Identification of hybridization in the nasal cavity of baboon hybrids, *Papio anubis* x *P. cynocephalus,* as an analogue for Neanderthal and Anatomically Modern Human hybrids

by

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

This study developed an informative model of a nasal cavity of a Neanderthal and Anatomically Modern Human (AMH) hybrid based on the morphological measurements and nonmetric features of nonhuman primate hybrids. This study examined morphometric measurements and nonmetric traits of the interior nasal cavity of two species of baboons (olive and yellow) and their first generation hybrids to determine how hybridization affects the internal anatomy of the nasal cavity. The nasal cavity was chosen because the nasal cavities of Neanderthals and AMH are recognized as uniquely different in size and shape.

This study found that functionally different regions within the baboon nasal cavity are altered in size and shape in response to hybridization. Changes in size and shape due to hybridization occurred in three regions, at the rhinion, choana, and mid-nasopharynx. In regions of more complex physiological function, the mid-bony cavity and the posterior nasopharynx, no size or shape response was observed, except a wider lateral recess. Males and females responded differently to hybridization; males showed heterosis and females showed heterosis in most areas, though dysgenesis in the inferior meatus. The opposing male and female trends may contribute to the greater sexual dimorphism observed in hybrids compared to parental taxa.

This study found that frequencies of nonmetric traits in the baboon hybrid nasal cavity were no different from frequencies in parental taxa, nor were regional frequency differences observed because anterior and posterior nonmetric traits occurred at the same frequency. However, males expressed a significantly higher frequency of nonmetric traits than females.

Assuming Neanderthal and AMH hybrid nasal cavities follow the trends observed in the baboon hybrid model, the Neanderthal and AMH hybrid nasal cavity would have a different shape and larger size at the rhinion, choana, and mid-nasopharynx, while the mid-bony cavity and posterior nasopharynx remained unchanged compared to parental taxa. However, because Neanderthals and AMH have been diverged for a longer time period, the traits of the nasal cavity may be very different in parental taxa due to adaptations to local conditions, which may result in hybrids with traits from one parent or the other. Further, an analysis of different hybridization scenarios between Neanderthals and AMH, based on observed hybridization in baboons and paleoanthropological evidence, suggests rapid gene swamping of the Neanderthal population by AMH during hybridization, as other authors have also concluded.

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Chapter 1

Introduction

One of the most inspiring and beautiful documentaries about the diversity of "Life on Earth," begins with Sir David Attenborough saying, "There are some four million different kinds of animals and plants in the world. Four million different solutions to the problems of staying alive." Since the 1979 documentary, scientists have calculated more precisely that there is an estimate of 7.7 million species of animals alone, of which only 12% or 953,434 have been described in the Catalogue of Life and the World Register of Marine Species (Mora et al., 2011). Humans are just one of these species that has developed and evolved since life began on earth ~3.5 billion years ago (Schopf, 1993).

Anthropologists study the tiny branch on the tree of life that diverged from other primates a mere 5-6 million years ago (Page and Goodman, 2001), which includes modern humans and Neanderthals. Common media coverage would suggest that Neanderthals are extinct, but perhaps they did have a solution to staying alive even though their climate abruptly changed and their food sources disappeared (Magniez and Boulbes, 2013). Perhaps hybridization between Neanderthals and Anatomically Modern Humans (AMH) preserved some of the Neanderthal DNA within the hybrid descendants, so that Neadnerthal DNA is present in some of the humans living today. In Sir Attenborough's words, "This is the story of how a few of them came to be as they are."

1.1 Evolutionary Theory of Hybridization

What happens when two species or populations, that have been isolated for thousands of years and adapted to their specific environments, finally come back into geographic contact with one another? The outcome changes the evolutionary history of both populations: they compete with one another until they are able to reach a balance point or one species must migrate or find a new niche, risk extinction, or interbreed to create hybrids. Interbreeding can recombine the populations or result in the disappearance of one or the other species due to gene swamping, and many degrees in between. Naturalists have observed hybridization throughout the animal kingdom, including many species of primates (Arnold and Meyer, 2006; Zinner et al., 2011).

Hybridization, or interbreeding, is the crossing of genetically distinct taxa or groups that leads to viable hybrid offspring. Hybridization is not confined to the occurrence of crossing between species, but can occur between genetically isolated subspecies or previously reproductively isolated populations of the same species (Mallet, 2005; Ackermann, 2010). Admixture is "the production of new genetic combinations in hybrid populations through recombination" (Ackermann, 2010: 259). The process of hybridization can lead to introgression, or gene flow and genetic exchange, of genes from one parental taxon moving into the genomes of the other parental taxon, in one or both directions between parental taxa (Levin, 2002; Mallet, 2005; Mallet, 2007).

