1,1],
cvUTP3nc$coef[1,1], cvUTP4nc$coef[1,1], cvUTM1nc$coef[1,1], cvUTM2nc$coef[1,1], cvUTM3nc$coef[1,1],
cvPremolarsnc$coef[1,1], cvMolarsnc$coef[1,1], cvToothrownc$coef[1,1], cvCaninenc$coef[1,1])
InterceptPvaluenc <- c(cvGroupnc$coef[1,4], cvUAPP2nc$coef[1,4], cvUAPP3nc$coef[1,4],
cvUAPP4nc$coef[1,4], cvUAPM1nc$coef[1,4], cvUAPM2nc$coef[1,4], cvUAPM3nc$coef[1,4],
cvUTP2nc$coef[1,4], cvUTP3nc$coef[1,4], cvUTP4nc$coef[1,4], cvUTM1nc$coef[1,4], cvUTM2nc$coef[1,4],
cvUTM3nc$coef[1,4], cvPremolarsnc$coef[1,4], cvMolarsnc$coef[1,4], cvToothrownc$coef[1,4],
cvCaninenc$coef[1,4])
pB1nc <- c(cvGroupnc$coef[2,4], cvUAPP2nc$coef[2,4], cvUAPP3nc$coef[2,4], cvUAPP4nc$coef[2,4],
cvUAPM1nc$coef[2,4], cvUAPM2nc$coef[2,4], cvUAPM3nc$coef[2,4], cvUTP2nc$coef[2,4],
cvUTP3nc$coef[2,4], cvUTP4nc$coef[2,4], cvUTM1nc$coef[2,4], cvUTM2nc$coef[2,4], cvUTM3nc$coef[2,4],
cvPremolarsnc$coef[2,4], cvMolarsnc$coef[2,4], cvToothrownc$coef[2,4], cvCaninenc$coef[2,4])
SEnc <- c(cvGroupnc$coef[2,2], cvUAPP2nc$coef[2,2], cvUAPP3nc$coef[2,2], cvUAPP4nc$coef[2,2],
cvUAPM1nc$coef[2,2], cvUAPM2nc$coef[2,2], cvUAPM3nc$coef[2,2], cvUTP2nc$coef[2,2],
cvUTP3nc$coef[2,2], cvUTP4nc$coef[2,2], cvUTM1nc$coef[2,2], cvUTM2nc$coef[2,2], cvUTM3nc$coef[2,2],
cvPremolarsnc$coef[2,2], cvMolarsnc$coef[2,2], cvToothrownc$coef[2,2], cvCaninenc$coef[2,2])
```

```
LcvGroupnc <- summary(lm(log(nocamels$stdev)~log(nocamels$avg)))
LcvUAPM1nc <- summary(lm(log(UAPM1nc$stdev)~(log(UAPM1nc$avg))))
LcvUAPM2nc <- summary(lm(log(UAPM2nc$stdev)~(log(UAPM2nc$avg))))
LcvUAPM3nc <- summary(lm(log(UAPM3nc$stdev)~(log(UAPM3nc$avg))))
LcvUAPP2nc <- summary(lm(log(UAPP2nc$stdev)~(log(UAPP2nc$avg))))
LcvUAPP3nc <- summary(lm(log(UAPP3nc$stdev)~(log(UAPP3nc$avg))))
LcvUAPP4nc <- summary(lm(log(UAPP4nc$stdev)~(log(UAPP4nc$avg))))
LcvUTM1nc <- summary(lm(log(UTM1nc$stdev)~(log(UTM1nc$avg))))
LcvUTM2nc <- summary(lm(log(UTM2nc$stdev)~(log(UTM2nc$avg))))
LcvUTM3nc <- summary(lm(log(UTM3nc$stdev)~(log(UTM3nc$avg))))
LcvUTP2nc <- summary(lm(log(UTP2nc$stdev)~(log(UTP2nc$avg))))
LcvUTP3nc <- summary(lm(log(UTP3nc$stdev)~(log(UTP3nc$avg))))
LcvUTP4nc <- summary(lm(log(UTP4nc$stdev)~(log(UTP4nc$avg))))
LcvMolarsnc <- summary(lm(log(Molarsnc$stdev)~(log(Molarsnc$avg))))
LcvPremolarsnc <- summary(lm(log(Premolarsnc$stdev)~(log(Premolarsnc$avg))))
LcvToothrownc <- summary(lm(log(Toothrownc$stdev)~(log(Toothrownc$avg))))
LcvMuzzlenc <- summary(lm(log(Muzzlenc$stdev)~(log(Muzzlenc$avg))))
LcvCaninenc <- summary(lm(log(Caninenc$stdev)~(log(Caninenc$avg))))

LadjR2nc <-  c(LcvGroupnc$adj.r.squared, LcvUAPP2nc$adj.r.squared, LcvUAPP3nc$adj.r.squared,
LcvUAPP4nc$adj.r.squared, LcvUAPM1nc$adj.r.squared, LcvUAPM2nc$adj.r.squared,
LcvUAPM3nc$adj.r.squared, LcvUTP2nc$adj.r.squared, LcvUTP3nc$adj.r.squared, LcvUTP4nc$adj.r.squared,
LcvUTM1nc$adj.r.squared, LcvUTM2nc$adj.r.squared, LcvUTM3nc$adj.r.squared, LcvPremolarsnc$adj.r.squared,
LcvMolarsnc$adj.r.squared, LcvToothrownc$adj.r.squared, LcvCaninenc$adj.r.squared)
LB1nc <- c(LcvGroupnc$coef[2,1], LcvUAPP2nc$coef[2,1], LcvUAPP3nc$coef[2,1], LcvUAPP4nc$coef[2,1],
LcvUAPM1nc$coef[2,1], LcvUAPM2nc$coef[2,1], LcvUAPM3nc$coef[2,1], LcvUTP2nc$coef[2,1],
LcvUTP3nc$coef[2,1], LcvUTP4nc$coef[2,1], LcvUTM1nc$coef[2,1], LcvUTM2nc$coef[2,1],
```

```
LcvUTM3nc$coef[2,1], LcvPremolarsnc$coef[2,1], LcvMolarsnc$coef[2,1], LcvToothrownc$coef[2,1],
LcvCaninenc$coef[2,1])
LInterceptnc <- c(LcvGroupnc$coef[1,1], LcvUAPP2nc$coef[1,1], LcvUAPP3nc$coef[1,1],
LcvUAPP4nc$coef[1,1], LcvUAPM1nc$coef[1,1], LcvUAPM2nc$coef[1,1], LcvUAPM3nc$coef[1,1],
LcvUTP2nc$coef[1,1], LcvUTP3nc$coef[1,1], LcvUTP4nc$coef[1,1], LcvUTM1nc$coef[1,1],
LcvUTM2nc$coef[1,1], LcvUTM3nc$coef[1,1], LcvPremolarsnc$coef[1,1], LcvMolarsnc$coef[1,1],
LcvToothrownc$coef[1,1], LcvCaninenc$coef[1,1])
LInterceptPvaluenc <- c(LcvGroupnc$coef[1,4], LcvUAPP2nc$coef[1,4], LcvUAPP3nc$coef[1,4],
LcvUAPP4nc$coef[1,4], LcvUAPM1nc$coef[1,4], LcvUAPM2nc$coef[1,4], LcvUAPM3nc$coef[1,4],
LcvUTP2nc$coef[1,4], LcvUTP3nc$coef[1,4], LcvUTP4nc$coef[1,4], LcvUTM1nc$coef[1,4],
LcvUTM2nc$coef[1,4], LcvUTM3nc$coef[1,4], LcvPremolarsnc$coef[1,4], LcvMolarsnc$coef[1,4],
LcvToothrownc$coef[1,4], LcvCaninenc$coef[1,4])
LpB1nc <- c(LcvGroupnc$coef[2,4], LcvUAPP2nc$coef[2,4], LcvUAPP3nc$coef[2,4], LcvUAPP4nc$coef[2,4],
LcvUAPM1nc$coef[2,4], LcvUAPM2nc$coef[2,4], LcvUAPM3nc$coef[2,4], LcvUTP2nc$coef[2,4],
LcvUTP3nc$coef[2,4], LcvUTP4nc$coef[2,4], LcvUTM1nc$coef[2,4], LcvUTM2nc$coef[2,4],
LcvUTM3nc$coef[2,4], LcvPremolarsnc$coef[2,4], LcvMolarsnc$coef[2,4], LcvToothrownc$coef[2,4],
LcvCaninenc$coef[2,4])
LSEnc <- c(LcvGroupnc$coef[2,2], LcvUAPP2nc$coef[2,2], LcvUAPP3nc$coef[2,2], LcvUAPP4nc$coef[2,2],
LcvUAPM1nc$coef[2,2], LcvUAPM2nc$coef[2,2], LcvUAPM3nc$coef[2,2], LcvUTP2nc$coef[2,2],
LcvUTP3nc$coef[2,2], LcvUTP4nc$coef[2,2], LcvUTM1nc$coef[2,2], LcvUTM2nc$coef[2,2],
LcvUTM3nc$coef[2,2], LcvPremolarsnc$coef[2,2], LcvMolarsnc$coef[2,2], LcvToothrownc$coef[2,2],
LcvCaninenc$coef[2,2])

NoCamelRegressionsCVLog <- data.frame(charnc, Interceptnc, InterceptPvaluenc, adjR2nc, B1nc, SEnc, pB1nc,
LInterceptnc, LInterceptPvaluenc, LadjR2nc, LB1nc, LSEnc, LpB1nc)
library("xlsx")
write.xlsx(NoCamelRegressionsCVLog, "C:/NoCamelRegressionsCVLog.xlsx")
```

```
nlsGroupnc <- summary(nls(stdev~a*avg^b, data=nocamels, start = list(a=0.005582, b=0.89063)))
nlsUAPP2nc <- summary(nls(stdev~a*avg^b, data=UAPP2nc, start = list(a=.003554, b=.96752)))
nlsUAPP3nc <- summary(nls(stdev~a*avg^b, data=UAPP3nc, start = list(a=.006703, b=1.45608)))
nlsUAPP4nc <- summary(nls(stdev~a*avg^b, data=UAPP4nc, start = list(a=.004926, b=1.368925)))
nlsUAPM1nc <- summary(nls(stdev~a*avg^b, data=UAPM1nc, start = list(a=0.006934, b=1.216415)))
nlsUAPM2nc <- summary(nls(stdev~a*avg^b, data=UAPM2nc, start = list(a=0.003887, b=1.402922)))
nlsUAPM3nc <- summary(nls(stdev~a*avg^b, data=UAPM3nc, start = list(a=0.002475, b=0.935304)))
nlsUTP2nc <- summary(nls(stdev~a*avg^b, data=UTP2nc, start = list(a=0.003083, b=0.436334)))
nlsUTP3nc <- summary(nls(stdev~a*avg^b, data=UTP3nc, start = list(a=.002411, b=.05085)))
nlsUTP4nc <- summary(nls(stdev~a*avg^b, data=UTP4nc, start = list(a=0.00341, b=1.095264)))
nlsUTM1nc <- summary(nls(stdev~a*avg^b, data=UTM1nc, start = list(a=0.002989, b=1.257573)))
nlsUTM2nc <- summary(nls(stdev~a*avg^b, data=UTM2nc, start = list(a=0.002138, b=1.548231)))
nlsUTM3nc <- summary(nls(stdev~a*avg^b, data=UTM3nc, start = list(a=0.001768, b=1.683582)))
nlsPremolarsnc <- summary(nls(stdev~a*avg^b, data=Premolarsnc, start = list(a=0.007217, b=0.731086)))
nlsMolarsnc <- summary(nls(stdev~a*avg^b, data=Molarsnc, start = list(a=0.000493, b=1.474455)))
nlsToothrownc <- summary(nls(stdev~a*avg^b, data=Toothrownc, start = list(a=0.000116, b=1.652252)))
nlsCaniformnc <- summary(nls(stdev~a*avg^b, data=Caninenc, start = list(a=0.04934, b=1.02592)))

RSSGroupnc <- sum((nlsGroupnc$residuals-mean(nlsGroupnc$residuals))^2)
RSSUAPP2nc <- sum((nlsUAPP2nc$residuals-mean(nlsUAPP2nc$residuals))^2)
RSSUAPP3nc <- sum((nlsUAPP3nc$residuals-mean(nlsUAPP3nc$residuals))^2)
RSSUAPP4nc <- sum((nlsUAPP4nc$residuals-mean(nlsUAPP4nc$residuals))^2)
RSSUAPM1nc <- sum((nlsUAPM1nc$residuals-mean(nlsUAPM1nc$residuals))^2)
RSSUAPM2nc <- sum((nlsUAPM2nc$residuals-mean(nlsUAPM2nc$residuals))^2)
RSSUAPM3nc <- sum((nlsUAPM3nc$residuals-mean(nlsUAPM3nc$residuals))^2)
RSSUTP2nc <- sum((nlsUTP2nc$residuals-mean(nlsUTP2nc$residuals))^2)
RSSUTP3nc <- sum((nlsUTP3nc$residuals-mean(nlsUTP3nc$residuals))^2)
RSSUTP4nc <- sum((nlsUTP4nc$residuals-mean(nlsUTP4nc$residuals))^2)
```

```
RSSUTM1nc <- sum((nlsUTM1nc$residuals-mean(nlsUTM1nc$residuals))^2)

RSSUTM2nc <- sum((nlsUTM2nc$residuals-mean(nlsUTM2nc$residuals))^2)

RSSUTM3nc <- sum((nlsUTM3nc$residuals-mean(nlsUTM3nc$residuals))^2)

RSSPremolarsnc <- sum((nlsPremolarsnc$residuals-mean(nlsPremolarsnc$residuals))^2)

RSSMolarsnc <- sum((nlsMolarsnc$residuals-mean(nlsMolarsnc$residuals))^2)

RSSToothrownc <- sum((nlsToothrownc$residuals-mean(nlsToothrownc$residuals))^2)

RSSCaniformnc <- sum((nlsCaniformnc$residuals-mean(nlsCaniformnc$residuals))^2)


RSSCVGroupnc <- sum((cvGroupnc$residuals-mean(cvGroupnc$residuals))^2)

RSSCVUAPP2nc <- sum((cvUAPP2nc$residuals-mean(cvUAPP2nc$residuals))^2)

RSSCVUAPP3nc <- sum((cvUAPP3nc$residuals-mean(cvUAPP3nc$residuals))^2)

RSSCVUAPP4nc <- sum((cvUAPP4nc$residuals-mean(cvUAPP4nc$residuals))^2)

RSSCVUAPM1nc <- sum((cvUAPM1nc$residuals-mean(cvUAPM1nc$residuals))^2)

RSSCVUAPM2nc <- sum((cvUAPM2nc$residuals-mean(cvUAPM2nc$residuals))^2)

RSSCVUAPM3nc <- sum((cvUAPM3nc$residuals-mean(cvUAPM3nc$residuals))^2)

RSSCVUTP2nc <- sum((cvUTP2nc$residuals-mean(cvUTP2nc$residuals))^2)

RSSCVUTP3nc <- sum((cvUTP3nc$residuals-mean(cvUTP3nc$residuals))^2)

RSSCVUTP4nc <- sum((cvUTP4nc$residuals-mean(cvUTP4nc$residuals))^2)

RSSCVUTM1nc <- sum((cvUTM1nc$residuals-mean(cvUTM1nc$residuals))^2)

RSSCVUTM2nc <- sum((cvUTM2nc$residuals-mean(cvUTM2nc$residuals))^2)

RSSCVUTM3nc <- sum((cvUTM3nc$residuals-mean(cvUTM3nc$residuals))^2)

RSSCVPremolarsnc <- sum((cvPremolarsnc$residuals-mean(cvPremolarsnc$residuals))^2)

RSSCVMolarsnc <- sum((cvMolarsnc$residuals-mean(cvMolarsnc$residuals))^2)

RSSCVToothrownc <- sum((cvToothrownc$residuals-mean(cvToothrownc$residuals))^2)

RSSCVCaniformnc <- sum((cvCaninenc$residuals-mean(cvCaninenc$residuals))^2)


nlscharnc <- c("All Characters", "UAPP2", "UAPP3", "UAPP4", "UAPM1", "UAPM2", "UAPM3", "UTP2",

"UTP3", "UTP4", "UTM1", "UTM2", "UTM3", "Premolars", "Molars", "Toothrow", "Caniform Teeth")
```

```
nlsRSSnc <- c(RSSGroupnc, RSSUAPP2nc, RSSUAPP3nc, RSSUAPP4nc, RSSUAPM1nc, RSSUAPM2nc,
RSSUAPM3nc, RSSUTP2nc, RSSUTP3nc, RSSUTP4nc, RSSUTM1nc, RSSUTM2nc, RSSUTM3nc,
RSSPremolarsnc, RSSMolarsnc, RSSToothrownc, RSSCaniformnc)
cvRSSnc <- c(RSSCVGroupnc, RSSCVUAPP2nc, RSSCVUAPP3nc, RSSCVUAPP4nc, RSSCVUAPM1nc,
RSSCVUAPM2nc, RSSCVUAPM3nc, RSSCVUTP2nc, RSSCVUTP3nc, RSSCVUTP4nc, RSSCVUTM1nc,
RSSCVUTM2nc, RSSCVUTM3nc, RSSCVPremolarsnc, RSSCVMolarsnc, RSSCVToothrownc,
RSSCVCaniformnc)
nlsB1nc <- c(nlsGroupnc$coef[2,1], nlsUAPP2nc$coef[2,1], nlsUAPP3nc$coef[2,1], nlsUAPP4nc$coef[2,1],
nlsUAPM1nc$coef[2,1], nlsUAPM2nc$coef[2,1], nlsUAPM3nc$coef[2,1], nlsUTP2nc$coef[2,1],
nlsUTP3nc$coef[2,1], nlsUTP4nc$coef[2,1], nlsUTM1nc$coef[2,1], nlsUTM2nc$coef[2,1], nlsUTM3nc$coef[2,1],
nlsPremolarsnc$coef[2,1], nlsMolarsnc$coef[2,1], nlsToothrownc$coef[2,1], nlsCaniformnc$coef[2,1])
nlsInterceptnc <- c(nlsGroupnc$coef[1,1], nlsUAPP2nc$coef[1,1], nlsUAPP3nc$coef[1,1], nlsUAPP4nc$coef[1,1],
nlsUAPM1nc$coef[1,1], nlsUAPM2nc$coef[1,1], nlsUAPM3nc$coef[1,1], nlsUTP2nc$coef[1,1],
nlsUTP3nc$coef[1,1], nlsUTP4nc$coef[1,1], nlsUTM1nc$coef[1,1], nlsUTM2nc$coef[1,1], nlsUTM3nc$coef[1,1],
nlsPremolarsnc$coef[1,1], nlsMolarsnc$coef[1,1], nlsToothrownc$coef[1,1], nlsCaniformnc$coef[1,1])
nlsInterceptPvaluenc <- c(nlsGroupnc$coef[1,4], nlsUAPP2nc$coef[1,4], nlsUAPP3nc$coef[1,4],
nlsUAPP4nc$coef[1,4], nlsUAPM1nc$coef[1,4], nlsUAPM2nc$coef[1,4], nlsUAPM3nc$coef[1,4],
nlsUTP2nc$coef[1,4], nlsUTP3nc$coef[1,4], nlsUTP4nc$coef[1,4], nlsUTM1nc$coef[1,4], nlsUTM2nc$coef[1,4],
nlsUTM3nc$coef[1,4], nlsPremolarsnc$coef[1,4], nlsMolarsnc$coef[1,4], nlsToothrownc$coef[1,4],
nlsCaniformnc$coef[1,4])
nlspB1nc <- c(nlsGroupnc$coef[2,4], nlsUAPP2nc$coef[2,4], nlsUAPP3nc$coef[2,4], nlsUAPP4nc$coef[2,4],
nlsUAPM1nc$coef[2,4], nlsUAPM2nc$coef[2,4], nlsUAPM3nc$coef[2,4], nlsUTP2nc$coef[2,4],
nlsUTP3nc$coef[2,4], nlsUTP4nc$coef[2,4], nlsUTM1nc$coef[2,4], nlsUTM2nc$coef[2,4], nlsUTM3nc$coef[2,4],
nlsPremolarsnc$coef[2,4], nlsMolarsnc$coef[2,4], nlsToothrownc$coef[2,4], nlsCaniformnc$coef[2,4])
nlsSEnc <- c(nlsGroupnc$coef[2,2], nlsUAPP2nc$coef[2,2], nlsUAPP3nc$coef[2,2], nlsUAPP4nc$coef[2,2],
nlsUAPM1nc$coef[2,2], nlsUAPM2nc$coef[2,2], nlsUAPM3nc$coef[2,2], nlsUTP2nc$coef[2,2],
nlsUTP3nc$coef[2,2], nlsUTP4nc$coef[2,2], nlsUTM1nc$coef[2,2], nlsUTM2nc$coef[2,2], nlsUTM3nc$coef[2,2],
nlsPremolarsnc$coef[2,2], nlsMolarsnc$coef[2,2], nlsToothrownc$coef[2,2], nlsCaniformnc$coef[2,2])
```

```
NLSRegressionsNC <- data.frame(nlscharnc, nlsRSSnc, cvRSSnc, nlsInterceptnc, nlsInterceptPvaluenc, nlsB1nc,
nlsSEnc, nlspB1nc )
library("xlsx")
write.xlsx(NLSRegressionsNC, "C:/NLSRegressionsNC.xlsx")

########Mahalanobis testing
o.bact <- subset(camel, Species == "Camelus bactrianus", select=c(L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P3,
L.P4, W.P3, W.P4))
o.drom <- subset(camel, Species == "Camelus dromedarius", select=c(L.M1, L.M2, L.M3, W.M1, W.M2, W.M3,
L.P3, L.P4, W.P3, W.P4))
o.guan <- subset(guan, select=c(L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P4, W.P4))
o.vicu <- subset(vicu, select=c(L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P4, W.P4))
na.bact <- na.omit(o.bact)
na.drom <- na.omit(o.drom)
na.guan <- na.omit(o.guan)
na.vicu <- na.omit(o.vicu)
mah.bact <- mahalanobis(na.bact, colMeans(na.bact), cov(na.bact))
mah.drom <- mahalanobis(na.drom, colMeans(na.drom), cov(na.drom))
mah.guan <- mahalanobis(na.guan, colMeans(na.guan), cov(na.guan))
mah.vicu <- mahalanobis(na.vicu, colMeans(na.vicu), cov(na.vicu))

#BACT
o2.bact <- subset(camel, Species == "Camelus bactrianus", select=c(X., zoo, L.M1, L.M2, L.M3, W.M1, W.M2,
W.M3, L.P3, L.P4, W.P3, W.P4))
no2.bact <- na.omit(o2.bact)
mah.bact <- c(mah.bact)
bactWho <- data.frame(no2.bact, mah.bact)
```

```
#DROM
o2.drom <- subset(camel, Species == "Camelus dromedarius", select=c(X., zoo, L.M1, L.M2, L.M3, W.M1, W.M2,
W.M3, L.P3, L.P4, W.P3, W.P4))
no2.drom <- na.omit(o2.drom)
mah.drom <- c(mah.drom)
dromWho <- data.frame(no2.drom, mah.drom)
#GUAN
o2.guan <- subset(guan, select=c(Num, Zoo, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P4, W.P4))
no2.guan <- na.omit(o2.guan)
mah.guan <- c(mah.guan)
guanWho <- data.frame(no2.guan, mah.guan)
#VICU
o2.vicu <- subset(vicu, select=c(num, zoo, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P4, W.P4))
no2.vicu <- na.omit(o2.vicu)
mah.vicu <- c(mah.vicu)
vicuWho <- data.frame(no2.vicu, mah.vicu)



#ONTOGENIES H1 by M1/M2/M3 AP/T
bactfitM1 <- summary(lm(bact$L.M1 ~ bact$H.M1))
dromfitM1 <- summary(lm(drom$L.M1 ~ drom$H.M1))
guanfitM1 <- summary(lm(guan$L.M1 ~ guan$H.M1))
vicufitM1 <- summary(lm(vicu$L.M1 ~ vicu$H.M1))
hylofitM1 <- summary(lm(hylo$L.M1 ~ hylo$H.M1))
ovisfitM1 <- summary(lm(ovis$L.M1 ~ ovis$H.M1))
muntfitM1 <- summary(lm(munt$L.M1 ~ munt$H.M1))
reevfitM1 <- summary(lm(reev$L.M1 ~ reev$H.M1))
leucfitM1 <- summary(lm(leuc$L.M1 ~ leuc$H.M1))
```

```
montfitM1 <- summary(lm(mont$L.M1 ~ mont$H.M1))
dorsfitM1 <- summary(lm(dors$L.M1 ~ dors$H.M1))
weynfitM1<- summary(lm(weyn$L.M1 ~ weyn$H.M1))
silvfitM1 <- summary(lm(silv$L.M1 ~ silv$H.M1))
nigifitM1 <- summary(lm(nigi$L.M1 ~ nigi$H.M1))

bactfitM2 <- summary(lm(bact$L.M2 ~ bact$H.M1))
dromfitM2 <- summary(lm(drom$L.M2 ~ drom$H.M1))
guanfitM2 <- summary(lm(guan$L.M2 ~ guan$H.M1))
vicufitM2 <- summary(lm(vicu$L.M2 ~ vicu$H.M1))
hylofitM2 <- summary(lm(hylo$L.M2 ~ hylo$H.M1))
ovisfitM2 <- summary(lm(ovis$L.M2 ~ ovis$H.M1))
muntfitM2 <- summary(lm(munt$L.M2 ~ munt$H.M1))
reevfitM2 <- summary(lm(reev$L.M2 ~ reev$H.M1))
leucfitM2 <- summary(lm(leuc$L.M2 ~ leuc$H.M1))
montfitM2 <- summary(lm(mont$L.M2 ~ mont$H.M1))
dorsfitM2 <- summary(lm(dors$L.M2 ~ dors$H.M1))
weynfitM2<- summary(lm(weyn$L.M2 ~ weyn$H.M1))
silvfitM2 <- summary(lm(silv$L.M2 ~ silv$H.M1))
nigifitM2 <- summary(lm(nigi$L.M2 ~ nigi$H.M1))

bactfitM3 <- summary(lm(bact$L.M3 ~ bact$H.M1))
dromfitM3 <- summary(lm(drom$L.M3 ~ drom$H.M1))
guanfitM3 <- summary(lm(guan$L.M3 ~ guan$H.M1))
vicufitM3 <- summary(lm(vicu$L.M3 ~ vicu$H.M1))
hylofitM3 <- summary(lm(hylo$L.M3 ~ hylo$H.M1))
ovisfitM3 <- summary(lm(ovis$L.M3 ~ ovis$H.M1))
muntfitM3 <- summary(lm(munt$L.M3 ~ munt$H.M1))
```