However, hybridization is a poorly understood, complex process in mammals. Though there are many observations of hybridization in the wild, confirmed by genetic analysis, understanding at the population level of what will happen to the taxa involved is still complicated by the numerous variables involved. Researchers have identified broad determinant variables, such as how long the re-encountering populations have been apart, how specialized they are to different environments, the population sizes, especially the number of each sex, and the selective pressures in the new hybrid zone (Haldane, 1922; Arnold, 1992; Barton, 2001; Levin, 2002; Holliday, 2008; Wolf et al., 2011; Charpentier et al., 2012). However, the outcome of a hybrid zone is still hard to predict in extant populations, let alone populations that existed tens of thousands of years ago. On the organismal level, the recombination of genomes to create unique combinations of alleles is only starting to be understood with relation to mutation rates, loci disequilibrium effects, and overall fitness (Wu, 2001). Researchers also struggle with relating hybrid phenotypes with genotypes, which means that there are no prescribed traits, particularly external, that researchers can look for in the wild to identify a hybrid. For example, Schillaci (Personal communication) only knew he was looking at wild macaque hybrids because they looked somehow different from the purebred populations. Similarly, hybrids between yellow and olive baboons in Amboseli, Kenya are identified primarily by their intermediate size and pelage on their heads and tails (Alberts and Altmann, 2001).

Most studies of these interbreeding events in wild populations are either based on external phenotypes, such as pelage colour and shape or general body proportions (Alberts and Altmann, 2001; Aguiar et al., 2008), or based on nuclear or mitochondrial DNA used to detect the hybrids biochemically (Tagliaro et al., 1997; Evans et al., 2001; Wyner et al., 2002; Zinner et al., 2009). However, soft tissue of Neanderthals and Pleistocene AMH are not preserved and ancient DNA is rare and difficult to work with (Pääbo et al., 2004; Gilbert et al., 2005; Smith et al., 2005; Willerslev and Cooper, 2005). Paleoanthropologists only have access to skeletal remains, yet

comparative studies of skeletal morphology of hybrids are rare, and have only been conducted on non-human extant primates (Ackermann et al., 2006; Ackermann and Bishop, 2009).

1.2 Hybridization between Neanderthal and Anatomically Modern Human

Anthropologists hold many views of recent human evolution, in particular, the involvement of Neanderthals in the ancestry of today's humans (Section 2.2.1). One view, the Replacement or Out of Africa hypotheses, holds that AMH, who evolved in Africa, are the direct ancestors of contemporary modern humans in Europe and Asia, with little or no genetic exchange with Neanderthals (Stringer and Andrews, 1988; Stringer, 2008; Tattersall and Schwartz, 2008). Alternatively, Wolpoff, Hawks and others argue for the Multiregional hypothesis, which means that AMH and Neanderthal populations, as well as other yet-to-be discovered ancient human populations, in different geographic areas were all within the same species through continuous interbreeding to create modern humans across Europe and Asia (Wolpoff et al., 2004). A middle ground between the two above theories is Fred Smith's Assimilation theory, which states that AMH migrated out of Africa into Eurasia where there was genetic exchange with some populations of Neanderthals, whose descendants then became modern humans (Smith et al., 2005).

The three above hypotheses have evolved from earlier explanations for the placement of Neanderthals in recent human evolution. Virchow initially dismissed the Neanderthal as pathological, but this hypothesis became less tenable as more skeletal remains with the same features were found across Europe (Drell, 2000). Researchers, in particular Boule and Keith, who are discussed in Section 2.2.4, believed that Neanderthals had established an alternative lineage from modern humans and were more closely related to apes than to contemporary humans (Catrmill and Smith, 2009: 295). Boule reconstructed the skeletal remains with bent knees and hunched back without an S-shape, emphasizing ape-like characteristics (Drell, 2000). However, Aleš Hrdlička believed that Neanderthals were direct ancestors to contemporary Europeans, who then left Europe to populate the rest of the world (Hrdlička, 1927; Cartmill and Smith, 2009: 295). Weidenrich similarly hypothesized that Neanderthals were directly ancestral, though only in Europe and West Asia (Cartmill and Smith, 2009: 295). W.W. Howells, F. C. Howell, and S. Sergi hypothesized that modern humans evolved from some archaic human ancestor somewhere in the Old World, possibly the early, but not late "classic", Neanderthals (Cartmill and Smith, 2009: 295).

After years of debate and speculation, many researchers are beginning to converge on the idea that at least some Neanderthals and AMH interbred, creating hybrids. Interbreeding left genetic markers of the Neanderthal genome in living European and Asian populations of today (Green et al., 2010). Additionally, x-linked chromosome segments from Neanderthals have also been found in 9% of non-African populations (Yotova et al., 2011). The possible advantages of these genes have been explored and hypothesized, perhaps providing immunity to previously un-encountered diseases in Europe for the immigrating AMH populations (Mendez et al., 2012).

For interbreeding to have occurred between AMH and Neanderthals, several criteria must have been met: the dates of each population in the same location must overlap, each population must recognize the other as possible mates, and there are no pre- or post-zygotic barriers preventing the biological development of the hybrid.

The dating of archaeological sites or remains at these sites have established that Neanderthals and AMH may have lived contemporaneously within the same geographic region for potentially almost 14,000 years in Europe. Dates determined by the evidence of AMH presence in Europe from the discovery of Aurignacian artifacts, associated with AMH, overlap with the dates in which Neanderthal skeletal remains are found (Mellars, 2006). The earliest radiometric dates of European archaeological sites that contain Aurignacian artifacts range from 42,800 years ago in Bulgaria to 30,200 years ago in various locations in Europe (Cartmill and Smith, 2009: 458). Dating of the earliest skeletal remains of AMH in Europe range from 28,2000-40,2000 years ago in Bulgaria (Bacho Kiro), Romania (Bordu Mare, Cioclovina, La Adam), Hungary (Görömböly-Tapolca, Istállós -kō), Austria (Miesslingtal), and the Czech Republic (Mladeč) (Ahern et al., 2013). The most recent skeletal remains classified as pure Neanderthal, as opposed to hybrid, have been dated to 28,000 +/- 400 years ago at Vindija and 29,195 +/- 965 years ago at Mezmaiskaya (Smith et al., 1999; Ovchinnikov et al., 2000; Cartmill and Smith, 2009: 347).

Dates of potential range overlap in Europe have also been determined by the examination of DNA. By the examination of the decay of loci disequilibrium in the Neanderthal genome, it is estimated that hybridization occurred between 47,000-65,000 years ago (Sankararaman et al., 2012; Mendez et al., 2012).

Earlier dates of overlap exist in the Near East. The Skhūl-Qafzeh modern humans in Israel are estimated to have existed between 80,000-100,000 years ago (Cartmill and Smith, 2009: 440), and moderns in general may have inhabited the Near East after at least 80,000 years ago or as early as 120,000 years ago (Cartmill and Smith, 2009; 444). Neanderthal remains in the Near East range from earliest, 265,000 years ago from Tabūn, to latest, 43,000-48,000 years ago from

the Wadi Amud (Cartmill and Smith, 2009: 350). Therefore, the ranges potentially overlapped for about 40,000-80,000 years.

The date when Neanderthals and AMH separated from their last common ancestor greatly varies from 690,000 to 270,000 years ago. Krings et al. (1997) estimated a date of 550,000-690,000 years ago for the date of divergence by analyzing Neanderthal mitochondrial DNA (mtDNA). Green et al. (2008) estimated a divergence date of 660,000 +/- 140,000 years by comparing Neanderthal and contemporary human mtDNA. By analyzing five Neanderthal mitochondrial genomes, Endicott et al. (2010) estimated a divergence date of 410,000-440,000 years ago. Using Neanderthal nuclear DNA (nDNA), Green et al. (2010) estimated that Neanderthals and contemporary humans separated 270,000-440,000 years ago. Holiday (2008) suggests that even the earliest divergence times probably did not result in an inability of Neanderthals and AMH to successfully interbreed and produce viable offspring by comparing this scenario to other divergent mammalian species who produce viable hybrids.

1.3 Identification of Hybridization from Skeletal Remains

Neanderthals are only represented by skeletal remains, from which some ancient DNA has been extracted to determine common ancestry and possible reciprocal hybridization with AMH in nuclear DNA and mtDNA studies (Krings et al., 1997; Nordborg, 1998; Ovchinnikov et al., 2000; Scholz et al., 2000; Hawks and Wolpoff, 2001; Stringer, 2002; Currat and Excoffier, 2004; Pearson, 2004; Serre et al., 2004; Wall and Hammer, 2006; Hawks, 2008; Serre and Pääbo, 2008; Green et al., 2010; Currat and Excoffier, 2011; Yotova et al., 2011; Mendez et al., 2012; Sankararaman et al., 2012). However, ancient DNA does not preserve well, and only examined in a subset of the many skeletal remains of Neanderthal and AMH (Pääbo et al., 2004; Gilbert et al., 2005; Smith et al., 2005; Willerslev and Cooper, 2005) (Section 2.2.3). Therefore, a model of hybridization from the skeletal remains is useful in the identification of hybrids in the fossil record.