```
reevfitM3 <- summary(lm(reev$L.M3 ~ reev$H.M1))
leucfitM3 <- summary(lm(leuc$L.M3 ~ leuc$H.M1))
montfitM3 <- summary(lm(mont$L.M3 ~ mont$H.M1))
dorsfitM3 <- summary(lm(dors$L.M3 ~ dors$H.M1))
weynfitM3<- summary(lm(weyn$L.M3 ~ weyn$H.M1))
silvfitM3 <- summary(lm(silv$L.M3 ~ silv$H.M1))
nigifitM3 <- summary(lm(nigi$L.M3 ~ nigi$H.M1))

bactfitTM1 <- summary(lm(bact$W.M1 ~ bact$H.M1))
dromfitTM1 <- summary(lm(drom$W.M1 ~ drom$H.M1))
guanfitTM1 <- summary(lm(guan$W.M1 ~ guan$H.M1))
vicufitTM1 <- summary(lm(vicu$W.M1 ~ vicu$H.M1))
hylofitTM1 <- summary(lm(hylo$W.M1 ~ hylo$H.M1))
ovisfitTM1 <- summary(lm(ovis$W.M1 ~ ovis$H.M1))
muntfitTM1 <- summary(lm(munt$W.M1 ~ munt$H.M1))
reevfitTM1 <- summary(lm(reev$W.M1 ~ reev$H.M1))
leucfitTM1 <- summary(lm(leuc$W.M1 ~ leuc$H.M1))
montfitTM1 <- summary(lm(mont$W.M1 ~ mont$H.M1))
dorsfitTM1 <- summary(lm(dors$W.M1 ~ dors$H.M1))
weynfitTM1<- summary(lm(weyn$W.M1 ~ weyn$H.M1))
silvfitTM1 <- summary(lm(silv$W.M1 ~ silv$H.M1))
nigifitTM1 <- summary(lm(nigi$W.M1 ~ nigi$H.M1))

bactfitTM2 <- summary(lm(bact$W.M2 ~ bact$H.M1))
dromfitTM2 <- summary(lm(drom$W.M2 ~ drom$H.M1))
guanfitTM2 <- summary(lm(guan$W.M2 ~ guan$H.M1))
vicufitTM2 <- summary(lm(vicu$W.M2 ~ vicu$H.M1))
hylofitTM2 <- summary(lm(hylo$W.M2 ~ hylo$H.M1))
```

```
ovisfitTM2 <- summary(lm(ovis$W.M2 ~ ovis$H.M1))
muntfitTM2 <- summary(lm(munt$W.M2 ~ munt$H.M1))
reevfitTM2 <- summary(lm(reev$W.M2 ~ reev$H.M1))
leucfitTM2 <- summary(lm(leuc$W.M2 ~ leuc$H.M1))
montfitTM2 <- summary(lm(mont$W.M2 ~ mont$H.M1))
dorsfitTM2 <- summary(lm(dors$W.M2 ~ dors$H.M1))
weynfitTM2<- summary(lm(weyn$W.M2 ~ weyn$H.M1))
silvfitTM2 <- summary(lm(silv$W.M2 ~ silv$H.M1))
nigifitTM2 <- summary(lm(nigi$W.M2 ~ nigi$H.M1))

bactfitTM3 <- summary(lm(bact$W.M3 ~ bact$H.M1))
dromfitTM3 <- summary(lm(drom$W.M3 ~ drom$H.M1))
guanfitTM3 <- summary(lm(guan$W.M3 ~ guan$H.M1))
vicufitTM3 <- summary(lm(vicu$W.M3 ~ vicu$H.M1))
hylofitTM3 <- summary(lm(hylo$W.M3 ~ hylo$H.M1))
ovisfitTM3 <- summary(lm(ovis$W.M3 ~ ovis$H.M1))
muntfitTM3 <- summary(lm(munt$W.M3 ~ munt$H.M1))
reevfitTM3 <- summary(lm(reev$W.M3 ~ reev$H.M1))
leucfitTM3 <- summary(lm(leuc$W.M3 ~ leuc$H.M1))
montfitTM3 <- summary(lm(mont$W.M3 ~ mont$H.M1))
dorsfitTM3 <- summary(lm(dors$W.M3 ~ dors$H.M1))
weynfitTM3<- summary(lm(weyn$W.M3 ~ weyn$H.M1))
silvfitTM3 <- summary(lm(silv$W.M3 ~ silv$H.M1))
nigifitTM3 <- summary(lm(nigi$W.M3 ~ nigi$H.M1))

sp <- c("Camelus bactrianus", "Camelus dromedarius", "Lama guanacoe", "Vicugna vicugna", "Hylochoerus
meinertzhagheni", "Cephalophus dorsalis", "Cephalophus leucogaster", " Cephalophus silvicultor", " Cephalophus
```

nigifirons", " Cephalophus weynsi", "Philantomba monticola", "Muntiacus muntjak", "Muntiacus reevesi", "Ovis dalli")

M1adjR2 <- c(bactfitM1$adj.r.squared, dromfitM1$adj.r.squared, guanfitM1$adj.r.squared, vicufitM1$adj.r.squared, hylofitM1$adj.r.squared, dorsfitM1$adj.r.squared, leucfitM1$adj.r.squared, silvfitM1$adj.r.squared, nigifitM1$adj.r.squared, weynfitM1$adj.r.squared, montfitM1$adj.r.squared, muntfitM1$adj.r.squared, reevfitM1$adj.r.squared, ovisfitM1$adj.r.squared)

M1Slope<- c(bactfitM1$coef[2,1], dromfitM1$coef[2,1], guanfitM1$coef[2,1], vicufitM1$coef[2,1], hylofitM1$coef[2,1], dorsfitM1$coef[2,1], leucfitM1$coef[2,1], silvfitM1$coef[2,1], nigifitM1$coef[2,1], weynfitM1$coef[2,1], montfitM1$coef[2,1], muntfitM1$coef[2,1], reevfitM1$coef[2,1], ovisfitM1$coef[2,1])

M1pSlope<- c(bactfitM1$coef[2,4], dromfitM1$coef[2,4], guanfitM1$coef[2,4], vicufitM1$coef[2,4], hylofitM1$coef[2,4], dorsfitM1$coef[2,4], leucfitM1$coef[2,4], silvfitM1$coef[2,4], nigifitM1$coef[2,4], weynfitM1$coef[2,4], montfitM1$coef[2,4], muntfitM1$coef[2,4], reevfitM1$coef[2,4], ovisfitM1$coef[2,4])

1StEr<- c(bactfitM1$coef[2,2], dromfitM1$coef[2,2], guanfitM1$coef[2,2], vicufitM1$coef[2,2], hylofitM1$coef[2,2], dorsfitM1$coef[2,2], leucfitM1$coef[2,2], silvfitM1$coef[2,2], nigifitM1$coef[2,2], weynfitM1$coef[2,2], montfitM1$coef[2,2], muntfitM1$coef[2,2], reevfitM1$coef[2,2], ovisfitM1$coef[2,2])

M1I <- c(bactfitM1$coef[1,1], dromfitM1$coef[1,1], guanfitM1$coef[1,1], vicufitM1$coef[1,1], hylofitM1$coef[1,1], dorsfitM1$coef[1,1], leucfitM1$coef[1,1], silvfitM1$coef[1,1], nigifitM1$coef[1,1], weynfitM1$coef[1,1], montfitM1$coef[1,1], muntfitM1$coef[1,1], reevfitM1$coef[1,1], ovisfitM1$coef[1,1])

M1pI <- c(bactfitM1$coef[1,4], dromfitM1$coef[1,4], guanfitM1$coef[1,4], vicufitM1$coef[1,4], hylofitM1$coef[1,4], dorsfitM1$coef[1,4], leucfitM1$coef[1,4], silvfitM1$coef[1,4], nigifitM1$coef[1,4], weynfitM1$coef[1,4], montfitM1$coef[1,4], muntfitM1$coef[1,4], reevfitM1$coef[1,4], ovisfitM1$coef[1,4])

M2adjR2 <- c(bactfitM2$adj.r.squared, dromfitM2$adj.r.squared, guanfitM2$adj.r.squared, vicufitM2$adj.r.squared, hylofitM2$adj.r.squared, dorsfitM2$adj.r.squared, leucfitM2$adj.r.squared, silvfitM2$adj.r.squared, nigifitM2$adj.r.squared, weynfitM2$adj.r.squared, montfitM2$adj.r.squared, muntfitM2$adj.r.squared, reevfitM2$adj.r.squared, ovisfitM2$adj.r.squared)

```
M2Slope<- c(bactfitM2$coef[2,1], dromfitM2$coef[2,1], guanfitM2$coef[2,1], vicufitM2$coef[2,1],
hylofitM2$coef[2,1], dorsfitM2$coef[2,1], leucfitM2$coef[2,1], silvfitM2$coef[2,1], nigifitM2$coef[2,1],
weynfitM2$coef[2,1], montfitM2$coef[2,1], muntfitM2$coef[2,1], reevfitM2$coef[2,1], ovisfitM2$coef[2,1])
M2pSlope<- c(bactfitM2$coef[2,4], dromfitM2$coef[2,4], guanfitM2$coef[2,4], vicufitM2$coef[2,4],
hylofitM2$coef[2,4], dorsfitM2$coef[2,4], leucfitM2$coef[2,4], silvfitM2$coef[2,4], nigifitM2$coef[2,4],
weynfitM2$coef[2,4], montfitM2$coef[2,4], muntfitM2$coef[2,4], reevfitM2$coef[2,4], ovisfitM2$coef[2,4])
M2StEr<- c(bactfitM2$coef[2,2], dromfitM2$coef[2,2], guanfitM2$coef[2,2], vicufitM2$coef[2,2],
hylofitM2$coef[2,2], dorsfitM2$coef[2,2], leucfitM2$coef[2,2], silvfitM2$coef[2,2], nigifitM2$coef[2,2],
weynfitM2$coef[2,2], montfitM2$coef[2,2], muntfitM2$coef[2,2], reevfitM2$coef[2,2], ovisfitM2$coef[2,2])
M2I <- c(bactfitM2$coef[1,1], dromfitM2$coef[1,1], guanfitM2$coef[1,1], vicufitM2$coef[1,1],
hylofitM2$coef[1,1], dorsfitM2$coef[1,1], leucfitM2$coef[1,1], silvfitM2$coef[1,1], nigifitM2$coef[1,1],
weynfitM2$coef[1,1], montfitM2$coef[1,1], muntfitM2$coef[1,1], reevfitM2$coef[1,1], ovisfitM2$coef[1,1])
M2pI <- c(bactfitM2$coef[1,4], dromfitM2$coef[1,4], guanfitM2$coef[1,4], vicufitM2$coef[1,4],
hylofitM2$coef[1,4], dorsfitM2$coef[1,4], leucfitM2$coef[1,4], silvfitM2$coef[1,4], nigifitM2$coef[1,4],
weynfitM2$coef[1,4], montfitM2$coef[1,4], muntfitM2$coef[1,4], reevfitM2$coef[1,4], ovisfitM2$coef[1,4])

M3adjR2 <- c(bactfitM3$adj.r.squared, dromfitM3$adj.r.squared, guanfitM3$adj.r.squared,
vicufitM3$adj.r.squared, hylofitM3$adj.r.squared, dorsfitM3$adj.r.squared, leucfitM3$adj.r.squared,
silvfitM3$adj.r.squared, nigifitM3$adj.r.squared, weynfitM3$adj.r.squared, montfitM3$adj.r.squared,
muntfitM3$adj.r.squared, reevfitM3$adj.r.squared, ovisfitM3$adj.r.squared)
M3Slope<- c(bactfitM3$coef[2,1], dromfitM3$coef[2,1], guanfitM3$coef[2,1], vicufitM3$coef[2,1],
hylofitM3$coef[2,1], dorsfitM3$coef[2,1], leucfitM3$coef[2,1], silvfitM3$coef[2,1], nigifitM3$coef[2,1],
weynfitM3$coef[2,1], montfitM3$coef[2,1], muntfitM3$coef[2,1], reevfitM3$coef[2,1], ovisfitM3$coef[2,1])
M3pSlope<- c(bactfitM3$coef[2,4], dromfitM3$coef[2,4], guanfitM3$coef[2,4], vicufitM3$coef[2,4],
hylofitM3$coef[2,4], dorsfitM3$coef[2,4], leucfitM3$coef[2,4], silvfitM3$coef[2,4], nigifitM3$coef[2,4],
weynfitM3$coef[2,4], montfitM3$coef[2,4], muntfitM3$coef[2,4], reevfitM3$coef[2,4], ovisfitM3$coef[2,4])
```

```
M3StEr<-  c(bactfitM3$coef[2,2], dromfitM3$coef[2,2], guanfitM3$coef[2,2], vicufitM3$coef[2,2],
hylofitM3$coef[2,2], dorsfitM3$coef[2,2], leucfitM3$coef[2,2], silvfitM3$coef[2,2], nigifitM3$coef[2,2],
weynfitM3$coef[2,2], montfitM3$coef[2,2], muntfitM3$coef[2,2], reevfitM3$coef[2,2], ovisfitM3$coef[2,2])
M3I <-  c(bactfitM3$coef[1,1], dromfitM3$coef[1,1], guanfitM3$coef[1,1], vicufitM3$coef[1,1],
hylofitM3$coef[1,1], dorsfitM3$coef[1,1], leucfitM3$coef[1,1], silvfitM3$coef[1,1], nigifitM3$coef[1,1],
weynfitM3$coef[1,1], montfitM3$coef[1,1], muntfitM3$coef[1,1], reevfitM3$coef[1,1], ovisfitM3$coef[1,1])
M3pI <-  c(bactfitM3$coef[1,4], dromfitM3$coef[1,4], guanfitM3$coef[1,4], vicufitM3$coef[1,4],
hylofitM3$coef[1,4], dorsfitM3$coef[1,4], leucfitM3$coef[1,4], silvfitM3$coef[1,4], nigifitM3$coef[1,4],
weynfitM3$coef[1,4], montfitM3$coef[1,4], muntfitM3$coef[1,4], reevfitM3$coef[1,4], ovisfitM3$coef[1,4])

TM1adjR2 <-  c(bactfitTM1$adj.r.squared, dromfitTM1$adj.r.squared, guanfitTM1$adj.r.squared,
vicufitTM1$adj.r.squared, hylofitTM1$adj.r.squared, dorsfitTM1$adj.r.squared, leucfitTM1$adj.r.squared,
silvfitTM1$adj.r.squared, nigifitTM1$adj.r.squared, weynfitTM1$adj.r.squared, montfitTM1$adj.r.squared,
muntfitTM1$adj.r.squared, reevfitTM1$adj.r.squared, ovisfitTM1$adj.r.squared)
TM1Slope<-  c(bactfitTM1$coef[2,1], dromfitTM1$coef[2,1], guanfitTM1$coef[2,1], vicufitTM1$coef[2,1],
hylofitTM1$coef[2,1], dorsfitTM1$coef[2,1], leucfitTM1$coef[2,1], silvfitTM1$coef[2,1], nigifitTM1$coef[2,1],
weynfitTM1$coef[2,1], montfitTM1$coef[2,1], muntfitTM1$coef[2,1], reevfitTM1$coef[2,1],
ovisfitTM1$coef[2,1])
TM1pSlope<-  c(bactfitTM1$coef[2,4], dromfitTM1$coef[2,4], guanfitTM1$coef[2,4], vicufitTM1$coef[2,4],
hylofitTM1$coef[2,4], dorsfitTM1$coef[2,4], leucfitTM1$coef[2,4], silvfitTM1$coef[2,4], nigifitTM1$coef[2,4],
weynfitTM1$coef[2,4], montfitTM1$coef[2,4], muntfitTM1$coef[2,4], reevfitTM1$coef[2,4],
ovisfitTM1$coef[2,4])
TM1StEr<-  c(bactfitTM1$coef[2,2], dromfitTM1$coef[2,2], guanfitTM1$coef[2,2], vicufitTM1$coef[2,2],
hylofitTM1$coef[2,2], dorsfitTM1$coef[2,2], leucfitTM1$coef[2,2], silvfitTM1$coef[2,2], nigifitTM1$coef[2,2],
weynfitTM1$coef[2,2], montfitTM1$coef[2,2], muntfitTM1$coef[2,2], reevfitTM1$coef[2,2],
ovisfitTM1$coef[2,2])
TM1I <-  c(bactfitTM1$coef[1,1], dromfitTM1$coef[1,1], guanfitTM1$coef[1,1], vicufitTM1$coef[1,1],
hylofitTM1$coef[1,1], dorsfitTM1$coef[1,1], leucfitTM1$coef[1,1], silvfitTM1$coef[1,1], nigifitTM1$coef[1,1],
```

```
weynfitTM1$coef[1,1], montfitTM1$coef[1,1], muntfitTM1$coef[1,1], reevfitTM1$coef[1,1],
ovisfitTM1$coef[1,1])
TM1pI <-  c(bactfitTM1$coef[1,4], dromfitTM1$coef[1,4], guanfitTM1$coef[1,4], vicufitTM1$coef[1,4],
hylofitTM1$coef[1,4], dorsfitTM1$coef[1,4], leucfitTM1$coef[1,4], silvfitTM1$coef[1,4], nigifitTM1$coef[1,4],
weynfitTM1$coef[1,4], montfitTM1$coef[1,4], muntfitTM1$coef[1,4], reevfitTM1$coef[1,4],
ovisfitTM1$coef[1,4])
TM2adjR2 <-  c(bactfitTM2$adj.r.squared, dromfitTM2$adj.r.squared, guanfitTM2$adj.r.squared,
vicufitTM2$adj.r.squared, hylofitTM2$adj.r.squared, dorsfitTM2$adj.r.squared, leucfitTM2$adj.r.squared,
silvfitTM2$adj.r.squared, nigifitTM2$adj.r.squared, weynfitTM2$adj.r.squared, montfitTM2$adj.r.squared,
muntfitTM2$adj.r.squared, reevfitTM2$adj.r.squared, ovisfitTM2$adj.r.squared)
TM2Slope<-  c(bactfitTM2$coef[2,1], dromfitTM2$coef[2,1], guanfitTM2$coef[2,1], vicufitTM2$coef[2,1],
hylofitTM2$coef[2,1], dorsfitTM2$coef[2,1], leucfitTM2$coef[2,1], silvfitTM2$coef[2,1], nigifitTM2$coef[2,1],
weynfitTM2$coef[2,1], montfitTM2$coef[2,1], muntfitTM2$coef[2,1], reevfitTM2$coef[2,1],
ovisfitTM2$coef[2,1])
TM2pSlope<-  c(bactfitTM2$coef[2,4], dromfitTM2$coef[2,4], guanfitTM2$coef[2,4], vicufitTM2$coef[2,4],
hylofitTM2$coef[2,4], dorsfitTM2$coef[2,4], leucfitTM2$coef[2,4], silvfitTM2$coef[2,4], nigifitTM2$coef[2,4],
weynfitTM2$coef[2,4], montfitTM2$coef[2,4], muntfitTM2$coef[2,4], reevfitTM2$coef[2,4],
ovisfitTM2$coef[2,4])
TM2StEr<-  c(bactfitTM2$coef[2,2], dromfitTM2$coef[2,2], guanfitTM2$coef[2,2], vicufitTM2$coef[2,2],
hylofitTM2$coef[2,2], dorsfitTM2$coef[2,2], leucfitTM2$coef[2,2], silvfitTM2$coef[2,2], nigifitTM2$coef[2,2],
weynfitTM2$coef[2,2], montfitTM2$coef[2,2], muntfitTM2$coef[2,2], reevfitTM2$coef[2,2],
ovisfitTM2$coef[2,2])
TM2I <-  c(bactfitTM2$coef[1,1], dromfitTM2$coef[1,1], guanfitTM2$coef[1,1], vicufitTM2$coef[1,1],
hylofitTM2$coef[1,1], dorsfitTM2$coef[1,1], leucfitTM2$coef[1,1], silvfitTM2$coef[1,1], nigifitTM2$coef[1,1],
weynfitTM2$coef[1,1], montfitTM2$coef[1,1], muntfitTM2$coef[1,1], reevfitTM2$coef[1,1],
ovisfitTM2$coef[1,1])
TM2pI <-  c(bactfitTM2$coef[1,4], dromfitTM2$coef[1,4], guanfitTM2$coef[1,4], vicufitTM2$coef[1,4],
hylofitTM2$coef[1,4], dorsfitTM2$coef[1,4], leucfitTM2$coef[1,4], silvfitTM2$coef[1,4], nigifitTM2$coef[1,4],
```

```
weynfitTM2$coef[1,4], montfitTM2$coef[1,4], muntfitTM2$coef[1,4], reevfitTM2$coef[1,4],
ovisfitTM2$coef[1,4])

TM3adjR2 <- c(bactfitTM3$adj.r.squared, dromfitTM3$adj.r.squared, guanfitTM3$adj.r.squared,
vicufitTM3$adj.r.squared, hylofitTM3$adj.r.squared, dorsfitTM3$adj.r.squared, leucfitTM3$adj.r.squared,
silvfitTM3$adj.r.squared, nigifitTM3$adj.r.squared, weynfitTM3$adj.r.squared, montfitTM3$adj.r.squared,
muntfitTM3$adj.r.squared, reevfitTM3$adj.r.squared, ovisfitTM3$adj.r.squared)
TM3Slope<- c(bactfitTM3$coef[2,1], dromfitTM3$coef[2,1], guanfitTM3$coef[2,1], vicufitTM3$coef[2,1],
hylofitTM3$coef[2,1], dorsfitTM3$coef[2,1], leucfitTM3$coef[2,1], silvfitTM3$coef[2,1], nigifitTM3$coef[2,1],
weynfitTM3$coef[2,1], montfitTM3$coef[2,1], muntfitTM3$coef[2,1], reevfitTM3$coef[2,1],
ovisfitTM3$coef[2,1])
TM3pSlope<- c(bactfitTM3$coef[2,4], dromfitTM3$coef[2,4], guanfitTM3$coef[2,4], vicufitTM3$coef[2,4],
hylofitTM3$coef[2,4], dorsfitTM3$coef[2,4], leucfitTM3$coef[2,4], silvfitTM3$coef[2,4], nigifitTM3$coef[2,4],
weynfitTM3$coef[2,4], montfitTM3$coef[2,4], muntfitTM3$coef[2,4], reevfitTM3$coef[2,4],
ovisfitTM3$coef[2,4])
TM3StEr<- c(bactfitTM3$coef[2,2], dromfitTM3$coef[2,2], guanfitTM3$coef[2,2], vicufitTM3$coef[2,2],
hylofitTM3$coef[2,2], dorsfitTM3$coef[2,2], leucfitTM3$coef[2,2], silvfitTM3$coef[2,2], nigifitTM3$coef[2,2],
weynfitTM3$coef[2,2], montfitTM3$coef[2,2], muntfitTM3$coef[2,2], reevfitTM3$coef[2,2],
ovisfitTM3$coef[2,2])
TM3I <- c(bactfitTM3$coef[1,1], dromfitTM3$coef[1,1], guanfitTM3$coef[1,1], vicufitTM3$coef[1,1],
hylofitTM3$coef[1,1], dorsfitTM3$coef[1,1], leucfitTM3$coef[1,1], silvfitTM3$coef[1,1], nigifitTM3$coef[1,1],
weynfitTM3$coef[1,1], montfitTM3$coef[1,1], muntfitTM3$coef[1,1], reevfitTM3$coef[1,1],
ovisfitTM3$coef[1,1])
TM3pI <- c(bactfitTM3$coef[1,4], dromfitTM3$coef[1,4], guanfitTM3$coef[1,4], vicufitTM3$coef[1,4],
hylofitTM3$coef[1,4], dorsfitTM3$coef[1,4], leucfitTM3$coef[1,4], silvfitTM3$coef[1,4], nigifitTM3$coef[1,4],
weynfitTM3$coef[1,4], montfitTM3$coef[1,4], muntfitTM3$coef[1,4], reevfitTM3$coef[1,4],
ovisfitTM3$coef[1,4])
```

```
ontogeny <- data.frame(sp, M1adjR2, M1Slope, M1pSlope, M1StEr, M1I, M1pI, M2adjR2, M2Slope, M2pSlope,
M2StEr, M2I, M2pI, M3adjR2, M3Slope, M3pSlope, M3StEr, M3I, M3pI, TM1adjR2, TM1Slope, TM1pSlope,
TM1StEr, TM1I, TM1pI, TM2adjR2, TM2Slope, TM2pSlope, TM2StEr, TM2I, TM2pI, TM3adjR2, TM3Slope,
TM3pSlope, TM3StEr, TM3I, TM3pI)
library("xlsx")
write.xlsx(ontogeny, "C:/ontogeny.xlsx")



#ONTOGENY OF THE MUZZLE AND OF DIASTEMAS
bactfitMuzzle <- summary(lm(bact$L.Muzzle ~ bact$H.M1))
dromfitMuzzle <- summary(lm(drom$L.Muzzle ~ drom$H.M1))
guanfitMuzzle <- summary(lm(guan$L.Muzzle ~ guan$H.M1))
vicufitMuzzle <- summary(lm(vicu$L.Muzzle ~ vicu$H.M1))
hylofitMuzzle <- summary(lm(hylo$Muzzle ~ hylo$H.M1))
ovisfitMuzzle <- summary(lm(ovis$L.Muzzle ~ ovis$H.M1))
muntfitMuzzle <- summary(lm(munt$L.Muzzle ~ munt$H.M1))
reevfitMuzzle <- summary(lm(reev$L.Muzzle ~ reev$H.M1))
leucfitMuzzle <- summary(lm(leuc$L.Muzzle ~ leuc$H.M1))
montfitMuzzle <- summary(lm(mont$L.Muzzle ~ mont$H.M1))
dorsfitMuzzle <- summary(lm(dors$L.Muzzle ~ dors$H.M1))
weynfitMuzzle<- summary(lm(weyn$L.Muzzle ~ weyn$H.M1))
silvfitMuzzle <- summary(lm(silv$L.Muzzle ~ silv$H.M1))
nigifitMuzzle <- summary(lm(nigi$L.Muzzle ~ nigi$H.M1))
MuzzleadjR2 <-  c(bactfitMuzzle$adj.r.squared, dromfitMuzzle$adj.r.squared, guanfitMuzzle$adj.r.squared,
vicufitMuzzle$adj.r.squared, hylofitMuzzle$adj.r.squared, dorsfitMuzzle$adj.r.squared,
leucfitMuzzle$adj.r.squared, silvfitMuzzle$adj.r.squared, nigifitMuzzle$adj.r.squared, weynfitMuzzle$adj.r.squared,
```

```
montfitMuzzle$adj.r.squared, muntfitMuzzle$adj.r.squared, reevfitMuzzle$adj.r.squared,
ovisfitMuzzle$adj.r.squared)
MuzzleSlope<-  c(bactfitMuzzle$coef[2,1], dromfitMuzzle$coef[2,1], guanfitMuzzle$coef[2,1],
vicufitMuzzle$coef[2,1], hylofitMuzzle$coef[2,1], dorsfitMuzzle$coef[2,1], leucfitMuzzle$coef[2,1],
silvfitMuzzle$coef[2,1], nigifitMuzzle$coef[2,1], weynfitMuzzle$coef[2,1], montfitMuzzle$coef[2,1],
muntfitMuzzle$coef[2,1], reevfitMuzzle$coef[2,1], ovisfitMuzzle$coef[2,1])
MuzzlepSlope<-  c(bactfitMuzzle$coef[2,4], dromfitMuzzle$coef[2,4], guanfitMuzzle$coef[2,4],
vicufitMuzzle$coef[2,4], hylofitMuzzle$coef[2,4], dorsfitMuzzle$coef[2,4], leucfitMuzzle$coef[2,4],
silvfitMuzzle$coef[2,4], nigifitMuzzle$coef[2,4], weynfitMuzzle$coef[2,4], montfitMuzzle$coef[2,4],
muntfitMuzzle$coef[2,4], reevfitMuzzle$coef[2,4], ovisfitMuzzle$coef[2,4])
MuzzleStEr<-  c(bactfitMuzzle$coef[2,2], dromfitMuzzle$coef[2,2], guanfitMuzzle$coef[2,2],
vicufitMuzzle$coef[2,2], hylofitMuzzle$coef[2,2], dorsfitMuzzle$coef[2,2], leucfitMuzzle$coef[2,2],
silvfitMuzzle$coef[2,2], nigifitMuzzle$coef[2,2], weynfitMuzzle$coef[2,2], montfitMuzzle$coef[2,2],
muntfitMuzzle$coef[2,2], reevfitMuzzle$coef[2,2], ovisfitMuzzle$coef[2,2])
MuzzleI <-  c(bactfitMuzzle$coef[1,1], dromfitMuzzle$coef[1,1], guanfitMuzzle$coef[1,1],
vicufitMuzzle$coef[1,1], hylofitMuzzle$coef[1,1], dorsfitMuzzle$coef[1,1], leucfitMuzzle$coef[1,1],
silvfitMuzzle$coef[1,1], nigifitMuzzle$coef[1,1], weynfitMuzzle$coef[1,1], montfitMuzzle$coef[1,1],
muntfitMuzzle$coef[1,1], reevfitMuzzle$coef[1,1], ovisfitMuzzle$coef[1,1])
MuzzlepI <-  c(bactfitMuzzle$coef[1,4], dromfitMuzzle$coef[1,4], guanfitMuzzle$coef[1,4],
vicufitMuzzle$coef[1,4], hylofitMuzzle$coef[1,4], dorsfitMuzzle$coef[1,4], leucfitMuzzle$coef[1,4],
silvfitMuzzle$coef[1,4], nigifitMuzzle$coef[1,4], weynfitMuzzle$coef[1,4], montfitMuzzle$coef[1,4],
muntfitMuzzle$coef[1,4], reevfitMuzzle$coef[1,4], ovisfitMuzzle$coef[1,4])
sp <- c("Camelus bactrianus", "Camelus dromedarius", "Lama guanacoe", "Vicugna vicugna", "Hylochoerus
meinertzhagheni", "Cephalophus dorsalis", "Cephalophus leucogaster", " Cephalophus silvicultor", " Cephalophus
nigifirons", " Cephalophus weynsi", "Philantomba monticola", "Muntiacus muntjak", "Muntiacus reevesi", "Ovis
dalli")
MuzzleOntogeny <- data.frame(sp, MuzzleadjR2, MuzzleSlope, MuzzlepSlope, MuzzleStEr, MuzzleI, MuzzlepI)
library("xlsx")
```

```
write.xlsx(MuzzleOntogeny, "C:/MuzzleOntogeny.xlsx")



bactDias <- subset(camel, Species == "Camelus bactrianus", select=c(adult, male, zoo, X., Age.Class, L.Muzzle,
L.C1, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars,
L.Molars, L.Toothrow, L.dias.inc, L.dias.ant, L.dias.pos))
dromDias <- subset(camel, Species == "Camelus dromedarius", select=c(adult, male, zoo, X., Age.Class, L.Muzzle,
L.C1, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars,
L.Molars, L.Toothrow, L.dias.inc, L.dias.ant, L.dias.pos))
muntDias <- subset(muntiacus, Species == "Muntiacus muntjak", select=c(adult, male, zoo, X., Age.Class,
L.Muzzle, L.C1, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4,
L.Premolars, L.Molars, L.Toothrow, L.Dias.pos))
reevDias <- subset(muntiacus, Species == "Muntiacus reevesi", select=c(adult, male, zoo, X., Age.Class, L.Muzzle,
L.C1, H.M1, L.M1, L.M2, L.M3, W.M1, W.M2, W.M3, L.P2, L.P3, L.P4, W.P2, W.P3, W.P4, L.Premolars,
L.Molars, L.Toothrow, L.Dias.pos))

bactfitDias1 <- summary(lm(bactDias$L.dias.inc ~ bactDias$H.M1))
dromfitDias1 <- summary(lm(dromDias$L.dias.inc ~ dromDias$H.M1))
guanfitDias1 <- summary(lm(guan$L.Dias.ant ~ guan$H.M1))
vicufitDias1 <- summary(lm(vicu$L.dias.ant ~ vicu$H.M1))

bactfitDias2 <- summary(lm(bactDias$L.dias.ant ~ bactDias$H.M1))
dromfitDias2 <- summary(lm(dromDias$L.dias.ant ~ dromDias$H.M1))
guanfitDias2 <- summary(lm(guan$L.Dias.pos ~ guan$H.M1))
vicufitDias2 <- summary(lm(vicu$L.dias.pos ~ vicu$H.M1))

bactfitDias3 <- summary(lm(bactDias$L.dias.pos ~ bactDias$H.M1))
```

```
dromfitDias3 <- summary(lm(dromDias$L.dias.pos ~ dromDias$H.M1))

hylofitDias <- summary(lm(hylo$L.Dias ~ hylo$H.M1))
muntfitDias <- summary(lm(muntDias$L.Dias.pos ~ muntDias$H.M1))
reevfitDias <- summary(lm(reevDias$L.Dias.pos ~ reevDias$H.M1))

Diassp <- c("Camelus bactrianus Dias 1", "Camelus dromedarius Dias 1", "Lama guanacoe Dias 1", "Vicugna
vicugna Dias 1", "Camelus bactrianus Dias 2", "Camelus dromedarius Dias 2", "Lama guanacoe Dias 2", "Vicugna
vicugna Dias 2", "Camelus bactrianus Dias 3", "Camelus dromedarius Dias 3", "Hylochoerus meinertzhagheni",
"Muntiacus muntjak", "Muntiacus reevesi")

DiasadjR2 <-  c(bactfitDias1$adj.r.squared, dromfitDias1$adj.r.squared, guanfitDias1$adj.r.squared,
vicufitDias1$adj.r.squared, bactfitDias2$adj.r.squared, dromfitDias2$adj.r.squared, guanfitDias2$adj.r.squared,
vicufitDias2$adj.r.squared, bactfitDias3$adj.r.squared, dromfitDias3$adj.r.squared, hylofitDias$adj.r.squared,
muntfitDias$adj.r.squared, reevfitDias$adj.r.squared)

DiasSlope<-  c(bactfitDias1$coef[2,1], dromfitDias1$coef[2,1], guanfitDias1$coef[2,1], vicufitDias1$coef[2,1],
bactfitDias2$coef[2,1], dromfitDias2$coef[2,1], guanfitDias2$coef[2,1], vicufitDias2$coef[2,1],
bactfitDias3$coef[2,1], dromfitDias3$coef[2,1], hylofitDias$coef[2,1], muntfitDias$coef[2,1],
reevfitDias$coef[2,1])

DiaspSlope<- c(bactfitDias1$coef[2,4], dromfitDias1$coef[2,4], guanfitDias1$coef[2,4], vicufitDias1$coef[2,4],
bactfitDias2$coef[2,4], dromfitDias2$coef[2,4], guanfitDias2$coef[2,4], vicufitDias2$coef[2,4],
bactfitDias3$coef[2,4], dromfitDias3$coef[2,4], hylofitDias$coef[2,4], muntfitDias$coef[2,4],
reevfitDias$coef[2,4])

DiasStEr<- c(bactfitDias1$coef[2,2], dromfitDias1$coef[2,2], guanfitDias1$coef[2,2], vicufitDias1$coef[2,2],
bactfitDias2$coef[2,2], dromfitDias2$coef[2,2], guanfitDias2$coef[2,2], vicufitDias2$coef[2,2],
```

```
bactfitDias3$coef[2,2], dromfitDias3$coef[2,2], hylofitDias$coef[2,2], muntfitDias$coef[2,2],
reevfitDias$coef[2,2])

DiasI <-  c(bactfitDias1$coef[1,1], dromfitDias1$coef[1,1], guanfitDias1$coef[1,1], vicufitDias1$coef[1,1],
bactfitDias2$coef[1,1], dromfitDias2$coef[1,1], guanfitDias2$coef[1,1], vicufitDias2$coef[1,1],
bactfitDias3$coef[1,1], dromfitDias3$coef[1,1], hylofitDias$coef[1,1], muntfitDias$coef[1,1],
reevfitDias$coef[1,1])

DiaspI <-  c(bactfitDias1$coef[1,4], dromfitDias1$coef[1,4], guanfitDias1$coef[1,4], vicufitDias1$coef[1,4],
bactfitDias2$coef[1,4], dromfitDias2$coef[1,4], guanfitDias2$coef[1,4], vicufitDias2$coef[1,4],
bactfitDias3$coef[1,4], dromfitDias3$coef[1,4], hylofitDias$coef[1,4], muntfitDias$coef[1,4],
reevfitDias$coef[1,4])

DiasOntogeny <- data.frame(Diassp, DiasadjR2, DiasSlope, DiaspSlope, DiasStEr, DiasI, DiaspI)
library("xlsx")
write.xlsx(DiasOntogeny, "C:/DiasOntogeny.xlsx")




##############################
#######FIGURE CREATION#####
##############################

###Correlation Plot for premolars and molars of camelids
plot(bact$L.Premolars, bact$L.Molars, xlab="Premolars Length (cm)", ylab="Molar length (cm)", cex=1.5,
cex.lab=1.3, cex.axis=1.3, cex.main=1.3, pch=1, xaxt='n', ylim=c(0,15), xlim=c(0,8), axes=FALSE)
axis(side=1, at=seq(0,8, by=2), tck=-.01)
```

```
axis(side=2, at=seq(0,15, by=2), tck=-.01)
par(new = TRUE)
plot(drom$L.Premolars, drom$L.Molars, xlab="", ylab="", cex.lab=1.3, cex.axis=1.3, cex.main=1.3, cex=1.5,
pch=15, xaxt='n', ylim=c(0,15), xlim=c(0,8), axes=FALSE, col="gray")
par(new = TRUE)
plot(guan$L.Premolars, guan$L.Molars, xlab="", ylab="", cex.lab=1.3, cex.axis=1.3, cex.main=1.3, cex=1.5,
pch=16, xaxt='n', ylim=c(0,15), xlim=c(0,8), axes=FALSE, col="gray")
par(new = TRUE)
plot(vicu$L.Premolars, vicu$L.Molars, xlab="", ylab="", cex.lab=1.3, cex.axis=1.3, cex.main=1.3, cex=1.5, pch=16,
xaxt='n', ylim=c(0,15), xlim=c(0,8), axes=FALSE)
legend(2.1, 4, pch=c(1,15,16, 16), col=c("black", "gray", "gray", "black"), c("C. bactrianus     CV=16.04, R2=.25,
p=.06", "C. dromedarius  CV=11.12, R2=-.04, p=.64", "L. guanaco        CV=10.75, R2=.46,  p=.01", "V. vicugna
CV=7.03,   R2=.75,  p=.0007"), bty="n", cex=1.5)
title("Correlations between Premolar Row and Molar Row", line=1)
abline(lm(bact$L.Molars ~ bact$L.Premolars))
abline(lm(drom$L.Molars ~ drom$L.Premolars))
abline(lm(guan$L.Molars ~ guan$L.Premolars))
abline(lm(vicu$L.Molars ~ vicu$L.Premolars))
box()


####CV line charts
linechart <- read.csv("linecharts.csv")
bactLC <- t(subset(linechart, Species == "bact", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
dromLC <- t(subset(linechart, Species == "drom", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
```

```
guanLC <- t(subset(linechart, Species == "guan", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
vicuLC <- t(subset(linechart, Species == "vicu", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
hyloLC <- t(subset(linechart, Species == "hylo", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
ovisLC <- t(subset(linechart, Species == "ovis", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
muntLC <- t(subset(linechart, Species == "munt", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
reevLC <- t(subset(linechart, Species == "reev", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
montLC <- t(subset(linechart, Species == "mont", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
leucLC <- t(subset(linechart, Species == "leuc", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
dorsLC <- t(subset(linechart, Species == "dors", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
weynLC <- t(subset(linechart, Species == "weyn", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
silvLC <- t(subset(linechart, Species == "silv", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
nigiLC <- t(subset(linechart, Species == "nigi", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
nigiLC <- t(subset(linechart, Species == "nigi", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1, AP.M2,
AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
```

```
guanlamaLC <- t(subset(linechart, Species == "guanlama", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1,
AP.M2, AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
muntiacusLC <- t(subset(linechart, Species == "muntiacus", select=c(AP.I3, AP.C1,  AP.P2, AP.P3, AP.P4, AP.M1,
AP.M2, AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
camelusLC <- t(subset(linechart, Species == "camelus", select=c(AP.I3, AP.C1, AP.P2, AP.P3, AP.P4, AP.M1,
AP.M2, AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
cephLC <- t(subset(linechart, Species == "cephalophus", select=c(AP.I3, AP.C1, AP.P2, AP.P3, AP.P4, AP.M1,
AP.M2, AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))
med.cephLC <- t(subset(linechart, Species == "med.cephalophus", select=c(AP.I3, AP.C1, AP.P2, AP.P3, AP.P4,
AP.M1, AP.M2, AP.M3, T..C1, T..P2, T.P3, T.P4, T.M1, T.M2, T.M3)))

characters <- c("AP I3", "AP C1", "AP P2", "AP P3", "AP P4", "AP M1", "AP M2", "AP M3", "T C1", "T P2", "T
P3", "T P4", "T M1", "T M2", "T M3")

par(mfrow=c(3,2))
plot(dromLC, type="b", ylab="", axes=FALSE, xaxt='n', xlab="", ylim=c(0,60))
axis(side=1, 1:15, labels=NA, cex.axis=1.2, las=2, tck=-.05)
axis(side=2, at=seq(0, 60, by=10), cex.axis=1.2, tck=-.05)
box()
title("Camelus", line=-1)
par(new=TRUE)
plot(bactLC, type="b", axes=FALSE, xlab="", ylab="Coefficient of Variation, as %", xaxt='n', ylim=c(0,60),
pch=16)
par(new=TRUE)
plot(camelusLC, type="b", axes=FALSE, xlab="", ylab="", xaxt='n', ylim=c(0,60), pch=15, col="gray")
legend(1, 61, pch=c(16, 1, 15), col=c("black", "black", "gray"), c("Camelus bactrianus", "Camelus dromedarius",
"Combined Camelus"), bty="n")
```

```
plot(guanLC, type="b", ylab="", axes=FALSE, xaxt='n', xlab="", ylim=c(0,60), pch=16)
par(new=TRUE)
plot(vicuLC, type="b", axes=FALSE, xlab="", ylab="", xaxt='n', ylim=c(0,60), pch=3)
par(new=TRUE)
plot(guanlamaLC, type="b", axes=FALSE, xlab="", ylab="", xaxt='n', ylim=c(0,60), pch=15, col="gray")
box()
title("Lama and Vicugna", line=-1)
axis(side=1, 1:15, labels=NA, cex.axis=1.2, las=2, tck=-.05)
axis(side=2, at=seq(0, 61, by=5), cex.axis=1.2, tck=-.05)
legend(1, 55, pch=c(16, 3, 15), col=c("black", "black", "gray"), c("Lama guanacoe", "Vicugna vicugna", "Combined
Lama and Vicugna"), bty="n")

plot(muntLC, type="b", ylab="", axes=FALSE, xaxt='n', xlab="", ylim=c(0,60))
axis(side=1, 1:15, labels=NA, cex.axis=1.2, las=2, tck=-.05)
axis(side=2, at=seq(0, 60, by=10), cex.axis=1.2, tck=-.05)
box()
title("Muntiacus", line=-1)
par(new=TRUE)
plot(reevLC, type="b", axes=FALSE, xlab="", ylab="Coefficient of Variation, as %", xaxt='n', ylim=c(0,60),
pch=16)
par(new=TRUE)
plot(muntiacusLC, type="b", axes=FALSE, xlab="", ylab="", xaxt='n', ylim=c(0,60), pch=15, col="gray")
legend(1, 61, pch=c(16, 1, 15), col=c("black", "black", "gray"), c("Muntiacus muntjak", "Muntiacus reevesi",
"Combined Muntiacus"), bty="n")

plot(montLC, type="b", ylab="", axes=FALSE, xaxt='n', xlab="", ylim=c(0,60), pch=1)
par(new=TRUE)
plot(leucLC, type="b", axes=FALSE, xlab="", ylab="", xaxt='n', ylim=c(0,60), pch=16)
```

```
par(new=TRUE)
plot(silvLC, type="b", axes=FALSE, xlab="", ylab="", xaxt='n', ylim=c(0,60), pch=3, col="black")
par(new=TRUE)
plot(med.cephLC, type="b", axes=FALSE, xlab="", ylab="", xaxt='n', ylim=c(0,60), pch=15, col="gray")
legend(1, 55, pch=c(1, 16, 3, 15), col=c("black", "black", "black", "gray"), c("Philantomba monticola",
"Cephalophus leucogaster", "Cephalophus silvicultor", "Combined medium duikers"), bty="n")
title("Cephalophus and Philantomba", line=-1)
axis(side=1, 1:15, labels=NA, cex.axis=1.2, las=2, tck=-.05)
axis(side=2, at=seq(0, 60, by=5), cex.axis=1.2, tck=-.05)
box()

plot(hyloLC, type="b", ylab="Coefficient of Variation, as %", axes=FALSE, xaxt='n', xlab="", ylim=c(0,60))
axis(side=1, 1:15, characters, cex.axis=1.2, las=2, tck=-.015)
axis(side=2, at=seq(0, 60, by=10), cex.axis=1.2, tck=-.015)
box()
title("Hylochoerus meinertzhageni", line=-1)

plot(ovisLC, type="b", ylab="", axes=FALSE, xaxt='n', xlab="", ylim=c(0,60))
axis(side=1, 1:15, characters, cex.axis=1.2, las=2, tck=-.015)
axis(side=2, at=seq(0, 60, by=10), cex.axis=1.2, tck=-.015)
box()
title("Ovis dalli", line=-1)



#CV graph for not significant regressions
par(mfrow=c(2,2))
plot(UAPP2$stdev~UAPP2$avg, main="L P2", ylab="Standard Deviations", xlab="Average, cm", pch=16,
cex=1.3)
```

```
abline(lm(UAPP2$stdev~UAPP2$avg), lty=2)
plot(UTP2$stdev~UTP2$avg, main="W P2", ylab="Standard Deviations", xlab="Average, cm", pch=16, cex=1.3)
abline(lm(UTP2$stdev~UTP2$avg), lty=2)
plot(UTP3$stdev~UTP3$avg, ylab="Standard Deviations", main="W P3", xlab="Average, cm", pch=16, cex=1.3)
abline(lm(UTP3$stdev~UTP3$avg), lty=2)
plot(Premolars$stdev~Premolars$avg, ylab="Standard Deviations", main="Premolar Row", xlab="Average, cm",
pch=16, cex=1.3)
abline(lm(Premolars$stdev~Premolars$avg), lty=2)
```

APPENDIX B

R SCRIPT FOR CHAPTER II

```
library(geomorph)
library(MASS)
library(base)
library(randomForest)
library(dplyr)
library(phytools)
library(geiger)
library(mixtools)
library(multigroup)

######Read in Data, General Procrustes Analysis####
duikers <- read.morphologika("duikers.txt")

Y.gpa <- gpagen(duikers)
categories <- strsplit(dimnames(duikers)[[3]], "_")
classifiers <- matrix(unlist(categories), ncol=5, byrow=T)
colnames(classifiers) <- c("ID", "Genus", "Group", "Species", "Sex")
classifiers <- as.data.frame(classifiers)
size <- read.csv("size.csv")
classifiers <- merge.data.frame(classifiers, size, by="ID", sort=F)

Y.gpa2d <- two.d.array(Y.gpa$coords)
categories2d <- strsplit(rownames(Y.gpa2d), "_")
classifiers2d <- matrix(unlist(categories2d), ncol=5, byrow=T)
colnames(classifiers2d) <- c("ID", "Genus", "Group", "Species", "Sex")
```

```
classifiers2d <- as.data.frame(classifiers2d)
classifiers2d <- merge.data.frame(classifiers2d, size, by="ID")

S.gpa <- Y.gpa$coords*classifiers$Size #using actual length

S.gpa2d <- two.d.array(S.gpa)
categories2dS <- strsplit(rownames(S.gpa2d), "_")
classifiers2dS <- matrix(unlist(categories2dS), ncol=5, byrow=T)
colnames(classifiers2dS) <- c("ID", "Genus", "Group", "Species", "Sex")
classifiers2dS <- as.data.frame(classifiers2dS)

####Color-coding####
colors_sp <- ifelse(classifiers$Species=="Mo", "purple", ifelse(classifiers$Species=="Mx", "purple4",
ifelse(classifiers$Species=="S", "black", ifelse(classifiers$Species=="D", "gray", ifelse(classifiers$Species=="L",
"darkgreen", ifelse(classifiers$Species=="R", "mediumseagreen", ifelse(classifiers$Species=="Ni", "green",
ifelse(classifiers$Species=="Nat", "yellowgreen", ifelse(classifiers$Species=="W", "skyblue", "blue4")))))))))
#Mo/max purple/pink. leuc-ruf-nig-nat are greens, silv-dors are black and gray, and weyn-call are blues.
pch_sp <- ifelse(classifiers$Species=="Mo", 17, ifelse(classifiers$Species=="Mx", 2,
ifelse(classifiers$Species=="S", 15, ifelse(classifiers$Species=="D", 0, ifelse(classifiers$Species=="L", 9,
ifelse(classifiers$Species=="R", 1, ifelse(classifiers$Species=="Ni", 13, ifelse(classifiers$Species=="Nat", 16,
ifelse(classifiers$Species=="W", 8, 3)))))))))) #Mont and Max are triangles. Dors and Silv are squares. The red
duikers cluster is circles. Weyn and callipygus are asterisk and plus.
colors_2 <- ifelse(classifiers$Species=="L", "gray", "black")

##########Principle Components Analysis############
PCA <- plotTangentSpace(Y.gpa$coords, verbose = T, groups=colors_sp)
bgPCA <- mgPCA(Y.gpa2d, classifiers2d$Species, graph=TRUE)
```

```
s_PCA <- plotTangentSpace(S.gpa, verbose = T, groups=colors_sp)
s_bgPCA <- mgPCA(S.gpa2d, classifiers2dS$Species, graph=TRUE)



######Discriminant Function Analysis
###PCA
lda_PCA <- lda(classifiers$Species~PCA$pc.scores[,1:17], priors=c(.06,.15,.28,.06,.05,.05,.09,.03,.08,.15)/1,
CV=TRUE)
ct1 <- table(classifiers$Species, lda_PCA$class)
ct1_d <- diag(prop.table(ct1))
sum_PCA <- sum(diag(prop.table(ct1)))

###BgPCA
lda_bgPCA <- lda(classifiers2d$Species~bgPCA$Con.Data[,1:17],
priors=c(.06,.15,.28,.06,.05,.05,.09,.03,.08,.15)/1, CV=TRUE)
ct2 <- table(classifiers2d$Species, lda_bgPCA$class)
ct2_d <- diag(prop.table(ct2))
sum_bgPCA <- sum(diag(prop.table(ct2)))

####bgPCA*size
lda_bgPCA_s <- lda(classifiers2dS$Species~s_bgPCA$Con.Data[,1:17],
priors=c(.06,.15,.28,.06,.05,.05,.09,.03,.08,.15)/1, CV=TRUE)
ct3 <- table(classifiers2dS$Species, lda_bgPCA_s$class)
ct3 <- data.frame(ct3)
ct3_d <- diag(prop.table(ct3))
sum_bgPCA_S <- sum(diag(prop.table(ct3)))

####PCA*size
```

```
lda_PCA_s <- lda(classifiers$Species~s_PCA$pc.scores[,1:17], priors=c(.06,.15,.28,.06,.05,.05,.09,.03,.08,.15)/1,
CV=TRUE)
ct4 <- table(classifiers$Species, lda_PCA_s$class)
ct4_d <- diag(prop.table(ct1))
sum_PCA_S <- sum(diag(prop.table(ct4)))

###Getting out misclassification information####
write.csv(ct1, "C:/Users/l_PCA.csv")
write.csv(ct2, "C:/Users/ l_bgPCA.csv")
write.csv(ct3, "C:/Users/ l_bgPCAs.csv")
write.csv(ct4, "C:/Users/1_PCAs.csv")

ct1 <- data.frame(ct1)
colnames(ct1) <- c("Species", "Identified_As", "PCA_DFA")
ct2 <- data.frame(ct2)
colnames(ct2) <- c("Species", "Identified_As", "bgPCA_DFA")
ct3 <- data.frame(ct3)
colnames(ct3) <- c("Species", "Identified_As", "bgPCA_S_DFA")
ct4 <- data.frame(ct4)
colnames(ct4) <- c("Species", "Identified_As", "PCA_S_DFA")
rt1 <- data.frame(rt1)
colnames(rt1) <- c("Species", "Identified_As", "PCA_rt")
rt2 <- data.frame(rt2)
colnames(rt2) <- c("Species", "Identified_As", "PCA_S_rt")
rt3 <- data.frame(rt3)
colnames(rt3) <- c("Species", "Identified_As", "bgPCA_rt")
rt4 <- data.frame(rt4)
colnames(rt4) <- c("Species", "Identified_As", "bgPCA_S_rt")
```

```
output <- cbind(ct1,ct2,ct3,ct4,rt1,rt2,rt3,rt4)

write.csv(output, "C:/Users/mistakesrflda.csv")



######RandomForest

###PCA

RF_PCA <- randomForest(PCA$pc.scores[,1:17], classifiers$Species, na.action="na.omit", importance=TRUE)

RF_PCA_I <- data.frame(RF_PCA$importance)

rt1 <- table(classifiers$Species, RF_PCA$predicted)

rt1_d <- diag(prop.table(rt1))

rf_sum_PCA <- sum(diag(prop.table(rt1)))


###PCA*size

RF_PCA_s <- randomForest(s_PCA$pc.scores[,1:17], classifiers$Species, na.action="na.omit", importance=TRUE)

RF_I_PCA_s <- data.frame(RF_PCA_s$importance)

rt2 <- table(classifiers$Species, RF_PCA_s$predicted)

rt2_d <- diag(prop.table(rt2))

rf_sum_PCA_s <- sum(diag(prop.table(rt2)))


####bgPCA

RF_bgPCA <- randomForest(bgPCA$Con.Data[,1:17], classifiers$Species, na.action="na.omit",

importance=TRUE)

RF_I_bgPCA <- data.frame(RF_bgPCA$importance)

rt3 <- table(classifiers$Species, RF_bgPCA$predicted)

rt3_d <- diag(prop.table(rt3))

rf_sum_bgPCA <- sum(diag(prop.table(rt3)))


####bgPCA*size
```

```
RF_bgPCA_s <- randomForest(s_bgPCA$Con.Data[,1:17], classifiers$Species, na.action="na.omit",
importance=TRUE)
RF_I_bgPCA_s <- data.frame(RF_bgPCA_s$importance)
rt4 <- table(classifiers$Species, RF_bgPCA_s$predicted)
rt4_d <- diag(prop.table(rt4))
rf_sum_bgPCA_s <- sum(diag(prop.table(rt4)))

###Misclassification Tables
write.csv(rt1, "C:/rf_PCA.csv")
write.csv(rt2, "C:/rf_PCAs.csv")
write.csv(rt3, "C:/rf_bgPCA.csv")
write.csv(rt4, "C:/rf_bgPCAs.csv")

#######Mean PCA
M.PCA <- aggregate(PCA$pc.scores~classifiers$Species, FUN=mean) #Get the mean PC score for each
rownames(M.PCA) <-
c("Cephalophus_callipygus","Cephalophus_dorsalis","Cephalophus_leucogaster","Philantomba_monticola",
"Philantomba_maxwellii", "Cephalophus_natalensis",
"Cephalophus_nigrifrons","Cephalophus_rufilatus","Cephalophus_silvicultor","Cephalophus_weynsi")
MPCA <- data.matrix(M.PCA, rownames.force=T)

##Fix my tree####
trs<-read.nexus("cephconsensus.nex") #this is a polytomy tree
trs <- multi2di(trs) #make it binary
c.tree <-treedata(trs, MPCA, sort=T) #combine with data


#####Tree Diagram #####
```

```
library(plotrix)
trs <-read.nexus("cephconsensus.nex") #this is a polytomy tree
trs <- multi2di(trs) #make it binary
means <- read.morphologika("means.txt")
means.gpa <- gpagen(means)
#make all my means#
l <- subset(classifiers$Size, classifiers$Species=="L")
max <- subset(classifiers$Size, classifiers$Species=="Mx")
mont <- subset(classifiers$Size, classifiers$Species=="Mo")
D <- subset(classifiers$Size, classifiers$Species=="D")
W <- subset(classifiers$Size, classifiers$Species=="W")
C <- subset(classifiers$Size, classifiers$Species=="C")
Ni <- subset(classifiers$Size, classifiers$Species=="Ni")
Nat <- subset(classifiers$Size, classifiers$Species=="Nat")
S <- subset(classifiers$Size, classifiers$Species=="S")
R <- subset(classifiers$Size, classifiers$Species=="R")
means_size <-
c(mean(l),mean(max),mean(mont),mean(D),mean(W),mean(C),mean(Ni),mean(Nat),mean(S),mean(R))
names_size <-
c("Cephalophus_leucogaster","Philantomba_maxwellii","Philantomba_monticola","Cephalophus_dorsalis","Cephal
ophus_weynsi","Cephalophus_callipygus","Cephalophus_nigrifrons","Cephalophus_natalensis","Cephalophus_silvi
cultor","Cephalophus_rufilatus")
means_size <- data.frame(means_size)
row.names(means_size) <- names_size
d.tree <-treedata(trs, means_size, sort=T)
pdatmatch<-d.tree[[2]]
ptrmatch<-d.tree[[1]]
plot.phylo(ptrmatch, type="phylogram", edge.width=.5, label.offset=1, use.edge.length=FALSE)
```

```
tiplabels(pch=16,  col="black", cex=as.numeric(pdatmatch/6))
tiplabels(pch=as.character(means_size), col="white", cex=.5)

plotGMPhyloMorphoSpace(trs, means.gpa$coords, tip.labels = FALSE, node.labels = FALSE, xaxis = 2, yaxis = 1,
zaxis = NULL,plot.param=list(n.cex=.3,t.cex=1,txt.cex=1), shadow = FALSE)

means <- read.morphologika("codenamesmeans.txt")
means.gpa <- gpagen(means)
means.gpa2d <- two.d.array(means.gpa$coords)
PCA_means <- plotTangentSpace(means.gpa$coords, verbose=T)
saved <- trs$tip.label
trs$tip.label <- c("CALL", "DORS", "LEUC", "NAT", "NIG", "RUF", "SILV", "WEYN", "MAX", "MONT")

par(mfrow=c(2,2))
phylomorphospace(trs, PCA_means$pc.scores[,c(1,2)], A=NULL, label=c("horizontal"), node.size=c(.57,2),
xlim=c(-.08, .08))
phylomorphospace(trs, PCA_means$pc.scores[,c(3,4)], A=NULL, label=c("horizontal"), node.size=c(.57,2),
xlim=c(-.05, .05))
phylomorphospace(trs, PCA_means$pc.scores[,c(5,6)], A=NULL, label=c("horizontal"), node.size=c(.57,2),
xlim=c(-.04, .04))
phylomorphospace(trs, PCA_means$pc.scores[,c(7,8)], A=NULL, label=c("horizontal"), node.size=c(.57,2),
xlim=c(-.03, .03))

###Cluster Analysis ####
library(mclust)
fit <- Mclust(Y.gpa2d)
fit2 <- Mclust(PCA$pc.scores[])
fit_s <- Mclust(classifiers$Size)
```

```
fit_MV_s <- Mclust(S.gpa2d)
summary(fit)
summary(fit2)
summary(fit_s)
summary(fit_MV_s)

dimens <- duikers2d[,c(1)]
plot(fit, dimens=duikers2d[,c(1)], what="density")
plot(fit2, what="density")
plot(fit_s, what="density")

plot(fit, dimens, what="scatterplot", colors)

library(pvclust)
classifiers2d$Species2 <- ifelse(classifiers2d$Species=="L", "LEUC", ifelse(classifiers2d$Species=="Nat", "NAT",
ifelse(classifiers2d$Species=="C", "CALL", ifelse(classifiers2d$Species=="Ni", "NIG",
ifelse(classifiers2d$Species=="W", "WEYN", ifelse(classifiers2d$Species=="S", "SILV",
ifelse(classifiers2d$Species=="D", "DORS", ifelse(classifiers2d$Species=="Mx", "MAX",
ifelse(classifiers2d$Species=="Mo", "MONT", "R")))))))))
row.names(Y.gpa2d) <- classifiers2d$Species2
Y.gpa2dT <- t(Y.gpa2d)

fit_pv <- pvclust(Y.gpa2dT)
fit_pv2 <- pvclust(Y.gpa2dT, method.hclust="ward",method.dist="euclidean")
fit_pv3 <- pvclust(Y.gpa2dT, method.hclust="single")
fit_pv4 <- pvclust(Y.gpa2dT, method.hclust="centroid")
fit_pv5 <- pvclust(Y.gpa2dT, method.hclust="single", method.dist="euclidean")
fit_pv6 <- pvclust(Y.gpa2dT, method.hclust="ward")
```

```
par(mfrow=c(2,2))
plot(fit_pv, cex=.4) # dendogram with p values
pvrect(fit_pv, alpha=.95)

plot(fit_pv2, cex=.4) # dendogram with p values
pvrect(fit_pv2, alpha=.95)

plot(fit_pv3, cex=.4) # dendogram with p values
pvrect(fit_pv3, alpha=.95)

plot(fit_pv4, cex=.4) # dendogram with p values
pvrect(fit_pv4, alpha=.95)

par(mfrow=c(1,1))
plot(fit_pv5) # dendogram with p values
pvrect(fit_pv5, alpha=.95)

plot(fit_pv6) # dendogram with p values
pvrect(fit_pv6, alpha=.95)



###Bayesian Information Criterion Plots####
par(mfrow=c(3,1))
plot(fit, what = "BIC", xlab = "Number of Estimated Components of Coordinate Data", cex=1.5)
plot(fit_s, what = "BIC", xlab = "Number of Estimated Components of Skull Length", cex=1.5)
plot(fit_MV_s, what = "BIC", xlab = "Number of Estimated Components of Scaled Coordinate Data", cex=1.5)
```

```
par(mfrow=c(1,1))



####Histogram of Size and Density####
hist(classifiers$Size, breaks=60, col="gray", xlab="", ylab="", ylim=c(0,15), xlim=c(10,30), yaxt='n', main="")
axis(4)
mtext("Count", side=4)
par(new=TRUE)
plot(fit_s, what = "density", xlab="Size, cm", ylim=c(0,15), xlim=c(10,30), main="", lwd=2) # plot results



####PCA figures
pch_sp <- ifelse(classifiers$Species=="Mo", 17, ifelse(classifiers$Species=="Mx", 2,
ifelse(classifiers$Species=="S", 15, ifelse(classifiers$Species=="D", 0, ifelse(classifiers$Species=="L", 15,
ifelse(classifiers$Species=="R", 1, ifelse(classifiers$Species=="Ni", 13, ifelse(classifiers$Species=="Nat", 16,
ifelse(classifiers$Species=="W", 8, 3)))))))) #Mont and Max are triangles. Dors and Silv are squares. The red
duikers cluster is circles. Weyn and callipygus are asterisk and plus.
colors_2 <- ifelse(classifiers$Species=="L", "gray", "black")

par(mfrow=c(3,1))
plot(PCA$pc.scores[,1], PCA$pc.scores[,2], pch=pch_sp, cex=1, col=colors_2, asp=T, main="PCA", xlab="PC1",
ylab="PC2")
legend("topright", legend=c("CALL", "DORS", "LEUC", "MAX", "MONT", "NAT", "NIG", "RUF", "SILV",
"WEYN"), pch=c(3, 0, 15, 2, 17, 13, 1, 15, 8), col=colors_2)
plot(mPCA$Data[,1], mPCA$Data[,2], pch=pch_sp, cex=1, col=colors_2, asp=T, main="Between-Groups PCA",
xlab="PC1", ylab="PC2")
plot(s2PCA$Data[,1], s2PCA$Data[,2], pch=pch_sp, cex=1, col=colors_2, asp=T, main="Between-Groups PCA
scaled by Skull Length", xlab="PC1", ylab="PC2")
```

APPENDIX C

R SCRIPT FOR CHAPTER III

```
library(MASS)
library(base)
library(dplyr)
library(stats)
library(mixtools)
library(diptest)
library(ape)
library(phytools)
library(rncl)
library(dip.test)

Skulls <- read.csv("TS1 Fossil Data.csv")
colnames(Skulls) <- c("juv", "Speciman", "Wear", "Diastema", "Museum Species", "HT", "JODA", "SK",
"Toothrow", "Premolar", "Molar", "IFW", "OW", "OH", "OL", "Malar", "PostorbW", "Braincase", "LacLength",
"LacDepth", "P2.P2", "Height", "Zyg", "Postglen", "Face", "NotFace", "Baxis", AB", "AM", "ZygRt", "MaxNotch",
"IF", "Paroc", "Occipit", "Well", "Ripple", "PalateStop", "PalateShape", "Bullae", "PostglenoidShp")
Skulls <- Skulls %>%
  filter(juv!="Juv") %>%
  filter(Code_Name!="Agriochoerus")

attach(Skulls)
dip.test(Diastema)
dip.test(SK)
dip.test(Molar)
dip.test(Premolar)
```

```
dip.test(IFW)

dip.test(OW)

dip.test(OH)

dip.test(LacLength)

dip.test(LacDepth)

dip.test(Postglen)

dip.test(P2.P2)

dip.test(Braincase)

dip.test(PostorbW)

dip.test(Malar)

dip.test(OL)

dip.test(Zyg)

dip.test(AB)


hist(Diastema)

hist(SK)

hist(Molar)

hist(Premolar)

hist(IFW)

hist(OW)

hist(OH)

hist(LacLength)

hist(LacDepth)

hist(Postglen)

hist(P2.P2)

hist(Braincase)

hist(PostorbW)

hist(Malar)
```

```
hist(OL)
hist(Zyg)
hist(AB)



detach(Skulls)

PCAdata <- na.omit(Skulls[,8:24])
Lac <- ifelse(PCAdata$LacDepth>.8, "Black", "Gray")
fit <- princomp(PCAdata, cor=TRUE)
plot(fit$scores[,1]~fit$scores[,2], col=Lac, pch=16)
plot(fit$scores[,2]~fit$scores[,3], col=Lac, pch=16)

PCAdata <- Skulls
Lacrimaletc <- PCAdata[,c("LacDepth", "LacLength")]
LD <- PCAdata[,c("LacDepth")]
LL <- PCAdata[,c("LacLength")]
Lacrimaletc <- as.matrix(Lacrimaletc)
LD <- as.matrix(LD)
LL <- as.matrix(LL)
Test <- boot.comp(Lacrimaletc, x=NULL, N=NULL, max.comp=2, B=100, sig=.06, mix.type=c("multmix"),
hist=TRUE)
LLtest <- boot.comp(LL, x=NULL, N=NULL, max.comp=4, B=100, sig=.06, mix.type=c("normalmix"),
hist=TRUE)
LDtest <- boot.comp(LD, x=NULL, N=NULL, max.comp=2, B=1000, sig=.1, mix.type=c("repnormmix"),
hist=TRUE)
```

```
all <- na.omit(PCAdata[,c("SK", "Height", "Zyg")])
all <- as.matrix(all)
Test <- boot.comp(all, x=NULL, N=NULL, max.comp=6, B=100, sig=.06, mix.type=c("mvnormalmix"),
hist=TRUE)

normalmixEM(LD, k=2, maxit=1000)
multmixEM(Lacrimaletc, k=2, maxit=1000)

##CORRELATION####
summary(lm((Skulls$Face~Skulls$SK)))
summary(lm((Skulls$Zyg~Skulls$SK)))
summary(lm((Skulls$Height~Skulls$SK)))
summary(lm((Skulls$P2.P2~Skulls$SK)))
summary(lm((Skulls$OH~Skulls$OL)))
summary(lm((Skulls$Premolar~Skulls$Molar)))
cor(Skulls$SK~Skulls$Zyg)



############################
####Teeth Dataset
############################
teeth <- read.csv("Table 2.S3 Teeth.csv")
UTeeth <- teeth[,c(15:17,24:26)] #Upper molar dimensions
UTeeth <- na.omit(UTeeth)
UTeeth <- as.matrix(UTeeth)
Test <- boot.comp(UTeeth, x=NULL, N=NULL, max.comp=6, B=100, sig=.06, mix.type=c("mvnormalmix"),
hist=TRUE)
```

```
LTeeth <- teeth[,c(33:35,42:44)] #Lower molar dimensions
LTeeth <- na.omit(LTeeth)
LTeeth <- as.matrix(LTeeth)
Test <- boot.comp(LTeeth, x=NULL, N=NULL, max.comp=6, B=100, sig=.06, mix.type=c("mvnormalmix"),
hist=TRUE)

P4 <- na.omit(teeth$U.P4.AP)
Test <- boot.comp(P4, x=NULL, N=NULL, max.comp=6, B=100, sig=.06, mix.type=c("normalmix"), hist=TRUE)



########################
###FIGURES###
########################

#Skull dimensions
par(mfrow=c(3,2))
plot(Skulls$Face~Skulls$SK, pch=16, cex=1.5, xlab="Skull Length, cm [CV=7.38]", ylab="Orbit to Incisors, cm
[CV=10.76]")
abline(lm((Skulls$Face~Skulls$SK)))
legend("bottomright", c("R2= .62", "E= .50*"))
plot(Skulls$Zyg~Skulls$SK, pch=16, cex=1.5, xlab="Skull Length, cm [CV=7.38]", ylab="Zygmatic Breadth, cm
[CV=9.81]")
abline(lm((Skulls$Zyg~Skulls$SK)))
legend("bottomright", c("R2= -.05", "E= .07"))
plot(Skulls$Height~Skulls$SK, pch=16, cex=1.5, xlab="Skull Length, cm [CV=7.38]", ylab="Muzzle Depth, cm
[CV=10.64]")
abline(lm((Skulls$Height~Skulls$SK)))
legend("bottomright", c("R2= .15", "E= .12*"))
```

```
plot(Skulls$P2.P2~Skulls$SK, pch=16, cex=1.5, xlab="Skull Length, cm [CV=7.38]", ylab="Muzzle Width, cm [CV=9.19]")
abline(lm((Skulls$P2.P2~Skulls$SK)))
legend("bottomright", c("R2= .47", "E= .21*"))
plot(Skulls$OH~Skulls$OL, pch=16, cex=1.5, xlab="Orbital Length, cm [CV=8.24]", ylab="Orbital Height, cm [CV=10.64]")
abline(lm((Skulls$OH~Skulls$OL)))
legend("bottomright", c("R2= .34", "E= .87*"))
plot(Skulls$Premolar~Skulls$Molar, pch=16, cex=1.5, xlab="Premolar Row Length, cm [CV=10.38]", ylab="Molar Row Length, cm [CV=9.96]")
abline(lm((Skulls$Premolar~Skulls$Molar)))
legend("bottomright", c("R2= .57", "E= .75*"))

#PLOTS with paroccipital shapes
par(mfrow=c(1,1))
col_paroc <- ifelse(Skulls$Paroc==0, "gray", ifelse(Skulls$Paroc=="?", "White", "black"))
plot(Skulls$Zyg~Skulls$SK, xlab="Skull Length, cm", ylab="Zygomatic Breadth, cm", col=col_paroc, pch=16, cex=1.5)

parshape <- Skulls %>%
  filter(Paroc != "?") %>%
  select(Paroc, Zyg, SK)
summary(aov(parshape$SK~parshape$Paroc))
summary(aov(parshape$Zyg~parshape$Paroc))
summary(lm(Skulls$P2.P2~Skulls$SK))
plot(Skulls$P2.P2~Skulls$SK)

####Does diastema dictate maxillary notch?
```

```
par(mfrow=c(1,2))
maxilla.color <- ifelse(Skulls$MaxNotch==0, "Black", ifelse(Skulls$MaxNotch==1, "Gray", "White"))
plot(Skulls$Diastema~Skulls$SK, pch=16, cex=1.5, col=maxilla.color, xlab="Skull Length, cm", ylab="C1:P1 Diastema, cm")
legend("topleft", pch=c(16,16), col=c("black", "gray"), c("Maxillary Notch At or Before P1", "Maxillary Notch After P1"))
plot(Skulls$Premolar~Skulls$SK, pch=16, cex=1.5, col=maxilla.color, xlab="Skull Length, cm", ylab="Premolar Length, cm")

#Pre-Orbital Fossa Distributions
par(mfrow=c(2,2))
hist(Skulls$LacLength, breaks=20, xlab="Pre-Orbital Fossa Length, cm", col="Gray", main="")
hist(Skulls$LacDepth, breaks=20, xlab="Pre-Orbital Fossa Depth, cm", col="Gray", main="")
plot(Skulls$LacDepth~Skulls$LacLength, pch=16, cex=1.5, xlab="Pre-Orbital Fossa Length, cm", ylab="Pre-Orbital Fossa Depth, cm")
arrows(2.25,.3,2.25,1.65, col="gray", angle=90, length=0, code=1)
plot(Skulls$LacLength~Skulls$LacDepth, pch=16,  cex=1.5, ylab="Pre-Orbital Fossa Length, cm", xlab="Pre-Orbital Fossa Depth, cm")
arrows(.82,1.3,.82,3, col="gray", angle=90, length=0, code=1)
par(mfrow=c(1,1))



###CV Line Plots
CVs <- read.csv("CV dental measurements.csv")

UAP <- CVs %>%
  filter(Maxornot == "Maxilla") %>%
```

```
  filter(type == "AP")
UT <- CVs %>%
  filter(Maxornot == "Maxilla") %>%
  filter(type == "T")
LAP  <- CVs %>%
  filter(Maxornot == "Mandible") %>%
  filter(type == "AP")
LT <- CVs %>%
  filter(Maxornot == "Mandible") %>%
  filter(type == "T")
label <- c("C1", "P1","P2", "P3", "P4", "M1", "M2", "M3")
par(mfrow=c(2,2))
plot(UAP$CV~UAP$Number, type="b", xaxt='n', xlab="", ylab="Coefficient of Variation %", ylim=c(0,20),
main="Upper Anterior-Posterior")
axis(side=1, 1:8, labels=label, cex.axis=1.2, las=2, tck=-.05)
plot(UT$CV~UT$Number, type="b", xaxt='n', xlab="", ylab="Coefficient of Variation %", ylim=c(0,20),
main="Upper Transverse")
axis(side=1, 1:8, labels=label, cex.axis=1.2, las=2, tck=-.05)
plot(LAP$CV~LAP$Number, type="b", xaxt='n', xlab="", ylab="Coefficient of Variation %", ylim=c(0,20),
main="Lower Anterior-Posterior")
axis(side=1, 1:8, labels=label, cex.axis=1.2, las=2, tck=-.05)
plot(LT$CV~LT$Number, type="b", xaxt='n', xlab="", ylab="Coefficient of Variation %", ylim=c(0,20),
main="Lower Transverse")
axis(side=1, 1:8, labels=label, cex.axis=1.2, las=2, tck=-.05)



####TREES
tree <- read_nexus_phylo("tree.nex")
```

```
par(mfrow=c(1,1))
hmm <- cophylo(tree$`tnt 1`,tree$`tnt 2`, assoc=NULL, rotate=TRUE)
plot(hmm)



col_paroc <- ifelse(Skulls$Paroccipital==0, "Red", ifelse(Skulls$Paroccipital=="?", "White", "black"))

##########################################
#MODERN COMPARATIVE TESTS AND SUCH#
##########################################
Modern <- read.csv("Data2016.5M.csv")
sexinfo <- read.csv("modernwork.csv")
sexinfo <- sexinfo %>%
  select(Sex, Number)
Modern <- merge.data.frame(Modern, sexinfo, by="Number")



Hylo <- Modern%>%
  filter(Species=="Hylochoerus")
Munt <- Modern%>%
  filter(Species=="Muntiacus muntjak")
Reev <- Modern%>%
  filter(Species=="Muntiacus reevesi")
Muntiacus <- rbind(Munt, Reev) %>%
  select(LacLength,LacDepth) %>%
  as.matrix()
Leuc <- Modern%>%
  filter(Species=="Cephalophus leucogaster")
```

```
Weyn <- Modern%>%
  filter(Species=="Cephalophus weynsi")
Cephalophus <-  rbind(Leuc, Weyn) %>%
  select(LacLength, LacDepth) %>%
  as.matrix()




Test <- boot.comp(Cephalophus, x=NULL, N=NULL, max.comp=4, B=100, sig=.06, mix.type=c("mvnormalmix"),
hist=TRUE)
Test <- boot.comp(Muntiacus, x=NULL, N=NULL, max.comp=4, B=100, sig=.06, mix.type=c("mvnormalmix"),
hist=TRUE)

###########Figures for Modern #############
Cephalophus <-  rbind(Leuc, Weyn) %>%
  select(Species, Sex, PFLength, PFDepth)
Muntiacus <- rbind(Munt, Reev) %>%
  select(Species, Sex, PFLength,PFDepth)

muntsp <- ifelse(Muntiacus$Species=="Muntiacus muntjak", "Black", "Gray")
cephsp <- ifelse(Cephalophus$Species=="Cephalophus leucogaster", "Black", "Gray")
muntsx <- ifelse(Muntiacus$Sex=="Male", 17, ifelse(Muntiacus$Sex=="Female", 16, 8))
cephsx <- ifelse(Cephalophus$Sex=="Male", 17, ifelse(Cephalophus$Sex=="Female", 16, 8)) #Females are circle,
males are triangles

par(mfrow=c(2,2))
```

```
hist(Cephalophus$PFLength, col="gray", main="Cephalophus", xlab="Pre-Orbital Fossa Length, cm", breaks=15)
hist(Muntiacus$PFLength, col="gray", main="Muntiacus", xlab="Pre-Orbital Fossa Length, cm", breaks=15)
plot(Cephalophus$PFLength,Cephalophus$PFDepth, cex=1.5, col=cephsp, pch=cephsx, xlab="Pre-Orbital Fossa
Length, cm", ylab="Pre-Orbital Fossa Depth, cm")
arrows(4.05,.6,4.05,1.2, col="gray", angle=90, length=0, code=1)
legend(3.8,1.13, c("Colors indicate species"))
plot(Muntiacus$PFLength,Muntiacus$PFDepth, cex=1.5, col=muntsp, pch=muntsx, xlab="Pre-Orbital Fossa
Length, cm", ylab="Pre-Orbital Fossa Depth, cm")
arrows(3.6,.6,3.6,1.5, col="gray", angle=90, length=0, code=1)
legend(3.5,.95, pch=c(17,16,8), c("Male", "Female", "Unknown"))
par(mfrow=c(1,1))

par(mfrow=c(2,2))
hist(Cephalophus$PFDepth, col="gray", main="Cephalophus", xlab="Pre-Orbital Fossa Depth, cm", breaks=15)
hist(Muntiacus$PFDepth, col="gray", main="Muntiacus", xlab="Pre-Orbital Fossa Depth, cm", breaks=15)
plot(Cephalophus$PFLength~Cephalophus$PFDepth, cex=1.5, col=cephsp, pch=cephsx, ylab="Pre-Orbital Fossa
Length, cm", xlab="Pre-Orbital Fossa Depth, cm")
arrows(.93,3,.93,5, col="gray", angle=90, length=0, code=1)
legend(.91,4.4, c("Colors indicate species"))
plot(Muntiacus$PFLength~Muntiacus$PFDepth, cex=1.5, col=muntsp, pch=muntsx, ylab="Pre-Orbital Fossa
Length, cm", xlab="Pre-Orbital Fossa Depth, cm")
arrows(1.25,2,1.25,4, col="gray", angle=90, length=0, code=1)
legend(1.29,2.8, pch=c(17,16,8), c("Male", "Female", "Unknown"))
par(mfrow=c(1,1))

#Hylo
hist(Hylo$IF_Width, breaks=5)
hist(Hylo$OrbW, breaks=5)
```

```
hist(Hylo$OrbH, breaks=5)

hist(Hylo$OrbL, breaks=5)

hist(Hylo$Malar, breaks=5)

hist(Hylo$Braincase, breaks=5)

hist(Hylo$Skull, breaks=5)

hist(Hylo$basicranial, breaks=5)

hist(Hylo$Zyg, breaks=5)



#Munt

hist(Munt$IF_Width, breaks=5)

hist(Munt$OrbW, breaks=5)

hist(Munt$OrbH, breaks=5)

hist(Munt$OrbL, breaks=5)

hist(Munt$Malar, breaks=5)

hist(Munt$Braincase, breaks=5)

hist(Munt$PFLength, breaks=5)

hist(Munt$PFDepth, breaks=5)

hist(Munt$Premolars, breaks=5)

hist(Munt$molars, breaks=5)

hist(Munt$Skull, breaks=5)

hist(Munt$basicranial, breaks=5)

hist(Munt$Zyg, breaks=5)

ModLac <- Munt[,c(9,10)]

ModLac <- as.matrix(ModLac)

ModLac <- na.omit(ModLac)
```

```
Test <- boot.comp(ModLac, x=NULL, N=NULL, max.comp=2, B=100, sig=.06, mix.type=c("mvnormalmix"),
hist=TRUE)
plot(Munt$PFLength~Munt$PFDepth)
```

APPENDIX D

SUPPLEMENTARY TABLE 2.1

Table S1.1. Measured data. Acronyms: L, Length; W, Width.

Museum	#	Species	L P2	L P3	L P4	L M1	L M2	L M3	W P2	W P3	W P4	W M1	W M2	W M3
AMNH	14889	*Ovis dalli*				1.68	2.06					1.05	1.19	
AMNH	14517	*Ovis dalli*				1.82						1.04		
AMNH	128025	*Ovis dalli*				1.8	1.82					0.98	1	
MCZ	11508	*Ovis dalli*				1.81						1.02		
MCZ	34514	*Ovis dalli*				1.84	2.14					1.1	1.04	
AMNH	123038	*Ovis dalli*	0.89	1.02	1.18	1.63	1.75		0.75	0.87	1.06	1.11	1.19	
MCZ	16280	*Ovis dalli*	0.69	0.79	0.94	1.71	1.87		0.7	0.83	0.96	1.12	1.04	
AMNH	31403	*Ovis dalli*	0.63	0.88	0.84	1.33	1.8	2.19	0.62	0.85	1.04	1.16	1.17	1.1
AMNH	123042	*Ovis dalli*					1.56	2.18					1.16	1.1
AMNH	128026	*Ovis dalli*			0.96	1.69	1.7	2.13			1.08	1.16	1.37	1.2
AMNH	129329	*Ovis dalli*	0.69	0.76		1.5	1.86	1.97	0.77	1.01		1.33	1.15	0.97
MCZ	35940	*Ovis dalli*	0.53	0.74	1.07	1.7	1.66	1.84	0.66	0.91	0.96	1.11	1.19	1.04
MCZ	37010	*Ovis dalli*	0.58	0.92	0.96	1.66	1.87	2.26	0.64	0.88	0.98	1.16	1.19	1.15
MCZ	16279	*Ovis dalli*	0.74	0.9	0.92	1.66	1.75	1.94	0.76	0.91	1.01	1.18	1.09	1.04
AMNH	16224	*Ovis dalli*	0.57	0.85	0.9	1.31	1.7	2.24	0.7	0.91	1.09	1.22	1.22	1.18
AMNH	125579	*Ovis dalli*	0.71	0.86	0.99	1.49	1.78	1.87	0.6	0.86	0.93	1.16	1.12	1.06
AMNH	19031	*Ovis dalli*	0.72	0.87	0.91	1.53	1.77	1.89	0.72	0.8	0.92	1.08	1.09	0.95
MCZ	35941	*Ovis dalli*	0.67	0.88	1.02	1.69	1.77	2.01	0.75	0.88	0.98	1.18	1.14	1.09
AMNH	123039	*Ovis dalli*	0.86	0.87	1.03	1.53	1.99	1.88	0.77	0.88	1.06	1.19	1.22	1.06
AMNH	19032	*Ovis dalli*		0.75		1.24	1.82	2.09		0.95		1.26	1.34	1.11
AMNH	14888	*Ovis dalli*		0.78	0.88	1.2	1.46	1.79		0.67	0.95	1.13	1.23	1.07
MCZ	25862	*Muntiacus muntjak*	0.74	0.75	0.73	0.99	1.09	1.09	0.75	0.94	1.01	1.1	1.22	1.25
MCZ	25863	*Muntiacus muntjak*	1.04		0.99	1.19	1.49	1.39	1.02		1.15	1.21	1.49	1.58
MCZ	6034	*Muntiacus muntjak*				0.94	0.96					1.14	1.17	
MCZ	38633	*Muntiacus muntjak*				1.13	1.35					1.33	1.42	
MCZ	6962	*Muntiacus muntjak*				1.08	1.13					1.09	1.22	
MCZ	13682	*Muntiacus muntjak*				1.26	1.41	1.39				1.5	1.53	1.41
MVZ	184217	*Muntiacus muntjak*	0.74	0.66	0.51	0.78	0.88	0.92	0.76	0.84	0.85	1.1	1.16	1.04
MCZ	13163	*Muntiacus muntjak*	0.81	0.78	0.66	0.8	0.96	1.14	0.92	0.97	1.04	1.32	1.43	1.31
MCZ	38111	*Muntiacus muntjak*	1	0.95	0.84	1.07	1.29	1.28	1.08	1.18	1.18	1.44	1.52	1.53
MCZ	7955	*Muntiacus muntjak*	0.94	0.94	0.86	1.07	1.28	1.21	1.01	1.08	1.16	1.42	1.52	1.44
MCZ	35917	*Muntiacus muntjak*	0.83	0.77	0.77	0.99	1.13	1.16	0.88	1	1.02	1.17	1.21	1.14
MCZ	34245	*Muntiacus muntjak*	0.84	0.82	0.71			1.16	0.63	0.87	0.95			1.21
MCZ	13164	*Muntiacus muntjak*	1.02	0.96	0.89	0.97	1.23	1.34	0.92	1.03	1.16	1.23	1.43	1.28
MCZ	25989	*Muntiacus muntjak*	0.88	0.8	0.81	1.1	1.25	1.19	0.9	1.03	1.14	1.27	1.36	1.39

Museum	#	Species	L P2	L P3	L P4	L M1	L M2	L M3	W P2	W P3	W P4	W M1	W M2	W M3
MCZ	35918	*Muntiacus muntjak*	0.84	0.8	0.76	0.99	1.17	1.24	1.05	1.09	1.18	1.31	1.44	1.39
MCZ	1839	*Muntiacus muntjak*	0.93	0.88	0.96	1.05	1.27	1.3	0.93	1.02	1.13	1.31	1.42	1.37
MCZ	16485	*Muntiacus reevesi*				1.05						0.93		
MCZ	16024	*Muntiacus reevesi*				0.98						0.87		
MCZ	11544	*Muntiacus reevesi*				0.91	1.12					1.02	0.99	
MCZ	16484	*Muntiacus reevesi*	0.7	0.74	0.72	0.92	1.17	1.08	0.78	0.82	0.83	1.04	1.19	1.16
MCZ	16483	*Muntiacus reevesi*	0.78	0.71	0.58	0.74	0.98	1.01	0.77	0.89	0.94	1.08	1.17	1.12
MCZ	11543	*Muntiacus reevesi*	0.74	0.66	0.58	0.81	1.01	1.01	0.75	0.79	0.9	1.21	1.2	1.2
MCZ	16494	*Muntiacus reevesi*	0.78	0.68	0.68	0.86	1.01	1.02	0.68	0.79	0.87	1.01	1.09	1.09
MCZ	51183	*Muntiacus reevesi*	0.7	0.71	0.65	0.89	0.99	0.97	0.85	0.92	0.94	1.17	1.2	1.14
MCZ	25858	*Muntiacus reevesi*	0.74	0.68	0.65	0.89	1.04	1.05	0.76	0.85	0.87	0.92	1.08	1.11
MCZ	25860	*Muntiacus reevesi*	0.72	0.68	0.6	0.75	0.91	0.92	0.73	0.88	0.91	1.06	1.24	1.24
AMNH	52874	*Cephalophus dorsalis*		0.99	0.71	1.04	1.27	1.31		1	1.09	1.18	1.44	1.33
AMNH	52880	*Cephalophus dorsalis*		0.84		1.07	1.21	1.21		0.95		1.34	1.37	1.2
AMNH	52881	*Cephalophus dorsalis*	0.93	0.97	0.8	1.03	1.19	1.13	0.73	0.91	0.98	1.17	1.34	1.28
AMNH	52898	*Cephalophus dorsalis*	0.96	0.92	0.86	0.9	1.11	1.15	0.72	0.91	1.03	1.27	1.49	1.46
AMNH	52900	*Cephalophus dorsalis*	0.92	0.92	0.73	0.94	1.2	1.17	0.75	0.89	0.94	1.21	1.41	1.3
AMNH	52987	*Cephalophus dorsalis*	0.92	0.86	0.76	1	1.15	1.28	0.68	0.8	0.96	1.17	1.3	1.29
AMNH	55391	*Cephalophus dorsalis*	0.86	0.96	0.82	1.01	1.2	1.17	0.8	0.95	0.96	1.39	1.48	1.33
AMNH	55393	*Cephalophus dorsalis*	0.88	0.9	0.75	0.91	1.17	1.14	0.79	0.99	0.99	1.25	1.32	1.22
AMNH	89617	*Cephalophus dorsalis*	0.75	0.75	0.7	0.8	0.99	1.01	0.65	0.82	0.87	0.97	1.22	1.11
AMNH	89619	*Cephalophus dorsalis*	0.92	0.87	0.76	0.98	1.14	1.12	0.78	0.99	1.12	1.25	1.46	1.33
AMNH	52883	*Cephalophus dorsalis*	0.92	0.89	0.79	0.95	1.17	1.13	0.71	0.83	0.94	1.22	1.37	1.31
AMNH	52896	*Cephalophus dorsalis*	1.03	0.86	0.79	0.7	0.89	0.99	0.65	0.76	0.92	1.08	1.23	1.27
AMNH	52903	*Cephalophus dorsalis*		0.83	0.84	0.92	1.24	1.15		0.92	0.99	1.14	1.32	1.35
AMNH	52905	*Cephalophus dorsalis*	0.91	0.91	0.85	0.83	1.08	1.04	0.69	0.87	1.01	1.2	1.47	1.3
AMNH	52916	*Cephalophus dorsalis*	0.81	0.75	0.69	0.76	1.03	1.04	0.66	0.86	0.96	1.34	1.5	1.39
AMNH	100285	*Cephalophus dorsalis*		0.61	0.7	0.79	0.88	0.92		0.9	0.91	1.41	1.51	1.38
AMNH	119821	*Cephalophus dorsalis*	0.91	0.81	0.81	0.9	1.17	1.11	0.88	0.97	1.04	1.21	1.49	1.4
AMNH	52824	*Cephalophus leucogaster*				0.95	1.26	1.23				1.04	1.17	1.06
AMNH	52827	*Cephalophus leucogaster*				0.92	1.21	1.1				1.02	1.22	1.15
AMNH	52831	*Cephalophus leucogaster*				1.04	1.21	1.19				1.12	1.2	1.06
AMNH	52834	*Cephalophus leucogaster*	0.83	0.88		0.87	1.27	1.31	0.77	0.84		1.14	1.3	1.1
AMNH	52804	*Cephalophus leucogaster*	0.68	0.77	0.61	0.9	1.13	1.19	0.56	0.73	0.9	1.09	1.24	1.12
AMNH	52835	*Cephalophus leucogaster*	0.79	0.78	0.69	0.94	1.16	1.18	0.71	0.77	0.91	1.24	1.27	1.24
AMNH	52836	*Cephalophus leucogaster*	0.8	0.83	0.7	0.95	1.15	1.22	0.63	0.73	1	1.08	1.31	1.14
AMNH	52840	*Cephalophus leucogaster*	0.7	0.67	0.6	0.9	1.02	1.06	0.66	0.77	0.97	1.1	1.26	1.05
AMNH	52842	*Cephalophus leucogaster*	0.75	0.78	0.7	1.01	1.24	1.1	0.73	0.9	1	1.15	1.26	1.12
AMNH	52849	*Cephalophus leucogaster*	0.7	0.7	0.7	0.97	1.17	1.19	0.68	0.72	0.91	1.09	1.28	1.18
AMNH	52851	*Cephalophus leucogaster*	0.73	0.7	0.61	0.88	1.15	1.11	0.57	0.75	0.89	1.04	1.18	1.08

Museum	#	Species	L P2	L P3	L P4	L M1	L M2	L M3	W P2	W P3	W P4	W M1	W M2	W M3
AMNH	52852	*Cephalophus leucogaster*	0.75	0.75	0.64	0.99	1.18	1.15	0.75	0.78	0.91	1.11	1.31	1.18
AMNH	52787	*Cephalophus leucogaster*	0.73	0.82	0.66	0.81	1.03	1.07	0.61	0.72	0.86	1.12	1.2	1.18
AMNH	52789	*Cephalophus leucogaster*	0.8	0.8	0.7	0.83	1.05	1.15	0.68	0.81	0.88	1.1	1.32	1.12
AMNH	52793	*Cephalophus leucogaster*	0.85	0.8	0.81	0.98	1.19	1.11	0.67	0.75	0.92	1.13	1.28	1.2
AMNH	52797	*Cephalophus leucogaster*	0.82	0.86	0.77	0.86	1.14	1.19	0.77	0.83	0.96	1.04	1.24	1.24
AMNH	52801	*Cephalophus leucogaster*	0.8	0.78	0.67	1.01	1.18	1.23	0.68	0.81	0.99	1.27	1.3	1.19
AMNH	52802	*Cephalophus leucogaster*	0.84	0.88	0.8	0.84	1.11	1.2	0.63	0.82	0.99	1.12	1.29	1.33
AMNH	52841	*Cephalophus leucogaster*	0.8	0.68	0.62	0.71	1.03	1.09	0.57	0.55	0.92	1.11	1.25	1.19
AMNH	52844	*Cephalophus leucogaster*	0.72	0.74	0.7	0.79	1.04	1.13	0.64	0.71	0.91	1.02	1.26	1.24
AMNH	52845	*Cephalophus leucogaster*	0.72	0.7	0.68	0.8	0.98	1.07	0.68	0.71	0.86	1.11	1.28	1.2
AMNH	52853	*Cephalophus leucogaster*	0.59	0.68	0.67	0.7	1.01	1.18	0.65	0.7	0.85	1.17	1.34	1.24
AMNH	52854	*Cephalophus leucogaster*	0.85	0.79	0.74	0.81	1.12	1.25	0.63	0.74	0.99	1.13	1.44	1.31
AMNH	52861	*Cephalophus leucogaster*	0.77	0.73	0.73	0.84	1.18	1.14	0.7	0.76	0.89	1.2	1.34	1.24
AMNH	89391	*Cephalophus leucogaster*	0.81	0.89	0.73	1	1.24	1.2	0.7	0.86	0.97	1.13	1.41	1.21
MCZ	32598	*Cephalophus nigifirons*	0.81	0.75		1.02	1.23	1.22	0.67	0.77		1.08	1.26	1.15
MCZ	8094	*Cephalophus nigifirons*	0.82	0.84	0.73	0.96	1.26	1.15	0.75	0.8	1.02	1.26	1.37	1.21
MCZ	14735	*Cephalophus nigifirons*	0.81	0.82	0.83	0.98	1.24	1.29	0.72	0.82	0.9	1.11	1.28	1.26
MCZ	31774	*Cephalophus nigifirons*	0.77	0.73	0.72	0.99	1.14	1.13	0.57	0.71	0.82	1.13	1.26	1.07
MCZ	32430	*Cephalophus nigifirons*	0.83	0.81	0.74	0.95	1.18	1.18	0.64	0.77	0.94	1.05	1.32	1.23
MCZ	32449	*Cephalophus nigifirons*	0.9	0.92	0.8	1.08	1.43	1.31	0.71	0.92	1.04	1.29	1.49	1.25
MCZ	32596	*Cephalophus nigifirons*	0.89	0.8	0.75	1.14	1.27	1.3	0.75	0.8	1.03	1.18	1.32	1.38
MCZ	32597	*Cephalophus nigifirons*	0.82	0.8	0.74	1.05	1.31	1.3	0.69	0.79	0.88	1.14	1.31	1.2
MCZ	32599	*Cephalophus nigifirons*	0.84	0.87	0.76	0.95	1.18	1.28	0.7	0.77	1.03	1.2	1.47	1.3
MCZ	32615	*Cephalophus nigifirons*	0.87	0.82	0.79	0.88	1.19	1.2	0.73	0.8	0.97	1.17	1.38	1.34
MCZ	26841	*Cephalophus nigifirons*	0.84	0.82	0.84	0.82	1.13	1.19	0.73	0.81	0.99	1.09	1.39	1.33
MCZ	31811	*Cephalophus nigifirons*			0.63	0.76	0.95	1			0.96	1.09	1.3	1.25
MCZ	32429	*Cephalophus nigifirons*	0.96	0.91	0.88	0.91	1.23	1.37	0.77	0.85	1.03	1.13	1.47	1.35
MCZ	32451	*Cephalophus nigifirons*	0.79	0.76	0.7	0.81	1.11	1.24	0.6	0.91	1.02	1.22	1.59	1.46
MCZ	32453	*Cephalophus nigifirons*	0.85	0.81	0.79	0.85	1.16	1.27	0.77	0.92	1.06	1.22	1.46	1.33
MCZ	32613	*Cephalophus nigifirons*	0.88	0.82	0.79	0.84	1.13	1.22	0.76	0.83	1.04	1.28	1.49	1.47
MCZ	32614	*Cephalophus nigifirons*	0.84	0.75	0.7	0.9	1.15	1.1	0.72	0.77	0.99	1.1	1.41	1.27
AMNH	53125	*Cephalophus silvicultor*	1.2	1.19	1.19	1.58	1.89	2.03	1.14	1.41	1.5	1.66	2.03	2.02
AMNH	53129	*Cephalophus silvicultor*	1.16	1.15	1.01	1.52	1.81	1.96	0.99	1.27	1.44	1.7	1.94	1.82
AMNH	53136	*Cephalophus silvicultor*	1.34	1.31	1.28	1.66	1.99	1.99	1.11	1.43	1.64	1.78	2.09	1.69
AMNH	194296	*Cephalophus silvicultor*	1.17	1.3	1.29	1.53	1.58	1.8	0.96	1.31	1.65	1.68	1.84	1.87
MCZ	8018	*Cephalophus silvicultor*	1.48	1.44	1.13	1.66	1.98	2.14	1.17	1.47	1.66	1.97	2.31	2.06
MCZ	17723	*Cephalophus silvicultor*	1.25	1.33	1.16	1.45	1.73	1.72	1.08	1.31	1.5	1.84	1.87	1.84

Museum	#	Species	L P2	L P3	L P4	L M1	L M2	L M3	W P2	W P3	W P4	W M1	W M2	W M3
MCZ	32588	*Cephalophus silvicultor*	1.33	1.18	1.1	1.34	1.72	2.07	1.14	1.42	1.72	1.98	2.32	2.17
AMNH	53132	*Cephalophus silvicultor*	1.16	1.1	1.04	1.13	1.59	1.69	1.17	1.37	1.46	1.87	1.98	1.86
MCZ	18622	*Cephalophus silvicultor*	1.25	1.22	1.08	1.35	1.56	1.71	1.09	1.36	1.59	1.85	2.17	1.95
AMNH	53067	*Cephalophus weynsi*	0.71	0.8		1.1	1.31	1.31	0.61	0.77		1.15	1.34	1.15
AMNH	53030	*Cephalophus weynsi*	0.77	0.74	0.7	1.08	1.3	1.25	0.68	0.83	0.93	1.24	1.34	1.22
AMNH	53037	*Cephalophus weynsi*	0.85	0.81	0.75	1.05	1.34	1.31	0.64	0.82	1.05	1.23	1.41	1.2
AMNH	53041	*Cephalophus weynsi*	0.8	0.8	0.77	1.08	1.2	1.16	0.69	0.85	0.82	1.2	1.33	1.19
AMNH	53055	*Cephalophus weynsi*	0.86	0.76	0.78	1.15	1.4	1.34	0.71	0.81	0.97	1.27	1.55	1.35
AMNH	53058	*Cephalophus weynsi*	0.85	0.9	0.82	1.06	1.34	1.41	0.76	0.91	1.02	1.28	1.53	1.3
AMNH	53070	*Cephalophus weynsi*	0.75	0.8	0.76	1	1.27	1.17	0.69	0.81	0.99	1.18	1.38	1.25
AMNH	53026	*Cephalophus weynsi*	0.8	0.83	0.72	1.04	1.25	1.29	0.64	0.83	0.94	1.1	1.34	1.24
AMNH	53048	*Cephalophus weynsi*	0.86	0.87	0.75	1.03	1.29	1.27	0.67	0.72	0.89	1.2	1.36	1.21
AMNH	53049	*Cephalophus weynsi*	0.81	0.63	0.82	0.83	1.13	1.21	0.64	0.82	0.91	1.1	1.38	1.3
AMNH	53062	*Cephalophus weynsi*			0.75	0.79	0.99	1.11			1.01	1.32	1.55	1.47
AMNH	53066	*Cephalophus weynsi*	0.82	0.82	0.85	0.95	1.2	1.3	0.49	0.87	0.97	1.11	1.44	1.33
AMNH	53073	*Cephalophus weynsi*		0.65	0.67	0.73	0.99	1.31		0.72	0.88	1.25	1.31	1.26
MCZ	8091	*Philantomba monticola*				0.74						0.7		
MCZ	31610	*Philantomba monticola*				0.62	0.76					0.66	0.69	
MCZ	32490	*Philantomba monticola*				0.69	0.77					0.75	0.89	
MCZ	40956	*Philantomba monticola*				0.62	0.65					0.66	0.76	
AMNH	52739	*Philantomba monticola*	0.45	0.5	0.43	0.69	0.77	0.76	0.36	0.46	0.58	0.75	0.83	0.75
AMNH	170437	*Philantomba monticola*	0.5	0.57	0.5	0.67	0.74	0.79	0.4	0.43	0.58	0.74	0.83	0.79
MCZ	18618	*Philantomba monticola*	0.5	0.5	0.51	0.63	0.74	0.7	0.33	0.39	0.47	0.59	0.8	0.8
MCZ	23021	*Philantomba monticola*	0.5	0.51	0.51	0.72	0.84	0.82	0.42	0.54	0.65	0.84	0.88	0.84
MCZ	23079	*Philantomba monticola*	0.48	0.46	0.45	0.6	0.67	0.79	0.34	0.4	0.54	0.63	0.71	0.7
MCZ	31818	*Philantomba monticola*	0.48	0.53	0.47	0.64	0.77	0.78	0.45	0.47	0.55	0.75	0.85	0.75
MCZ	32196	*Philantomba monticola*	0.47	0.47	0.41	0.64	0.7	0.66	0.37	0.43	0.56	0.72	0.8	0.72
MCZ	32480	*Philantomba monticola*	0.54	0.55	0.5	0.67	0.75	0.82	0.43	0.45	0.56	0.71	0.84	0.83
MCZ	32602	*Philantomba monticola*	0.53	0.52	0.54	0.63	0.78	0.8	0.41	0.44	0.58	0.69	0.82	0.77
MCZ	32605	*Philantomba monticola*	0.45	0.51	0.46	0.67	0.77	0.85	0.4	0.51	0.65	0.7	0.84	0.78
MCZ	40957	*Philantomba monticola*	0.5	0.46	0.47	0.61	0.7	0.73	0.33	0.51	0.6	0.64	0.76	0.7
AMNH	170420	*Philantomba monticola*		0.43	0.45	0.52	0.64	0.75		0.38	0.57	0.77	0.87	0.87
AMNH	170430	*Philantomba monticola*	0.45	0.45	0.51	0.61	0.75	0.75	0.36	0.43	0.62	0.72	0.8	0.8
AMNH	170431	*Philantomba monticola*	0.51	0.53	0.48	0.55	0.69	0.79	0.4	0.47	0.58	0.68	0.78	0.77
MCZ	32603	*Philantomba monticola*	0.49	0.58	0.56	0.68	0.82	0.8	0.47	0.52	0.65	0.77	0.84	0.76
MCZ	32604	*Philantomba monticola*	0.49	0.51	0.49	0.49	0.63	0.65	0.35	0.37	0.48	0.66	0.78	0.75
MCZ	1135	*Lama guanicoe*				2.04	2.3					1.49	1.59	
MCZ	1050	*Lama guanicoe*		1.01	1.25	1.67	2.13	2.7		0.32	1.12	1.77	1.91	1.76
MCZ	1744	*Lama guanicoe*		0.84	1.31	1.96	2.48	2.15		0.68	1.21	1.74	1.59	1.52
MCZ	1745	*Lama guanicoe*		1.2	1.22	1.97	2.27	2.47		0.49	1.47	1.85	1.95	1.71
MCZ	1746	*Lama guanicoe*		0.76	1.22	1.89	2.11	2.15		0.56	1.22	1.78	1.73	1.59
MCZ	20972	*Lama guanicoe*		0.76	1.33	1.75	2.33	2.27		0.59	1.07	1.6	1.63	1.47

Museum	#	Species	L P2	L P3	L P4	L M1	L M2	L M3	W P2	W P3	W P4	W M1	W M2	W M3
MCZ	1134	*Lama guanicoe*			1.34	1.96	1.96	2.5			1.86	1.77	1.82	1.86
MCZ	1882	*Lama guanicoe*		0.6	1.24	1.78	1.64	2.45		0.4	1.03	1.62	1.75	1.92
MCZ	1884	*Lama guanicoe*		0.96	1.05	1.4	1.67	1.86		0.44	1.12	1.33	1.58	1.51
MCZ	5399	*Lama guanicoe*		1.27	1.35	1.69	2.03	2.33		0.53	1.23	1.66	1.87	1.84
MCZ	6171	*Lama guanicoe*		0.63	1.18	1.62	1.54	1.92		0.43	0.97	1.6	1.97	1.9
MCZ	19108	*Lama guanicoe*			1.43	1.7	2.16	2.79			1.06	2	2.07	1.82
MCZ	29878	*Lama guanicoe*		1.3	1.14	1.39	1.68	2.25		0.45	1.24	1.44	1.74	1.9
MCZ	61749	*Lama guanicoe*		0.94	1.05	1.6	2	2.15		0.6	1.34	2.05	2.18	1.9
MCZ	5243	*Vicugna vicugna*												
MCZ	5244	*Vicugna vicugna*												
MCZ	6170	*Vicugna vicugna*				1.95						1.29		
MCZ	7132	*Vicugna vicugna*				1.92						1.29		
MCZ	40983	*Vicugna vicugna*				1.79	1.85					1.06		
FMNH	49753	*Vicugna vicugna*				1.79						1.1		
AMNH	244136	*Vicugna vicugna*				1.73						1.09		
AMNH	15997	*Vicugna vicugna*				1.54	1.9					1.26	1.29	
MCZ	58030	*Vicugna vicugna*				1.58	1.86					1.18	0.96	
FMNH	92748	*Vicugna vicugna*				1.63	1.83					1.13	1.09	
AMNH	46	*Vicugna vicugna*		0.79	1.03	1.63	1.97	1.97		0.54	1.08	1.46	1.33	1.27
MCZ	7877	*Vicugna vicugna*				1.49	1.85					1.16	1.09	
FMNH	36047	*Vicugna vicugna*		0.52	0.95	1.32	1.76	1.73		0.44	0.81	1.31	1.17	1.09
FMNH	121665	*Vicugna vicugna*		0.7	0.79	1.37	1.62	1.81		0.36	1.06	1.32	1.33	1.2
MCZ	1883	*Vicugna vicugna*		0.66	0.98	1.33	1.77	1.82		0.42	0.91	1.41	1.63	1.36
MCZ	6167	*Vicugna vicugna*		0.81	1.06	1.21	1.61	1.82		0.45	0.91	1.35	1.48	1.37
MCZ	6168	*Vicugna vicugna*			0.99	1.22	1.68	1.82			0.69	1.41	1.64	1.5
MCZ	6169	*Vicugna vicugna*			0.87	1.12	1.26	1.69			0.71	1.34	1.39	1.43
FMNH	21505	*Vicugna vicugna*			1.02	1.04	1.24	1.71			0.72	1.27	1.4	1.46
MCZ	42785	*Vicugna vicugna*		0.58	0.89	1.46	1.61	1.78		0.37	0.84	1.45	1.32	1.13
MCZ	42923	*Vicugna vicugna*		0.47	0.78	1.21	1.29	1.69		0.4	0.96	1.42	1.32	1.35
AMNH	2911	*Camelus bactrianus*	0.89											
AMNH	14109	*Camelus bactrianus*	2.24	1.64	2.18	2.96	4.27	4.48	1.49	1.71	2.14	2.7	2.62	3.87
AMNH	14110	*Camelus bactrianus*	1.17	1.73	2.32	3.19	4.01	4.47	1.02	1.69	2.44	2.52	2.72	2.84
AMNH	14113	*Camelus bactrianus*	2.03	2.11	2.62	3.33	4.15	4.81	1.37	1.8	2.83	3.32	3.45	2.97
AMNH	80232	*Camelus bactrianus*	1.27	2.07	2.35	3.38	3.66	4.01	0.69	1.55	2.27	2.77	3.03	2.12
AMNH	80233	*Camelus bactrianus*	1.46	1.9	2.16	2.64	2.96	3.95	1.46	1.9	2.16	2.33	2.85	2.76
AMNH	90117	*Camelus bactrianus*	2.33	1.98	2.25	3.2	4.33	4.02	1.56	1.48	2.93	2.93	3.23	3.04
AMNH	90380	*Camelus bactrianus*	1.24			4.33			0.86			2.72		
AMNH	139842	*Camelus bactrianus*	2.08	2.12	2.16	3.12	3.98	4.76	1.45	2.09	3.08	3.41	3.07	3.07
FMNH	18847	*Camelus bactrianus*	1.43	1.85	2.15	2.73	3.4	4.46	0.95	1.7	2.44	2.71	2.72	2.51
FMNH	18848	*Camelus bactrianus*				4.25	5.02					2.66	2.63	
FMNH	21708	*Camelus bactrianus*	1.2	1.8	2.4	2.9	3.51	4.61	0.97	1.67	2.5	3.31	3.44	2.93
FMNH	60503	*Camelus bactrianus*	1.37	2.06	2.56	3.41	3.97	4.99	1.36	1.72	3.08	3.49	3.6	3.6
FMNH	64438	*Camelus bactrianus*	1.92	1.79	2.35	2.79	3.45	4.64	1.04	1.99	2.56	2.68	3.16	3.36

Museum	#	Species	L P2	L P3	L P4	L M1	L M2	L M3	W P2	W P3	W P4	W M1	W M2	W M3
VPL M	8822	*Camelus bactrianus*	2.61	1.67	2.24	4.07	4.23	5.08	1.69	1.85	2.86	3.53	4.2	4.1
MVZ	74673	*Camelus bactrianus*	1.03	2.06	2.65	4.5	4.76			1.84	2.65	3.18	3.06	
AMNH	14107	*Camelus dromedarius*	1.36	2.19	1.99	2.25	2.96	4.07	0.72	1.45	2.55	3.04	3.17	2.97
AMNH	14108	*Camelus dromedarius*				4.23						2.6		
AMNH	14111	*Camelus dromedarius*	1.78	1.94	2.41	2.83	3.45	4.5	1.05	1.77	2.57	3.31	3.35	3.02
AMNH	14112	*Camelus dromedarius*	1.06	1.59	1.86	2.34	3.49	3.96	0.74	1.66	2.31	3.16	3.2	2.74
AMNH	80198	*Camelus dromedarius*	1.85	2.14	2.34	2.48	3.17	4.24	0.93	1.64	2.46	2.73	2.94	2.57
AMNH	201157	*Camelus dromedarius*		2.06	2.53	3.05	3.76	4.72		1.82	2.83	2.91	3.05	2.8
FMNH	42446	*Camelus dromedarius*	0.92	1.62	1.95	2.55	3.43	4.18	0.69	1.64	2.28	3.05	3.09	2.66
FMNH	42447	*Camelus dromedarius*	1.25	2.05	2.33	2.83	3.14	4.16	0.58	1.76	2.49	3	3.35	3.02
FMNH	42448	*Camelus dromedarius*	0.9	1.65	2.19	2.63	3.38	4.24	0.67	1.44	2.23	2.63	3.38	2.64
FMNH	42449	*Camelus dromedarius*				3.76						2.71		
FMNH	42451	*Camelus dromedarius*	1.1	2.16	2.42	2.68	3.33	4.02	0.7	1.34	2.4	3.26	3.29	2.79
FMNH	129800	*Camelus dromedarius*	1.35	2.16	2.4	3.51	4.43	4.33	0.77	1.63	2.6	3.4	3.42	2.76
VPL M	4170	*Camelus dromedarius*	1.71	2.47	2.18	3.38	4.14	3.48	1.09	1.82	2.63	3.33	3.14	2.83
MCZ	1049	*Camelus dromedarius*	1.56	1.91	2.44	2.89	4.03	4.29	1.02	1.61	2.46	2.93	3.1	2.82
MCZ	8058	*Camelus dromedarius*	1.6	1.88	2.4	3	3.72	4.37	1.06	1.65	2.46	2.95	3.12	2.83
MCZ	10787	*Camelus dromedarius*		2.16	2.55	3.12	4.32	4.27		1.73	2.37	2.82	2.92	2.57
MCZ	16891	*Camelus dromedarius*	0.63	1.94	2.44	3.11	4.5			1.77	2.23	2.8	2.76	
MCZ	42152	*Camelus dromedarius*	1.1	1.58	2.3	2.39	2.95	3.91	0.6	1.6	2.28	2.63	3.05	3.06
MCZ	47405	*Camelus dromedarius*	1.15	2.07	1.89	2.49	3.03	3.88	0.76	1.84	2.31	3.29	3.25	2.81
MCZ	51314	*Camelus dromedarius*	1.27	2.31	2.16	2.89	3.74	4.08	0.74	1.44	2.32	2.96	3.29	2.79
MCZ	57837	*Camelus dromedarius*	1.41	2.1	2.08	2.92	3.6	4.38	0.86	1.78	2.73	3.17	3.36	3.21
MCZ	60131	*Camelus dromedarius*	2.21	2.49	2.1	2.51	2.96	4.24	1.6	2.23	2.76	3.11	3.56	3.54
MVZ	101026	*Camelus dromedarius*	1.25	1.8	2.32	3.62	4.22	4.36	0.88	1.62	2.57	3.02	2.87	2.57

APPENDIX E

SUPPLEMENTARY TABLE 2.2

Table S1.2. Measured data. Acronyms: L, Length; W, Width, H, Height. Measurement uncertainty also listed.

Museum	#	Species	W C1	W I3	H M1	Premolars	Molars	Toothrow	Uncertainty (m)
AMNH	14889	*Ovis dalli*							0.000098
AMNH	14517	*Ovis dalli*			0.8				0.000074
AMNH	128025	*Ovis dalli*							0.000185
MCZ	11508	*Ovis dalli*							0.0001
MCZ	34514	*Ovis dalli*			0.97				0.000185
AMNH	123038	*Ovis dalli*			1.06	3.03	5.5	8.26	0.000152
MCZ	16280	*Ovis dalli*			0.9	2.59			0.000125
AMNH	31403	*Ovis dalli*			1	2.33	5.24	7.36	0.000335
AMNH	123042	*Ovis dalli*							0.00026
AMNH	128026	*Ovis dalli*			1.26	2.59	5.53	7.93	0.000187
AMNH	129329	*Ovis dalli*			1.4	1.71	5.43	6.97	0.000026
MCZ	35940	*Ovis dalli*			0.95	2.52	5.23	7.6	0.000006
MCZ	37010	*Ovis dalli*			1.24	2.43	5.73	8.06	0.000181
MCZ	16279	*Ovis dalli*			0.89	2.56	5.53	7.82	0.000194
AMNH	16224	*Ovis dalli*			0.66	2.42	5.18	7.24	0.000056
AMNH	125579	*Ovis dalli*			0.82	2.47	5.05	7.39	0.000162
AMNH	19031	*Ovis dalli*			0.96	2.41	5.23	7.48	0.000091
MCZ	35941	*Ovis dalli*			1.18	2.67	5.61	8.08	0.000092
AMNH	123039	*Ovis dalli*			1.27	2.64	5.27	7.57	0.000647
AMNH	19032	*Ovis dalli*			1.7		4.97	6.73	0.000283
AMNH	14888	*Ovis dalli*			0.45	2.18	4.63	6.99	0.000098
MCZ	25862	*Muntiacus muntjak*	0.48		0.52	2.44	3.16	5.41	0.000057
MCZ	25863	*Muntiacus muntjak*			0.5	3.2	3.94	6.89	0.00003
MCZ	6034	*Muntiacus muntjak*							0.000052
MCZ	38633	*Muntiacus muntjak*	0.4		0.5				0.00012
MCZ	6962	*Muntiacus muntjak*							0.00009
MCZ	13682	*Muntiacus muntjak*			0.67		3.81		0.000083
MVZ	184217	*Muntiacus muntjak*			0.19	2.13	2.66	4.7	0.00146
MCZ	13163	*Muntiacus muntjak*	0.58		0.16	2.19	3.03	5.55	0.000108
MCZ	38111	*Muntiacus muntjak*			0.46	2.83	3.62	6.29	0.000082
MCZ	7955	*Muntiacus muntjak*			0.42	2.87	3.53	6.16	0.000013
MCZ	35917	*Muntiacus muntjak*	0.47		0.46	2.42	3.13	5.6	0.000185
MCZ	34245	*Muntiacus muntjak*							0.00011

Museum	#	Species	W C1	W I3	H M1	Premolars	Molars	Toothrow	Uncertainty (m)
MCZ	13164	*Muntiacus muntjak*	0.54		0.3	2.72	3.38	6.18	0.000105
MCZ	25989	*Muntiacus muntjak*			0.46	2.69	3.52	6.15	0.000064
MCZ	35918	*Muntiacus muntjak*	0.68		0.23	2.6	3.49	6.03	0.000068
MCZ	1839	*Muntiacus muntjak*			0.47	2.83	3.53	6.14	0.000044
MCZ	16485	*Muntiacus reevesi*							0.000009
MCZ	16024	*Muntiacus reevesi*			0.44				0.000082
MCZ	11544	*Muntiacus reevesi*			0.62				0.00005
MCZ	16484	*Muntiacus reevesi*	0.25		0.27	2.26	3.05	5.12	0.000176
MCZ	16483	*Muntiacus reevesi*	0.43		0.27	2.93	2.85	4.96	0.000137
MCZ	11543	*Muntiacus reevesi*	0.41		0.3	2.1	2.82	4.63	0.000072
MCZ	16494	*Muntiacus reevesi*	0.22		0.25	2.12	2.82	4.74	0.000112
MCZ	51183	*Muntiacus reevesi*	0.88		0.24	2.14	2.82	4.92	0.000082
MCZ	25858	*Muntiacus reevesi*	0.5		0.43	2.02	2.88	4.9	0.000123
MCZ	25860	*Muntiacus reevesi*	0.53		0.25	2.07	2.53	4.43	0.000112
AMNH	52874	*Cephalophus dorsalis*			0.62	2.83	3.38	5.95	0.000188
AMNH	52880	*Cephalophus dorsalis*			0.65		3.27		0.000028
AMNH	52881	*Cephalophus dorsalis*			0.57	2.8	3.19	5.79	0.000205
AMNH	52898	*Cephalophus dorsalis*			0.44	2.84	3.16	5.81	0.000223
AMNH	52900	*Cephalophus dorsalis*			0.5	2.74	3.13	5.74	0.000119
AMNH	52987	*Cephalophus dorsalis*			0.53	2.64	3.35	5.8	0.00015
AMNH	55391	*Cephalophus dorsalis*			0.5	2.61	3.35	5.78	0.00014
AMNH	55393	*Cephalophus dorsalis*			0.44	2.61	3.09	5.43	0.000111
AMNH	89617	*Cephalophus dorsalis*			0.4	2.2	2.84	4.92	0.000064
AMNH	89619	*Cephalophus dorsalis*			0.66	2.72	3.07	5.66	0.000133
AMNH	52883	*Cephalophus dorsalis*			0.54	2.56	3.24	5.53	0.000068
AMNH	52896	*Cephalophus dorsalis*			0.31	2.69	2.69	5.18	0.00017
AMNH	52903	*Cephalophus dorsalis*			0.48	2.82	3.17	5.75	0.000182
AMNH	52905	*Cephalophus dorsalis*			0.43	2.69	3.04	5.59	0.000192
AMNH	52916	*Cephalophus dorsalis*			0.48	2.33	2.88	5.16	0.000093
AMNH	100285	*Cephalophus dorsalis*			0.25		2.7		0.000132
AMNH	119821	*Cephalophus dorsalis*			0.38	2.68	3.13	5.58	0.000053
AMNH	52824	*Cephalophus leucogaster*			0.53		3.11		0.00007
AMNH	52827	*Cephalophus leucogaster*			0.49		3.12		0.000165
AMNH	52831	*Cephalophus leucogaster*			0.55		3.27		0.000053
AMNH	52834	*Cephalophus leucogaster*			0.62	2.86	3.45	5.89	0.000093
AMNH	52804	*Cephalophus leucogaster*			0.46	2.18	2.97	4.94	0.000113
AMNH	52835	*Cephalophus leucogaster*			0.51	2.39	3.09	5.25	0.000073
AMNH	52836	*Cephalophus leucogaster*			0.6	2.38	3.13	5.29	0.000186
AMNH	52840	*Cephalophus leucogaster*			0.54	2.21	2.76	4.79	0.000119
AMNH	52842	*Cephalophus leucogaster*			0.58	2.29	3.25	5.39	0.000099

Museum	#	Species	W C1	W I3	H M1	Premolars	Molars	Toothrow	Uncertainty (m)
AMNH	52849	*Cephalophus leucogaster*			0.5	2.36	3.13	5.25	0.000161
AMNH	52851	*Cephalophus leucogaster*			0.46	2.3	2.93	5.09	0.000071
AMNH	52852	*Cephalophus leucogaster*			0.54	2.39	3.14	5.36	0.000091
AMNH	52787	*Cephalophus leucogaster*			0.38	2.25	2.87	4.93	0.000111
AMNH	52789	*Cephalophus leucogaster*			0.41	2.29	2.91	5.17	0.000282
AMNH	52793	*Cephalophus leucogaster*			0.46	2.49	3.01	5.43	0.000104
AMNH	52797	*Cephalophus leucogaster*			0.37	2.17	3.01	5.06	0.000298
AMNH	52801	*Cephalophus leucogaster*			0.47	2.35	3.28	5.51	0.000117
AMNH	52802	*Cephalophus leucogaster*			0.25	2.55	3.18	5.52	0.000074
AMNH	52841	*Cephalophus leucogaster*			0.15	2.08	3.03	4.99	0.000259
AMNH	52844	*Cephalophus leucogaster*			0.41	2.31	3.14	5.23	0.000064
AMNH	52845	*Cephalophus leucogaster*			0.39	2.15	2.85	4.84	0.000079
AMNH	52853	*Cephalophus leucogaster*			0.38	2.26	3.05	5.18	0.000073
AMNH	52854	*Cephalophus leucogaster*			0.37	2.45	3.27	5.54	0.000162
AMNH	52861	*Cephalophus leucogaster*			0.37	2.25	3.09	5.1	0.000134
AMNH	89391	*Cephalophus leucogaster*			0.61	2.61	3.43	5.81	0.001729
MCZ	32598	*Cephalophus nigifirons*			0.57	2.55	3.23	5.5	0.000157
MCZ	8094	*Cephalophus nigifirons*			0.47	2.56	3.29	5.65	0.000106
MCZ	14735	*Cephalophus nigifirons*			0.43	2.5	3.24	5.47	0.000014
MCZ	31774	*Cephalophus nigifirons*			0.55	2.17	2.97	4.95	0.000849
MCZ	32430	*Cephalophus nigifirons*			0.57	2.36	3.12	5.33	0.000018
MCZ	32449	*Cephalophus nigifirons*			0.63	2.57	3.51	5.82	0.000084
MCZ	32596	*Cephalophus nigifirons*			0.69	2.48	3.52	5.75	0.000109
MCZ	32597	*Cephalophus nigifirons*			0.58	2.22	3.45	5.51	0.000088
MCZ	32599	*Cephalophus nigifirons*			0.46	2.44	3.27	5.52	0.000024
MCZ	32615	*Cephalophus nigifirons*			0.43	2.53	3.19	5.5	0.000016
MCZ	26841	*Cephalophus nigifirons*			0.37	2.43	3.18	5.51	0.000098
MCZ	31811	*Cephalophus nigifirons*			0.08		2.81		0.000004
MCZ	32429	*Cephalophus nigifirons*			0.45	2.52	3.42	5.69	0.000002
MCZ	32451	*Cephalophus nigifirons*			0.21	2.26	3.39	5.49	0.000107
MCZ	32453	*Cephalophus nigifirons*			0.28	2.5	3.21	5.39	0.000059
MCZ	32613	*Cephalophus nigifirons*			0.3	2.53	3.3	5.6	0.000187
MCZ	32614	*Cephalophus nigifirons*			0.45	2.3	3.1	5.18	0.000133
AMNH	53125	*Cephalophus silvicultor*			0.94	3.96	4.95	8.55	0.00012
AMNH	53129	*Cephalophus silvicultor*			0.85	3.85	4.93	8.65	0.00005
AMNH	53136	*Cephalophus silvicultor*			1.04	4.29	5.37	9.23	0.000226
AMNH	194296	*Cephalophus silvicultor*			0.92	3.89	4.77	8.49	0.000242

Museum	#	Species	W C1	W I3	H M1	Premolars	Molars	Toothrow	Uncertainty (m)
MCZ	8018	*Cephalophus silvicultor*			0.98	4.1	5.34	9.17	0.000201
MCZ	17723	*Cephalophus silvicultor*			0.83	3.64	4.79	8.24	0.00008
MCZ	32588	*Cephalophus silvicultor*			0.73	3.56	5.17	8.47	0.000131
AMNH	53132	*Cephalophus silvicultor*			0.53	3.48	4.57	7.8	0.000214
MCZ	18622	*Cephalophus silvicultor*			0.66	3.46	4.76	8.11	0.000171
AMNH	53067	*Cephalophus weynsi*			0.88	2.42	3.63	5.84	0.000102
AMNH	53030	*Cephalophus weynsi*			0.64	2.45	3.44	5.71	0.000017
AMNH	53037	*Cephalophus weynsi*			0.57	2.51	3.41	5.69	0.000188
AMNH	53041	*Cephalophus weynsi*			0.66	2.41	3.3	5.6	0.000008
AMNH	53055	*Cephalophus weynsi*			0.54	2.44	3.51	5.78	0.000183
AMNH	53058	*Cephalophus weynsi*			0.55	2.41	3.6	5.63	0.000064
AMNH	53070	*Cephalophus weynsi*			0.64	2.33	3.13	5.3	0.000037
AMNH	53026	*Cephalophus weynsi*			0.52	2.4	3.31	5.51	0.000162
AMNH	53048	*Cephalophus weynsi*			0.6	2.52	3.19	5.47	0.000265
AMNH	53049	*Cephalophus weynsi*			0.39	2.23	3.1	5.33	0.000242
AMNH	53062	*Cephalophus weynsi*			0.06		3.28	5.51	0.000126
AMNH	53066	*Cephalophus weynsi*			0.39	2.49	3.47	5.74	0.00001
AMNH	53073	*Cephalophus weynsi*			0.24		2.95		0.000019
MCZ	8091	*Philantomba monticola*			0.46				0.000084
MCZ	31610	*Philantomba monticola*			0.29				0.000051
MCZ	32490	*Philantomba monticola*							0.000017
MCZ	40956	*Philantomba monticola*							0.000014
AMNH	52739	*Philantomba monticola*			0.41	1.48	2.1	3.49	0.000075
AMNH	170437	*Philantomba monticola*			0.4	1.62	2.1	3.58	0.000084
MCZ	18618	*Philantomba monticola*			0.31	1.54	1.93	3.25	0.000121
MCZ	23021	*Philantomba monticola*			0.4	1.67	2.14	3.68	0.000051
MCZ	23079	*Philantomba monticola*			0.3	1.41	1.95	3.24	0.00007
MCZ	31818	*Philantomba monticola*			0.29	1.45	2.11	3.52	0.00009
MCZ	32196	*Philantomba monticola*			0.35	1.42	1.96	3.33	0.000152
MCZ	32480	*Philantomba monticola*			0.36	1.48	2.12	3.46	0.000061
MCZ	32602	*Philantomba monticola*			0.33	1.52	2.09	3.52	0.000076
MCZ	32605	*Philantomba monticola*			0.4	1.5	2.19	3.58	0.000131
MCZ	40957	*Philantomba monticola*			0.32	1.49	1.97	3.31	0.000018
AMNH	170420	*Philantomba monticola*			0.25	1.42	1.94	3.2	0.000094
AMNH	170430	*Philantomba monticola*			0.26	1.43	1.97	3.23	0.00007
AMNH	170431	*Philantomba monticola*			0.2	1.46	1.91	3.25	0.000193
MCZ	32603	*Philantomba monticola*			0.34	1.7	2.14	3.58	0.000097
MCZ	32604	*Philantomba monticola*			0.33	1.43	1.84	3.18	0.000027
MCZ	1135	*Lama guanicoe*	0.99		1.01				0.00058
MCZ	1050	*Lama guanicoe*	0.69	0.86	1.13	2.23	6.2	8.22	0.000105
MCZ	1744	*Lama guanicoe*	0.46	0.44	1.3	2.05	6.36	8.17	0.000072
MCZ	1745	*Lama guanicoe*	0.36	0.43	1.09	2.21	6.64	8.63	0.00014

Museum	#	Species	W C1	W I3	H M1	Premolars	Molars	Toothrow	Uncertainty (m)
MCZ	1746	*Lama guanicoe*	0.42	0.37	1.02	1.94	6.25	7.83	0.000566
MCZ	20972	*Lama guanicoe*		0.3	1.12	2.07	6.12	7.78	0.000133
MCZ	1134	*Lama guanicoe*	0.69	0.69	0.8	1.92	5.87	6.84	0.00027
MCZ	1882	*Lama guanicoe*	0.32	0.38	0.55	1.73	5.72	7.19	0.00018
MCZ	1884	*Lama guanicoe*	0.4	0.52	0.92	1.92	4.77	6.08	0.000133
MCZ	5399	*Lama guanicoe*	0.55	0.58	0.66	1.73	5.79	7.19	0.00031
MCZ	6171	*Lama guanicoe*	0.35	0.47	0.57	1.32	4.95	5.97	0.000025
MCZ	19108	*Lama guanicoe*	0.43	0.44	0.7		6.42	7.33	0.00016
MCZ	29878	*Lama guanicoe*	0.57	0.63	0.53	1.8	5.24	6.62	0.000096
MCZ	61749	*Lama guanicoe*	0.61	0.6	0.45	1.63	5.5	6.89	0.000147
MCZ	5243	*Vicugna vicugna*							0.00006
MCZ	5244	*Vicugna vicugna*							0.000068
MCZ	6170	*Vicugna vicugna*							0.000054
MCZ	7132	*Vicugna vicugna*							0.000055
MCZ	40983	*Vicugna vicugna*							0.000108
FMNH	49753	*Vicugna vicugna*			0.58				0.000054
AMNH	244136	*Vicugna vicugna*			0.47				0.000138
AMNH	15997	*Vicugna vicugna*	0.31	0.25	0.8				0.000121
MCZ	58030	*Vicugna vicugna*			0.58				0.000031
FMNH	92748	*Vicugna vicugna*			1.36				0.000026
AMNH	46	*Vicugna vicugna*	0.47	0.47	0.84	1.84	5.44	7.17	0.000146
MCZ	7877	*Vicugna vicugna*							0.000067
FMNH	36047	*Vicugna vicugna*	0.42	0.41	0.84	1.41	4.72	6.04	0.000047
FMNH	121665	*Vicugna vicugna*	0.39	0.39	0.66	1.31	4.52	5.77	0.000286
MCZ	1883	*Vicugna vicugna*	0.31	0.29	0.58	1.51	4.72	6.17	0.000091
MCZ	6167	*Vicugna vicugna*	0.31	0.31	0.42	1.47	4.38	5.55	0.000053
MCZ	6168	*Vicugna vicugna*	0.29	0.26	0.62	1.36	4.44	5.58	0.000101
MCZ	6169	*Vicugna vicugna*	0.44	0.44	0.51	1.12	3.92	4.96	0.000103
FMNH	21505	*Vicugna vicugna*	0.47	0.49	0.19	1.2	3.99	4.96	0.000126
MCZ	42785	*Vicugna vicugna*	0.28	0.3	0.93	1.25	4.7	5.68	0.000248
MCZ	42923	*Vicugna vicugna*	0.24	0.27	0.31	1.24	4.08	4.68	0.000098
AMNH	2911	*Camelus bactrianus*							0.000034
AMNH	14109	*Camelus bactrianus*	1.65		1.39	4.11	11.31	15.07	0.000237
AMNH	14110	*Camelus bactrianus*	1.14		2.28	3.9	11.26	14.76	0.000208
AMNH	14113	*Camelus bactrianus*	2.27		2.66	4.65	12	16.13	0.000093
AMNH	80232	*Camelus bactrianus*	0.97		1.96	4.39	10.57	14.78	0.000066
AMNH	80233	*Camelus bactrianus*	1.47		1.39	4.03	6.88	13.26	0.000203
AMNH	90117	*Camelus bactrianus*	2.71		0.53	4.19	11.31	14.86	0.00016
AMNH	90380	*Camelus bactrianus*			2.06				0.000198
AMNH	139842	*Camelus bactrianus*	2.2		1.89	4.68	11.84	17.06	0.000346
FMNH	18847	*Camelus bactrianus*	1.77		2.01	3.95	10.36	14.02	0.0004
FMNH	18848	*Camelus bactrianus*			2.55				0.000002
FMNH	21708	*Camelus bactrianus*	1.46		1.57	4.3	10.7	14.57	0.000126

Museum	#	Species	W C1	W I3	H M1	Premolars	Molars	Toothrow	Uncertainty (m)
FMNH	60503	*Camelus bactrianus*			2.33	4.45	12.14	15.96	0.000107
FMNH	64438	*Camelus bactrianus*	1.32		1.52	4.06	10.64	14.14	0.000072
VPL M	8822	*Camelus bactrianus*	3.14		2.28	4.55	13.06	17.15	0.000179
MVZ	74673	*Camelus bactrianus*			2.85	4.55			0.000233
AMNH	14107	*Camelus dromedarius*	0.98		0.83	3.98	9.5	13.45	0.000234
AMNH	14108	*Camelus dromedarius*	0.53		1.9				0.00017
AMNH	14111	*Camelus dromedarius*	1.64		1.8	4.35	10.45	14.82	0.000197
AMNH	14112	*Camelus dromedarius*	1.04		1.06	3.98	9.91	13.42	0.000016
AMNH	80198	*Camelus dromedarius*	1.65		1.59	4.45	10.02	14.24	0.000757
AMNH	201157	*Camelus dromedarius*			2.28	4.43	11.93	15.06	0.000583
FMNH	42446	*Camelus dromedarius*	0.85		1.72	3.79	10.21	13.87	0.000181
FMNH	42447	*Camelus dromedarius*	0.92		0.97	4.37	9.82	13.87	0.000094
FMNH	42448	*Camelus dromedarius*	0.93		1.45	4.27	10.02	13.78	0
FMNH	42449	*Camelus dromedarius*	0.5		1.74				0.00033
FMNH	42451	*Camelus dromedarius*	0.88		1.99	4.17	10.28	14.19	0.000112
FMNH	129800	*Camelus dromedarius*	1		2.3	4.52	8.98	15.59	0.000382
VPL M	4170	*Camelus dromedarius*	1.92		2.12	4.9	10.53	15.05	0.000074
MCZ	1049	*Camelus dromedarius*	1.64		2.25	4.35	10.87	14.87	0.00005
MCZ	8058	*Camelus dromedarius*	1.82		1.49	4.53	10.6	14.81	0.000058
MCZ	10787	*Camelus dromedarius*			2.47	4.64	11.02	15.33	0.000276
MCZ	16891	*Camelus dromedarius*	0.78		2.36	4.35			0.000097
MCZ	42152	*Camelus dromedarius*	0.83		1.1	3.88	8.95	12.55	0.000148
MCZ	47405	*Camelus dromedarius*	0.97		0.45	3.87	9.13	12.83	0.00006
MCZ	51314	*Camelus dromedarius*	0.93		2.2	4.37	10.39	14.4	0.000076
MCZ	57837	*Camelus dromedarius*	0.91		1.09	4.18	10.73	14.4	0.000017
MCZ	60131	*Camelus dromedarius*	2.32		0.49	5.27	9.23	13.48	0.000182
MVZ	101026	*Camelus dromedarius*	1.19		2.05	4.12	11.39	15.17	0.000548

APPENDIX F

SUPPLEMENTARY TABLE 4.1

Tables S3.1 – Discrete and continuous measurements of Eporeodon bullatus. Acronyms: IF, infraorbital foramen; POF, pre-orbital fossa; L, length; W, width; OR, orbit; SK, skull; Br, Braincase; BC, basicrania; AB, auditory bullae. This table is split up into several tables in this appendix because of size constraints. The full table in excel format is as supplementary data.

Speciman #	Wear stage (1-4)	Diastema	SK L	Tooth row	Premolar row	Molar row	Width at IF	O W	O H	O L	Malar Depth	Postorbital Width	Br W	POF L	POF D
AMNH FM 7402															
AMNH FM 7496	3.0	1.2	21.9	10.3	5.4	4.9	5.6	7.6	3.8	3.7	1.6	3.6	6.6	2.3	1.1
AMNH FM 7498	3.0	0.3	18.4	8.7	4.1	4.6	4.9	5.9	3.6	2.9	1.6	3.8	6.0	1.9	0.4
AMNH FM 7500	3.0	0.6	20.3	9.0	4.6	4.4	6.0	8.3	3.5	3.4	1.8	4.8	6.4	2.4	0.6
AMNH FM 7502	3.0	0.7	20.4	9.3	4.6	4.7	5.1	7.0	3.8	3.3	1.5	4.0	6.5	2.5	1.6
AMNH FM 7504	3.0	1.0	21.1	9.5	4.7	4.8	5.7	6.8			1.6	4.5	6.6	2.0	0.7
AMNH FM 7505	4.0	0.5	17.5	6.1	3.0	3.2	5.1	5.7	3.3	3.1	1.6	3.1	6.0	1.6	0.6
AMNH FM 7509	3.0	0.5	19.6	9.2	4.2	5.0	4.6	6.2	3.9	3.1	1.4	3.7	5.9	2.0	0.6
AMNH FM 7514	3.0						4.1	5.3	3.3	3.0	1.4	4.1	5.6	1.8	0.7
AMNH FM 7564	1.0	0.5	18.3				5.2	6.7	2.9	3.0	1.7	4.2	6.3	1.8	0.5
AMNH FM 7567	2.0	0.6	21.4	9.6	4.8	4.8	5.1	7.2	3.5	3.8	1.3	4.4	6.8	2.7	1.0
AMNH FM 7621	1.0	0.9					4.5	6.2	3.5	3.2	1.4	4.6	4.6	2.4	0.7
AMNH FM 7632	2.0	0.7	20.3	9.2	4.4	4.9	5.0	7.4	3.8	3.2	1.6	4.1	6.3	2.9	0.9
AMNH FM 7637	4.0	0.7	21.1	9.7	4.9	4.9	4.3	7.3	3.2	3.4	1.6	4.4		2.1	0.9
AMNH FM 7654	3.0	0.3	19.2	9.2	4.4	4.9	5.5	6.7	3.8	3.3	1.6	3.8	6.3	2.1	0.6
AMNH FM 7672	4.0	0.6	16.8	8.4	4.1	4.3	4.7	6.0	3.5	2.9	1.2	3.4	5.4	2.0	0.5
AMNH FM 7695	3.0	0.6	20.6	9.8	4.8	5.0	4.4	6.4	3.5	3.0	1.3	3.8	5.7	2.0	0.9
AMNH FM 7725	3.0	0.7	19.6	9.0	4.2	4.8	5.4	6.8	2.9	2.9	1.5	4.8	6.1	2.1	0.7
Burke S 51725	2.0	0.5	18.3	8.7	4.2	4.5	5.3	6.4	3.8	3.2	1.4	4.0	6.5	2.3	0.6
Burke S 58118	2.0		19.1	8.8	4.2	4.6	4.8	6.6	3.5	3.3	1.8	4.1	5.6	2.1	0.6
CM 1584	2.0		17.4	8.1	4.0	4.1	3.9	6.2	3.1	3.0	1.2	3.2	5.8	1.8	0.4
CM 725	1.0					4.7	4.5	5.8	2.9	2.9	1.7	3.4	5.7	1.7	0.4
FMNH 12725	2.0	0.9	18.2	9.2	4.7	4.5	4.9	7.1	3.0	3.0	1.4	3.9	6.4	1.4	0.3
FMNH P 26401	2.0	0.6	21.1	10.3	4.7	5.6	4.5	7.7	3.3	3.5	1.7	4.4	6.9	1.9	0.6
JODA 250	2.0	0.8	21.6	9.9	4.7	5.1	5.0	7.2	3.7	3.2	1.6	3.7	6.1	2.4	0.9

Speciman #	Wear stage (1-4)	Diastema	SK L	Tooth row	Premolar row	Molar row	Width at IF	O W	O H	O L	Malar Depth	Postorbital Width	Br W	POF L	POF D
UCMP 1911	2.0	0.7	20.0	8.5	4.1	4.4	5.3	7.0	4.0	3.5	1.5	4.0	6.4	2.0	0.7
UCMP 75280	4.0	0.6	19.9	8.8	4.3	4.4	5.0	6.1	2.8	3.0	1.8	4.0	6.1	1.9	0.6
UCMP 76529	3.0	0.7	21.6	10.4	5.2	5.2	5.0	7.0	4.1	3.4	1.6	4.3	6.3	2.6	1.1
YPM 10142	2.0					4.2	5.3	7.0	2.7	2.7	1.4	4.0	6.1	2.1	0.7
YPM 11016	2.0	0.6	18.4	8.1	4.0	4.0	4.8	5.8	3.3	3.0	1.5	3.7	6.2	2.0	0.6
YPM 13118	2.0	0.5	18.2	9.0	4.3	4.8	4.1	6.0	3.1		1.8	3.2	5.7	1.8	0.7
YPM 13119	2.0	0.7	18.5	9.2	4.4	4.8	3.9	5.9	3.2		1.6	3.5	4.9	2.0	0.7
YPM 13948	2.0	0.8	20.7	10.0	4.7	5.4	4.9	7.1	3.5	3.2	1.8	3.6	6.1	1.6	0.5

Speciman #	Palate Width at P2	Muzzle Height	Zygomatic Breadth	Width at Postglenoid Processes	O to Premaxilla	O to occipital condyle	BC Axis	AB H
AMNH FM 7402								
AMNH FM 7496	5.2	5.3	13.6	9.0	8.9	13.0	154.7	2.3
AMNH FM 7498	3.8	4.7	11.6	7.7	8.3	10.1	151.7	1.7
AMNH FM 7500	4.9	4.7		9.4	9.1	11.2	143.5	2.3
AMNH FM 7502	4.6	4.4	13.6	9.0	9.2	11.3	152.3	1.5
AMNH FM 7504	5.2	4.8		9.2	9.3	12.4	159.3	2.0
AMNH FM 7505	4.8	3.7	14.3	8.6	8.6	8.9	153.2	1.4
AMNH FM 7509	4.6	5.1	11.3	8.3	8.2	11.6	160.7	2.0
AMNH FM 7514			9.8	7.6				2.0
AMNH FM 7564			11.9	8.3	8.5	9.8	152.7	
AMNH FM 7567	4.9	5.0		8.8	9.6	11.9	152.3	2.0
AMNH FM 7621			10.5	8.1			148.7	1.9
AMNH FM 7632	4.6	4.7	12.5	8.4	8.0	12.3	159.2	1.8
AMNH FM 7637	4.8	5.2	13.1	8.1	9.2	11.9	153.0	1.8
AMNH FM 7654	5.0	5.2	13.4	8.7	8.7	10.5	145.5	1.7
AMNH FM 7672	4.0	4.4	12.8	8.1	6.1	10.7	155.3	2.0
AMNH FM 7695	4.3	4.0	11.2	8.1	8.2	12.5	151.0	2.1
AMNH FM 7725	5.1	4.1	14.3	8.6	8.4	11.3	146.2	1.4
Burke S 51725	4.6	4.5	12.8	9.2	6.7	11.6	148.4	2.0
Burke S 58118	4.8	5.1	12.9	8.8	8.3	10.8	149.4	1.7
CM 1584	4.3	4.5		7.6	7.1	10.3	155.6	2.0
CM 725				8.1			153.0	1.5
FMNH 12725	4.4	4.5	12.6	9.2	7.1	11.2	156.1	1.2
FMNH P 26401	4.9	5.4		9.5	8.0	13.1	150.8	2.0
JODA 250	5.1	4.7	13.3	9.1	9.5	12.1	157.0	1.8
UCMP 1911	4.8	4.6	15.2	9.1	8.9	11.1	170.4	2.0
UCMP 75280	4.8	4.9	13.1	8.6	8.5	11.5	156.2	2.0
UCMP 76529	5.4	5.0	13.1	8.6	9.7	11.9	157.5	2.1

Speciman #	Palate Width at P2	Muzzle Height	Zygomatic Breadth	Width at Postglenoid Processes	O to Premaxilla	O to occipital condyle	BC Axis	AB H
YPM 10142	4.4	3.2		8.0			166.3	2.0
YPM 11016	3.7	4.6	11.9	8.2	7.6	10.9	145.0	1.8
YPM 13118	4.3	5.1		6.7	7.8	10.4	153.8	1.6
YPM 13119	4.5	4.9		7.2	7.7	10.8	155.2	1.2
YPM 13948	5.2	5.2	12.5	8.7	9.4	11.4	148.7	2.0

Speciman #	Auditory Meatus Shape	Zygomatic root	Maxillary notch	IF placement	Parocciptial	Basiocciput Ridge	Enamel Well	Enamel Ridges	Palate End Point	Palate End Shane	Shape of Bullae	Postglenoid
AMNH FM 7402	0	1	0	0	0	0	0	0	0	0	1	0
AMNH FM 7496	2	1	0	1	0	0	0	1	2	?	0	1
AMNH FM 7498	1	1	0	1	1	1	0	0	2	0	1	1
AMNH FM 7500	?	1	0	1	1	1	0	0	2	0	0	1
AMNH FM 7502	3	0	0	1	1	1	0	0	2	0	1	1
AMNH FM 7504	3	1	?	0	0	1	0	0	2	0	0	1
AMNH FM 7505	0	1	0	2	1	1	?	?	2	0	1	1
AMNH FM 7509	0	1	0	2	1	1	0	0	2	0	0	1
AMNH FM 7514	2	?	?	?	1	1	?	?	?	?	0	1
AMNH FM 7564	0	?	?	?	1	1	?	?	2	?	?	1
AMNH FM 7567	1	0	0	0	1	1	0	1	2	?	0	1
AMNH FM 7621	2	?	?	?	1	1	?	?	2	0	1	1
AMNH FM 7632	3	0	0	0	1	0	1	0	2	0	0	1
AMNH FM 7637	2	1	1	1	0	1	0	0	2	0	0	1
AMNH FM 7654	3	1	0	1	1	1	0	0	2	0	0	1
AMNH FM 7672	3	0	?	0	1	1	0	0	2	0	1	1
AMNH FM 7695	3	2	1	1	0	1	1	0	2	?	0	1
AMNH FM 7725	0	0	?	1	1	0	0	0	2	0	1	1
Burke S 51725	3	1	0	0	1	1	0	1	2	0	1	1
Burke S 58118	3	1	0	0	1	1	0	0	2	0	0	1
CM 1584	0	1	0	0	1	1	1	0	1	0	0	1
CM 725	2	1	?	2	0	1	?	?	1	?	0	1
FMNH 12725	?	0	0	?	0	1	?	?	2	?	0	1
FMNH P 26401	?	1	?	0	1	1	?	?	2	0	0	1
JODA 250	3	2	1	1	0	0	0	0	2	0	0	1
UCMP 1911	3	0	0	1	1	1	0	1	2	0	1	1
UCMP 75280	0	1	0	1	1	1	0	0	2	0	1	1
UCMP 76529	3	0	0	1	0	1	1	1	2	?	0	1
YPM 10142	2	0	?	2	1	1	0	0	2	0	0	1
YPM 11016	3	0	0	2	1	1	0	1	2	0	1	1
YPM 13118	?	1	0	0	1	1	?	?	2	0	0	1

YPM 13119	2	0	0	0	1	1	?	?	1	1	1	1
YPM 13948	3	1	0	0	1	1	?	?	2	0	1	1

APPENDIX G

SUPPLEMENTARY TABLE 4.2

Table S3.2 – Comparative discrete and continuous measurements of extant artiodactyls. Acronyms: IF, infraorbital foramen; POF, pre-orbital fossa; L, length; W, width; OR, orbit; SK, skull; Br, Braincase; BC, basicrania; AB, auditory bullae.

Specimen #	Species	AB H	POF L	POF W	IF W	O W	O H	O L	Malar Depth	postorbital [illegible]	Br W	Premolar Row	Molar Row	SK L	O to premaxilla	O to occipital [illegible]	BC axis	Zygomatic W	Palate End	Palate Shape
AMNH 52836	*Cephalophus leucogaster*		3.5	0.8															After M2	U
AMNH 52787	*Cephalophus leucogaster*		3.5	0.9															After M2	V
AMNH 52789	*Cephalophus leucogaster*		3	1															At M3	U
AMNH 52793	*Cephalophus leucogaster*		3	0.8															After M2	V
AMNH 52797	*Cephalophus leucogaster*		3	1.0															After M2	V
AMNH 52801	*Cephalophus leucogaster*		4	1.0															After M2	V
AMNH 52802	*Cephalophus leucogaster*		5	1.0															M3	U
AMNH 52804	*Cephalophus leucogaster*		4	1.0															M3	V
AMNH 52824	*Cephalophus leucogaster*		1	0.9															After M2	W
AMNH 52827	*Cephalophus leucogaster*		2	0.6															After M2	V
AMNH 52831	*Cephalophus leucogaster*		9	1.0															After M2	U
AMNH 52834	*Cephalophus leucogaster*		4	0.9															Mid M2	V
AMNH 52835	*Cephalophus leucogaster*		5	0.9															after M2	U
AMNH 52840	*Cephalophus leucogaster*		3	1.0															At M1	V
AMNH 52841	*Cephalophus leucogaster*		3	0.8															After M3	U

Specimen #	Species	AB H	POF L	POF W	IF W	O W	O H	O L	Malar Depth	postorbital	Br W	Premolar Row	Molar Row	SK L	O to premaxilla	O to occipital	BC axis	Zygomatic W	Palate End	Palate Shape
AMNH 52842	*Cephalophus leucogaster*		3.7	1.1															M2	U
AMNH 52844	*Cephalophus leucogaster*		3.4	1.0															M3	U
AMNH 52845	*Cephalophus leucogaster*		3.2	0.9															M3	U
AMNH 52849	*Cephalophus leucogaster*		3.4	0.9															M2	V
AMNH 52851	*Cephalophus leucogaster*		3.3	1.1															M3	U
AMNH 52058	*Cephalophus weynsi*		3.6	0.8															After M2	V
AMNH 53026	*Cephalophus weynsi*		3.7	0.7															M3	V
AMNH 53030	*Cephalophus weynsi*		3.7	0.8															M2	V
AMNH 53037	*Cephalophus weynsi*		4.4	0.8															M3	U
AMNH 53041	*Cephalophus weynsi*		3.8	0.8															after M2	V
AMNH 53048	*Cephalophus weynsi*		3.9	0.7															After M2	U
AMNH 53049	*Cephalophus weynsi*		4.3	0.9															After M2	V
AMNH 53055	*Cephalophus weynsi*		4.3	0.9															After M2	V/U
AMNH 53062	*Cephalophus weynsi*		3.7	0.9															M3	U
AMNH 53066	*Cephalophus weynsi*		3.8	0.8															M2	V
AMNH 53067	*Cephalophus weynsi*		4.1	0.9															M3	U
AMNH 53070	*Cephalophus weynsi*		3.5	0.7															after M2	U
AMNH 53073	*Cephalophus weynsi*		3.7	0.9															after M2	V
AMNH 36431	*Hylochoerus meinertzhagheni*	4.8			6.2	9.8	4.1	4.1	6.3		10.5			36.3			132.7	20.3	After M3	W
AMNH 36438	*Hylochoerus meinertzhagheni*	4.2			6.3	11.0	4.0	4.2	6.2		11.6			36.6			138.0	21.1	After M3	W
AMNH 53665	*Hylochoerus meinertzhagheni*	4.4			4.6	9.6	3.9	4.4	4.8		8.7			34.9			135.5	18.6	After M3	W

Specimen #	Species	AB H	POF L	POF W	IF W	O W	O H	O L	Malar Depth	postorbital	Br W	Premolar Row	Molar Row	SK L	O to premaxilla	O to occipital	BC axis	Zygomatic W	Palate End	Palate Shape
AMNH 53670	*Hylochoerus meinertzhagheni*	4.1			5.6	9.1	4.2	4.5	4.9		8.8			33.3			146.2	17.6	After M3	U
AMNH 81803	*Hylochoerus meinertzhagheni*	4.4			6.0	10.5	4.2	4.4	5.8		10.7			32.6			142.0	20.1	After M3	U
AMNH 89456	*Hylochoerus meinertzhagheni*	3.8			5.6	10.4	4.9	4.0	6.4		9.1			33.2			137.0	21.8	After M3	U
AMNH No numfemale	*Hylochoerus meinertzhagheni*	4.0			5.6	9.7	4.7	4.2	5.0		8.2			35.3			142.3	18.9	After M3	U
AMNH No Number Male	*Hylochoerus meinertzhagheni*	4.7			6.2	10.8	4.1	4.4	7.5		10.5			37.7			149.5	26.4	After M3	W
MCZ 12410	*Hylochoerus meinertzhagheni*	3.5			5.1	8.6	4.1	3.9	3.6		7.7			28.1			144.9	16.4	After M3	W
MCZ 21202	*Hylochoerus meinertzhagheni*	4.5			5.2	9.8	4.3	4.0	4.8		9.3			34.7			157.5	18.5	After M3	W
MCZ 27851	*Hylochoerus meinertzhagheni*	4.9			6.8	11.7	4.3	4.4	8.4		11.1			37.0			143.8	26.4	After M3	W
MCZ 7955	*Muntiacus muntjak*		3.2	1.0	3.8	6.1	4.0	3.6	0.4		5.8	2.9	3.5				138.0	9.8	After M3	U
MCZ 1839	*Muntiacus muntjak*		3.2	1.0	3.5	5.5	3.6	3.7	0.4		5.7	2.8	3.5				142.7	8.8	At M3	W
MCZ 13164	*Muntiacus muntjak*		3.2	1.3	3.6	6.3	4.0	3.8	0.4		6.3	2.7	3.4	18.9			143.9	9.9	At M3	U
MCZ 13163	*Muntiacus muntjak*		2.8	0.9	3.4	5.3	3.6	3.7	0.2		5.8	2.2	3.0	17.9			137.9	8.6	After M3	W
MCZ 25862	*Muntiacus muntjak*		2.3	0.9	3.1	5.2	3.2	3.3	0.2		5.5	2.4	3.2	15.7			142.7	8.0	At M3	U
MCZ 25832	*Muntiacus muntjak*		2.3	1.0	3.4	5.6	3.4	3.4	0.3		5.9	3.2	3.9	17.7			145.4	9.5	At M3	U
MCZ 25989	*Muntiacus muntjak*		2.7	0.9	3.5	6.0	3.7	3.7	0.4		5.8	2.7	3.5	17.3			137.7	8.7	At M3	U
MCZ 34245	*Muntiacus muntjak*		2.6	0.8	3.1	4.7	3.5	3.5	0.2		5.3	2.4	3.1	17.3			140.9	8.0	After M3	U
MCZ 35917	*Muntiacus muntjak*		2.6	1.1	3.2	5.5	3.3	3.3	0.3		5.7	2.4	3.1	16.8			142.6	8.7	At M3	U/V
MCZ 35918	*Muntiacus muntjak*		2.9	1.0	3.6	6.2	3.5	3.5	0.4		5.9	2.6	3.5	18.1			130.3	8.6	After M3	W
MCZ 38111	*Muntiacus muntjak*		2.9	1.1	3.8	6.0	3.7	3.7	0.3		6.0	2.8	3.6				147.9	9.5	At M3	U/W
MVZ 184217	*Muntiacus muntjak*		2.6	0.9	3.0	4.7	3.0	2.9	0.2		4.8	2.1	2.7	13.7			142.9	7.1	After M3	V
MCZ 11544	*Muntiacus reevesi*		3.2	1.0															After M3	U

Specimen #	Species	AB H	POF L	POF W	IF W	O W	O H	O L	Malar Depth	postorbital	Br W	Premolar Row	Molar Row	SK L	O to premaxilla	O to occipital	BC axis	Zygomatic W	Palate End	Palate Shape
MCZ 16024	*Muntiacus reevesi*		2.2	0.8															After M3	U
MCZ 11543	*Muntiacus reevesi*		3.4	1.1															After M3	U
MCZ 16483	*Muntiacus reevesi*		3.5	1.2															After M3	U/V
MCZ 16484	*Muntiacus reevesi*		3.1	1.0															After M3	V
MCZ 16494	*Muntiacus reevesi*		3.0	1.1															After M3	W
MCZ 25858	*Muntiacus reevesi*		3.8	1.3															After M3	U/W
MCZ 25860	*Muntiacus reevesi*		3.1	1.4															After M3	U
MCZ 51183	*Muntiacus reevesi*		3.8	1.3															At M3	V
AMNH 244136	*Vicugna vicugna*	0.9																		U
FMNH 49753	*Vicugna vicugna*	1.2																		
MCZ 5243	*Vicugna vicugna*	1.2																		
MCZ 5244	*Vicugna vicugna*	1.0																		
MCZ 7877	*Vicugna vicugna*	1.1																		
MCZ 6170	*Vicugna vicugna*	1.4																		
MCZ 7132	*Vicugna vicugna*	1.5																		
MCZ 58030	*Vicugna vicugna*	1.3																		
AMNH 46	*Vicugna vicugna*	1.1																	M1	V
AMNH 15997	*Vicugna vicugna*	1.4																	M2	V
FMNH 21505	*Vicugna vicugna*	1.2																		U
FMNH 36407	*Vicugna vicugna*	1.2																	M2	U
FMNH 92748	*Vicugna vicugna*	1.0																		
FMNH 121665	*Vicugna vicugna*	0.8																		
MCZ 1883	*Vicugna vicugna*	1.4																		
MCZ 6167	*Vicugna vicugna*	1.6																		

Specimen #	Species	AB H	POF L	POF W	IF W	O W	O H	O L	Malar Depth	postorbital	Br W	Premolar Row	Molar Row	SK L	O to premaxilla	O to occipital	BC axis	Zygomatic W	Palate End	Palate Shape
MCZ 42923	*Vicugna vicugna*	0.7																		
MCZ 42785	*Vicugna vicugna*	0.9																		
MCZ 40983	*Vicugna vicugna*	1.2																		
MCZ 6169	*Vicugna vicugna*	0.9																		
MCZ 6168	*Vicugna vicugna*	1.2																		

APPENDIX H

SUPPLEMENTARY TABLE 4.3

Table S3.3 – Descriptions of discrete character states.

Character	0	1	2	3
Enamel Well on P4	Not Present	Present		
Ridges on Lingual Surface of the labial cone of P4	Not Present	Present		
Placement above Maxillary Notch	Anterior to P1	Posterior to P1		
Place where the anterior section of the zygomatic arch roots	M1	M2	M3	
Direction of the lateral edge of the paroccipital process	Parallel with the skull's axis	perpendicular to the skull's axis		
Ridge on the basiocciput	Absent	Present		
Shape of the end of the palate	U-shaped	V-shaped	W-shaped	
Ending point of the palate	At M2	At M3	After M3	
Shape of the auditory meatus	Square, short tube, or amorphous	Long tube or ridge	Triangle	Trumpet-shaped (triangular, flaring at the end)
Shape of the Auditory Bullae	Oval	Circular		
Postglenoid process shape	Peg-like, isolated from Bullae	Thick ridge that is close to or touching bullae		
Placement of the infraorbital foramen	Above P3	Between P3/P4	Above P4	Above M1

APPENDIX I

SUPPLEMENTARY TABLE 4.4

Table S3.4 – Teeth measurements data. Split into multiple tables for better legibility. Available as supplementary excel file.

Catalog #	U C H	U C1 L	U Diastema	U P1 L	U P2 L	U P3 L	U P4 L	U M1 L	U M2 L	U M3 L	U TRL
JODA 940											
JODA 12231											
JODA 1944											
JODA 16006							11.05				
JODA 374											
JODA 16148											
JODA 905	5.20		0.00	10.10							
JODA 4851											
JODA 7237											
JODA 10136											
JODA 16158											
JODA 15402											
JODA 13135											
JODA 1009											
JODA 6298											
JODA 7225											
JODA 849						11.68					
JODA 12261											
JODA 1955		x									
JODA 12253											
JODA 14045						12.18					
JODA 1214							10.14				
JODA 15417											
JODA 7744											
JODA 7918											
JODA 982						13.58					

Catalog #	U C H	U C1 L	U Diastema	U P1 L	U P2 L	U P3 L	U P4 L	U M1 L	U M2 L	U M3 L	U TRL
JODA 11558											
JODA 866											
JODA 3042							10.53				
JODA 1884											
JODA 6718											
JODA 15496								13.25			
JODA 6160											
JODA 14121								13.49			
JODA 1899								15.65			
JODA 938											
JODA 1369											
JODA 4838											
JODA 8634											
JODA 375											
JODA 4982									17.15		
JODA 6441									17.18		
JODA 6329										17.54	
JODA 1850										18.54	
JODA 16181										17.40	
JODA 14208											
JODA 1150											
JODA 6815										19.36	
JODA 751										18.12	
JODA 5852											
JODA 1379										19.61	
JODA 7748										19.42	
JODA 2802											
JODA 7460										20.09	
JODA 10805										21.05	
JODA 916										21.20	
JODA 4963											
JODA 4939											
JODA 15531				9.16				13.53			
JODA 7399											

Catalog #	U C H	U C1 L	U Diastema	U P1 L	U P2 L	U P3 L	U P4 L	U M1 L	U M2 L	U M3 L	U TRL
JODA 15449											
JODA 6467						11.64	9.99				
JODA 7429				10.13				16.25			
JODA 6816						11.31	10.73				
JODA 4202				11.20				15.28			
JODA 15802							10.07	13.03			
JODA 677											
JODA 3383							9.53	12.66			
JODA 16099							9.69	14.15			
JODA 16325											
JODA 7930											
JODA 7533											
JODA 14908											
JODA 4996											
JODA 1933											
JODA 6326								11.90		19.13	
JODA 2771	11.35	6.44	7.37								
JODA 1206		9.98	6.30	11.26	10.23						
JODA 16291								15.27	17.23		
JODA 3788				9.10				12.37			
JODA 15712								15.02	17.36		
JODA 2748								15.38	19.42		
JODA 7972											
JODA 684											
JODA 6588											
JODA 11564											
JODA 15807									16.39	18.16	
JODA 1770									17.16	20.09	
JODA 1406											
JODA 8619									17.04	20.27	
JODA 1426									16.81	22.04	
JODA 7992							13.47	14.81	18.36		
JODA 4865											

Catalog #	U C H	U C1 L	U Diastema	U P1 L	U P2 L	U P3 L	U P4 L	U M1 L	U M2 L	U M3 L	U TRL
JODA 839								11.00	14.90		
JODA 4938									19.42	22.12	
JODA 15975											
JODA 12067											
JODA 8599							11.54	13.52	16.01		
JODA 365				9.64		11.85	12.72		18.85		
JODA 2747											
JODA 379											
JODA 4335									12.98		74.59
JODA 7465											
JODA 13165											
JODA 7819		9.95		8.49	9.45	11.05	9.99	12.43	17.14		
JODA 7451											
JODA 10803								14.46	16.95		93.00
JODA 4201	13.27	6.05	3.95	9.17	8.95	10.50	11.03	13.57	16.04		
JODA 12080											
JODA 3741	12.23	7.47	5.66	10.56	11.48	14.47	11.94			19.42	
JODA 3349					9.80	10.66	10.15	13.69	17.29	19.60	
JODA 7438					12.80	12.26	11.30	12.90	17.17	22.63	
JODA 6317											
JODA 6631								13.63	14.12	17.57	98.00
JODA 1865							9.74	13.31	15.69	16.80	98.38
JODA 14111											
JODA 6612		7.87	4.95	10.91				18.06	21.39		114.00
JODA 7798						12.18	11.31	12.86	12.97	17.99	87.00
JODA 15358						10.34	10.32	13.81	16.46	17.54	
JODA 1892				9.80	10.50	9.92	9.03	12.98	15.35	14.46	88.00
JODA 10812				9.80	11.23	10.43	10.21	12.73	14.64	17.22	93.00
YPM 12420		8.43	7.82	5.90	10.52	9.42	8.88	10.68	13.40	13.42	86.22
JODA 7118	16.95	8.79	2.31	12.28				16.72	18.50	21.99	95.00
JODA 8765						12.37	10.09	14.67	18.55	22.37	105.59
JODA 6216											
AMNH FM 7821		11.29	5.71	9.77				12.13	17.08	20.12	106.91
JODA 10815						12.09	10.66	14.93	18.85	23.64	117.14

Catalog #	U C H	U C1 L	U Diastema	U P1 L	U P2 L	U P3 L	U P4 L	U M1 L	U M2 L	U M3 L	U TRL
JODA 10840	21.09	10.48				10.88	10.23	12.74	17.18	19.11	103.58
JODA 16335											
JODA 10824		10.52	6.79	9.38	10.02	10.66	9.63	11.76	15.79	19.52	104.37
JODA 10747	15.73	7.54	6.02	10.54	11.59	11.70		14.45	17.92	19.75	108.51
JODA 4200		10.04	7.05	11.14	10.90	10.71	10.22	12.64	16.07	19.21	105.16
JODA 910	15.61	10.93	6.29	9.79	9.66	10.19	10.12	11.69	14.20	18.88	100.31
JODA 3259	17.24	10.41	5.76		11.49	11.66	10.94	14.46	17.08	20.25	112.72
JODA 1945		9.61	7.73	9.85	9.69	11.69	10.24	12.14	14.79	19.05	118.27
JODA 3576	18.45	11.03	6.91	11.15	11.69	11.33	10.45	11.92	16.19	20.86	107.58
JODA 250		10.02	8.09	11.23	13.86	12.74	10.81	13.79	18.84	21.46	112.95
JODA 8642	17.34	10.92	7.32	10.14	10.90	10.61	9.34	12.65	16.88	19.00	105.71
JODA 1946		9.87	7.18	11.44	10.86	13.60	10.45	13.10	16.54	22.73	115.85
JODA 10809	18.24	9.09	7.06	10.50	12.45	12.49	11.62	12.37	17.42	21.61	109.38
JODA 10813	22.86	9.06	9.25	10.08	10.85	11.87	10.48	13.81	18.06	21.15	112.78
JODA 3012											
JODA 1886											
JODA 10757		11.85	5.76	9.97	11.01	10.82	9.73	14.73	17.75	19.62	105.53
JODA 12060											
JODA 1268											
JODA 1302								15.09	18.79		
JODA 1389											
JODA 3347											
JODA 3787		8.73	7.52	10.62	9.98	10.80	10.49	13.17	17.01	18.90	108.57
JODA 4323	18.00	7.93	4.84	8.96	12.29	11.27	9.59	11.07	14.30	18.52	94.63
JODA 4206	15.68	8.78	7.15	10.10	10.63	10.44	11.28	12.09	15.11	17.11	96.12
JODA 6315		10.21	3.29	11.78	13.55	12.80	11.72	15.64	18.92	22.78	109.51
JODA 10825	19.97	10.93	6.33	12.65	13.10	13.25	12.00	14.41	18.78	22.97	115.57

Catalog #	U C1 W	U P1 W	U P2 W	U P3 W	U P4 W	U M1 W	U M2 W	U M3 W	J P1 H	J C1 L	J P1 L	J P2 L	J P3 L	J P4 L
JODA 940														
JODA 12231														
JODA 1944														12.50

Catalog #	U C1 W	U P1 W	U P2 W	U P3 W	U P4 W	U M1 W	U M2 W	U M3 W	J P1 H	J C1 L	J P1 L	J P2 L	J P3 L	J P4 L
JODA 16006														
JODA 374							11.65							
JODA 16148					13.96									
JODA 905														
JODA 4851											10.69			
JODA 7237												10.73		
JODA 10136													12.02	
JODA 16158													12.65	
JODA 15402											12.13			
JODA 13135														
JODA 1009														
JODA 6298														
JODA 7225													14.03	
JODA 849				10.59										
JODA 12261														13.17
JODA 1955														14.09
JODA 12253														
JODA 14045				11.09										
JODA 1214					13.28									
JODA 15417														
JODA 7744														
JODA 7918														
JODA 982				11.60										
JODA 11558														
JODA 866														
JODA 3042					15.27									
JODA 1884									13.33		7.55			
JODA 6718														
JODA 15496						14.89								
JODA 6160														17.16
JODA 14121						15.03								
JODA 1899						12.97								
JODA 938												9.06	10.58	
JODA 1369														
JODA 4838														
JODA 8634														
JODA 375									13.60		11.96			
JODA 4982								16.79						
JODA 6441							17.14							
JODA 6329								17.36						
JODA 1850								16.58						
JODA 16181								17.78						

Catalog #	U C1 W	U P1 W	U P2 W	U P3 W	U P4 W	U M1 W	U M2 W	U M3 W	J P1 H	J C1 L	J P1 L	J P2 L	J P3 L	J P4 L
JODA 14208												10.74	12.24	
JODA 1150														
JODA 6815								18.04						
JODA 751								19.88						
JODA 5852														
JODA 1379								18.99						
JODA 7748								19.24						
JODA 2802														
JODA 7460								19.60						
JODA 10805								19.00						
JODA 916							19.92							
JODA 4963													12.51	13.23
JODA 4939													11.75	13.44
JODA 15531		5.48				14.48								
JODA 7399													13.50	13.65
JODA 15449									22.10		14.55			
JODA 6467				11.35	13.00									
JODA 7429		5.38				14.38								
JODA 6816				11.01	14.45									
JODA 4202		6.94				14.70								
JODA 15802					12.18	13.05								
JODA 677														
JODA 3383					13.50	14.42								
JODA 16099					12.19	15.95								
JODA 16325														
JODA 7930														
JODA 7533														
JODA 14908														
JODA 4996														
JODA 1933														
JODA 6326						13.04		17.75						
JODA 2771	10.46								9.25		11.26			
JODA 1206	9.77	7.28	8.14											
JODA 16291						14.36	16.32							
JODA 3788		3.71	5.99	9.00	10.88	13.70								
JODA 15712						15.72	18.23							
JODA 2748						15.34	17.71							
JODA 7972														
JODA 684									20.00		12.28			
JODA 6588														
JODA 11564														
JODA 15807							18.72	19.01						

Catalog #	U C1 W	U P1 W	U P2 W	U P3 W	U P4 W	U M1 W	U M2 W	U M3 W	J P1 H	J C1 L	J P1 L	J P2 L	J P3 L	J P4 L
JODA 1770							16.92	19.18						
JODA 1406									11.97		11.88	10.97	11.79	
JODA 8619							17.74	18.89						
JODA 1426							17.46	19.34						
JODA 7992					13.59	17.02								
JODA 4865													9.39	17.20
JODA 839						17.00	19.00	20.44						
JODA 4938							19.49	21.86						
JODA 15975												11.25	11.01	13.02
JODA 12067														
JODA 8599					14.22	16.55	18.56							
JODA 365		5.36		10.08	12.00		16.50							
JODA 2747											12.00	12.61	12.91	14.22
JODA 379									24.00		15.77			
JODA 4335								18.50						
JODA 7465										6.73	12.37	10.73	12.49	12.11
JODA 13165													12.80	12.05
JODA 7819					12.97	14.70	17.18							
JODA 7451									12.00		11.26	9.98	11.86	12.83
JODA 10803		5.21				14.58	14.56							
JODA 4201	6.93	5.18	5.89	8.24	11.65	14.95	17.23							
JODA 12080												11.83	13.54	
JODA 3741	11.19	6.88	8.72	8.55	14.46			20.45						
JODA 3349			7.89	9.54	14.05	14.50	17.85	19.01						
JODA 7438			8.38	11.28	14.09	16.05	19.05	19.04						
JODA 6317												11.35	13.12	14.91
JODA 6631						15.26	17.08	17.38						
JODA 1865					13.22	15.10	18.70	20.19						
JODA 14111									15.75		11.92			
JODA 6612	11.01	5.56				17.27	21.54							
JODA 7798				11.65	15.05	14.80	18.45	18.81						
JODA 15358				9.45	13.86	15.85	18.06	18.08						12.17
JODA 1892		6.03	7.62	9.21	11.34	13.29	15.33	16.73						
JODA 10812												10.80	8.83	10.72
YPM 12420	8.29	7.06	5.84	8.04	10.85	12.62	14.53	16.26						
JODA 7118	10.20	7.06				16.45	18.47	17.00						
JODA 8765				10.54	14.17	15.82	19.21	19.50						
JODA 6216													12.37	13.31
AMNH FM 7821	5.74	5.10	5.78	9.77	14.51	13.38	19.04	19.03						
JODA 10815				10.74	13.96	15.09	18.06	20.59						
JODA 10840	10.51			10.41	13.62	14.69	16.69	17.93						

Catalog #	U C1 W	U P1 W	U P2 W	U P3 W	U P4 W	U M1 W	U M2 W	U M3 W	J P1 H	J C1 L	J P1 L	J P2 L	J P3 L	J P4 L
JODA 16335												12.74	14.65	15.61
JODA 10824	13.38	4.99	6.84	10.05	10.58	14.19	17.31	18.88						
JODA 10747	9.88	6.17	7.66	10.97		15.39	18.82	20.53						
JODA 4200	11.90	6.06	8.08	10.42	13.89	15.24	19.86	20.42						
JODA 910	13.60	6.82	8.71	11.34	13.91	14.63	17.47	18.48						
JODA 3259	12.97		7.46	10.45	13.26	13.61	17.48	18.42						
JODA 1945	12.23	6.78	8.05	10.57	14.30	15.84	18.78	18.91						
JODA 3576	11.51	7.08	8.04	9.54	12.38	14.47	16.63	17.88						
JODA 250	10.58	7.34	8.05	10.27	13.30	14.91	18.95	19.01						
JODA 8642	13.99	6.56	8.04	10.69	14.21	15.86	17.95	18.78						
JODA 1946	10.98	6.50	9.20	10.66	13.49	14.95	18.86	20.76						
JODA 10809	9.61	5.30	7.25	10.05	13.32	14.28	16.70	18.29						
JODA 10813	11.85	7.14	7.97	10.10	13.30	13.98	17.72	18.26						
JODA 3012											13.53		14.19	14.60
JODA 1886									8.43	8.22	10.76	11.90	12.24	13.07
JODA 10757	11.92	5.43	9.03	10.19	13.23	15.50	17.92	18.40					11.93	11.83
JODA 12060														
JODA 1268											10.35	10.53	12.65	12.59
JODA 1302						14.58	16.84			7.56	13.21	10.14	12.19	16.38
JODA 1389										7.69	12.09		11.65	13.70
JODA 3347												12.81	13.21	14.50
JODA 3787	10.28	6.07	7.72	9.89	13.44	14.50	17.42	17.37	10.73	6.77	11.76	10.50	11.06	12.36
JODA 4323	8.67	6.03	8.36	10.12	13.43	15.06	17.03	16.79	11.65		8.56	10.84	11.41	13.02
JODA 4206	10.57	5.26	8.29	9.98	13.15	13.77	15.94	17.79	12.41	6.16	11.72	12.16	11.99	12.46
JODA 6315	11.75	6.84	9.16	11.41	14.88	18.07	19.81	21.51		7.93	13.70	12.29	13.88	15.90
JODA 10825	13.12	5.67	8.13	9.77	13.86	14.00	19.00	21.11		7.25	15.43	12.48	15.39	15.22

Catalog #	J M1 L	J M2 L	J M3 L	J P1 W	J C1 W	J P1 W	J P2 W	J P3 W	J P4 W	J M1 W	J M2 W	J M3 W
JODA 940									7.53			
JODA 12231									7.68			
JODA 1944									7.76			
JODA 16006												
JODA 374												
JODA 16148												
JODA 905												
JODA 4851						5.67						
JODA 7237							5.67					
JODA 10136								7.30				

Catalog #	J M1 L	J M2 L	J M3 L	J P1 W	J C1 W	J P1 W	J P2 W	J P3 W	J P4 W	J M1 W	J M2 W	J M3 W
JODA 16158								6.78				
JODA 15402						7.67						
JODA 13135	12.38									8.94		
JODA 1009	12.81									8.53		
JODA 6298	12.40									9.41		
JODA 7225								8.09				
JODA 849												
JODA 12261									9.22			
JODA 1955									8.90			
JODA 12253	12.99									10.16		
JODA 14045												
JODA 1214												
JODA 15417	14.31									9.19		
JODA 7744	14.13										9.85	
JODA 7918		14.73									9.45	
JODA 982												
JODA 11558	14.45									10.81		
JODA 866		15.10									10.28	
JODA 3042												
JODA 1884						5.67						
JODA 6718		15.76									12.11	
JODA 15496												
JODA 6160									11.07			
JODA 14121												
JODA 1899												
JODA 938							3.41	5.70				
JODA 1369		17.26									12.86	
JODA 4838		17.32									12.87	
JODA 8634			21.68									11.59
JODA 375						7.75						
JODA 4982												
JODA 6441												
JODA 6329												
JODA 1850												

Catalog #	J M1 L	J M2 L	J M3 L	J P1 W	J C1 W	J P1 W	J P2 W	J P3 W	J P4 W	J M1 W	J M2 W	J M3 W
JODA 16181												
JODA 14208							5.44	7.79				
JODA 1150			25.47									10.96
JODA 6815												
JODA 751												
JODA 5852			24.37									13.68
JODA 1379												
JODA 7748												
JODA 2802			27.50									11.46
JODA 7460												
JODA 10805												
JODA 916												
JODA 4963								6.83	8.80			
JODA 4939								7.44	9.21			
JODA 15531												
JODA 7399								7.07	9.51			
JODA 15449						8.39						
JODA 6467												
JODA 7429												
JODA 6816												
JODA 4202												
JODA 15802												
JODA 677	13.18	15.12								9.64	11.45	
JODA 3383												
JODA 16099												
JODA 16325	14.10	16.32								9.42	12.15	
JODA 7930	13.93	16.03								10.47	11.90	
JODA 7533	14.90	16.96								10.40	11.40	
JODA 14908	13.86								7.52	9.79		
JODA 4996		14.32	19.23								11.33	11.67
JODA 1933		14.99	21.71								12.38	11.57
JODA 6326												
JODA 2771						6.30						

Catalog #	J M1 L	J M2 L	J M3 L	J P1 W	J C1 W	J P1 W	J P2 W	J P3 W	J P4 W	J M1 W	J M2 W	J M3 W
JODA 1206												
JODA 16291												
JODA 3788												
JODA 15712												
JODA 2748												
JODA 7972	15.18						4.43	7.30	8.62	9.86		
JODA 684						6.83						
JODA 6588												
JODA 11564		18.13	26.94								13.10	13.40
JODA 15807												
JODA 1770												
JODA 1406						7.17	5.16	6.63	8.16			
JODA 8619												
JODA 1426												
JODA 7992												
JODA 4865	13.68							5.61	6.63	9.37		
JODA 839												
JODA 4938												
JODA 15975	13.28						6.22	7.72	9.95	10.50		
JODA 12067	12.91	15.43	21.52							10.06	12.01	12.78
JODA 8599												
JODA 365												
JODA 2747	13.74					6.64	3.32	5.68	7.67	10.21		
JODA 379	14.80	16.69				8.02				10.21	11.67	
JODA 4335												
JODA 7465					5.89	7.47	5.89	7.80	9.84			
JODA 13165	12.96	16.69						6.76	9.09	9.97	12.56	
JODA 7819												
JODA 7451	12.86					5.31	5.31	7.90	8.49	9.27		
JODA 10803												
JODA 4201												
JODA 12080	14.43	16.09	25.38				5.62	7.11		9.75	11.97	12.37
JODA 3741												
JODA 3349												

Catalog #	J M1 L	J M2 L	J M3 L	J P1 W	J C1 W	J P1 W	J P2 W	J P3 W	J P4 W	J M1 W	J M2 W	J M3 W
JODA 7438												
JODA 6317	13.70						6.61	8.07	10.44	10.58		
JODA 6631												
JODA 1865												
JODA 14111	12.62	15.02		91.00		6.14			7.35	10.57	12.03	12.50
JODA 6612												
JODA 7798												
JODA 15358	13.65	14.40	24.60						8.10	9.04	11.41	11.64
JODA 1892												
JODA 10812	11.99	13.01	20.12									
YPM 12420												
JODA 7118												
JODA 8765												
JODA 6216	12.86	14.60	25.68	#####				7.30	9.69	10.40	12.35	13.23
AMNH FM 7821												
JODA 10815												
JODA 10840												
JODA 16335	15.39	17.76	27.24	#####			6.64	8.65	11.47	11.54	14.00	14.16
JODA 10824												
JODA 10747												
JODA 4200												
JODA 910												
JODA 3259												
JODA 1945												
JODA 3576												
JODA 250												
JODA 8642												
JODA 1946												
JODA 10809												
JODA 10813												
JODA 3012	14.60	15.67	23.16	#####		8.00		8.56	11.43	9.97	11.87	12.62
JODA 1886	13.54	15.96	23.27	#####	5.11	6.78	6.71	8.32	9.85	10.71	13.19	13.12
JODA 10757	13.52	15.02	23.85					7.65	8.61	10.28	10.80	11.66

Catalog #	J M1 L	J M2 L	J M3 L	J P1 W	J C1 W	J P1 W	J P2 W	J P3 W	J P4 W	J M1 W	J M2 W	J M3 W
JODA 12060	13.61	16.83	24.65	97.16								
JODA 1268	12.82	14.04	21.77	99.65		6.16	5.40	7.22	9.02	9.15	10.81	10.98
JODA 1302	13.65	15.59		93.00	4.47	6.17	4.84	6.85	8.19	11.16	12.68	
JODA 1389	13.61	15.56	22.10	#####	4.07	6.24		7.07	9.33	10.38	11.52	11.84
JODA 3347	14.55	15.09	26.41	#####			7.30	7.73	9.15	10.96	12.83	15.09
JODA 3787	13.65	15.35	22.81	98.17	5.28	6.59	5.85	6.49	9.69	9.70	11.50	11.78
JODA 4323	12.97	13.89	22.63	98.42		6.02	5.73	6.79	9.05	9.27	10.30	10.84
JODA 4206	11.51	13.87	20.54	89.73	4.94	6.91	5.44	6.41	8.80	9.37	10.82	10.83
JODA 6315	14.94	17.58	26.64	#####	5.57	7.86	5.42	7.08	10.16	10.14	12.52	13.86
JODA 10825	13.51	16.56	29.34	#####	5.61	8.65	6.41	7.07	9.66	9.79	12.32	13.77

APPENDIX J

SUPPLEMENTARY TABLE 4.5

Table S3.5 – CV data for teeth measurements, for use in R script.

CV	Count	Measurement	Measurement Type	Maxilla or Mandible
26.07	16	C	H	Maxilla
15.67	28	C1	L	Maxilla
12.07	33	P1	L	Maxilla
11.47	27	P2	L	Maxilla
9.72	37	P3	L	Maxilla
8.96	42	P4	L	Maxilla
11.03	54	M1	L	Maxilla
10.42	52	M2	L	Maxilla
10.75	49	M3	L	Maxilla
17.86	27	C1	W	Maxilla
14.52	31	P1	W	Maxilla
12.52	27	P2	W	Maxilla
8.66	37	P3	W	Maxilla
8.30	43	P4	W	Maxilla
7.62	53	M1	W	Maxilla
9.05	50	M2	W	Maxilla
7.02	50	M3	W	Maxilla
34.20	13	P1	H	Maxilla
9.52	8	C1	L	Mandible
15.68	23	P1	L	Mandible
9.03	21	P2	L	Mandible
11.09	32	P3	L	Mandible
11.74	29	P4	L	Mandible
6.48	40	M1	L	Mandible
7.86	34	M2	L	Mandible
10.79	25	M3	L	Mandible
11.95	8	C1	W	Mandible
13.61	23	P1	W	Mandible
17.86	21	P2	W	Mandible
10.63	32	P3	W	Mandible
12.68	35	P4	W	Mandible
6.71	37	M1	W	Mandible
8.53	33	M2	W	Mandible
9.51	24	M3	W	Mandible

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