Over the last 40 years, researchers have attempted to answer the question of hybrid identification in regards to Neanderthals and AMH. From the type specimen of the species, Neanderthal 1, found in 1856 in Neander Valley, Germany, and other early Neanderthal specimens, anthropologists were able to establish the suite of traits that compile a "classic" Neanderthal. As stated by Hrdlička:

> They [Neanderthal traits] include a moderate stature, heavy build, and a good-sized, thick, oblong skull, with pronounced supraorbital torus, low forehead, low vault, protruding

occiput, large, full, upper maxilla, large nose, large teeth, and a large, heavy lower jaw with receding chin. (Hrdlička, 1927)

The list of "classical" Neanderthal traits has been extended and refined since 1927 to include an 'inflated' morphology of the infra-orbital plate, anteroinferior projection of glabella relative to the browridge, prognathic face, pronounced juxtamastoid eminence, occipital bun, small mastoid process, and large piriform (nasal) aperture (Dean et al., 1998; Hublin, 2002; Tattersall and Schwartz, 2008; Harvati et al., 2010). Anatomically Modern Humans are characterized with high neurocranial vaults with expanded parietals, occipital rounding, long and prominent mastoid processes, prominent chins, small dentition, and gracile skeletal structure (Trinkaus, 2005; Hublin, 2013). Ahern (2008) and many others have recently argued that some of these classic Neanderthal traits are not found exclusively in Neanderthals, but also appear in other populations. Ahern (2008) and Ahern et al. (2013) argue that these traits may be seen in the Upper Paleolithic AMH due to admixture from Neanderthals.

After defining and quantifying species-specific, or derived, features, anthropologists can hypothesize about what features a hybrid would have. Some anthropologists propose a "mosaic" of features, in which, for example, a Neanderthal and AMH hybrid might contain a prominent chin (a feature of AMH) as well as lingual bridging of the mandibular foramen (a Neanderthal feature), a trait that has been observed in Oase 1 (Trinkaus et al., 2003). Indeed, most conceptions of Neanderthal and AMH morphology are based on a "mosaic" of features (Duarte et al., 1999; Tattersall and Schwartz, 1999; Wolpoff et al., 2001; Harvati et al., 2007; Soficaru et al., 2007). However, hybridization in primates also recognizes hybrids with "intermediate" morphology of features observed along a gradient, such as stocky build to gracile build (Alberts and Altmann, 2001; Arnold and Meyer, 2006). Still other researchers propose that the hybrid would have features more of one or the other parental species, thus making hybridization invisible, concealed in the morphological diversity of the parental species (Jiggins and Mallet, 2000). Anthropologists have not come to a consensus on what features a hybrid of Neanderthals and AMH might have.

However, a final group of researchers decided to look for specific features, which they call "anomalies" and can be congenital malformations, or rare nonmetric traits that occur at higher rates in hybrids compared to either parental species (Ackermann et al., 2006). Therefore, a higher frequency of nonmetric traits may indicate hybridization in that population.

1.4 Hybridization in the Baboon Nasal Cavity

This study analyzed the hybrid nasal cavity from baboon skeletal remains. The morphology of internal structures in hybrids has never been studied and will have a different, possibly lesser, response to hybridization than external skeletal morphology (Bastir and Rosas, 2013). The nasal cavity also spans across the palate to the critically functioning areas of the sphenoid below the orbits, where a variety of strong stabilizing selective pressures act to maintain vision, respiration, and basal cranium structure. I hypothesized that the outcome of hybridization will alter the anterior region (bony palate) more because it is not surrounded by critically functioning areas, whereas the posterior region (nasopharynx) will remain unchanged.

The nasal cavity is of particular interest in recent human evolution and hybridization because Neanderthal nasal cavities are remarkably different from AMH (Schwartz and Tattersall, 1996; Dean et al., 1998). Rae et al. (2006; 2011) disproved the earlier view that the Neanderthal nasal cavity was an adaptation to the colder European climate. Climate variables, such as temperature and humidity, influence nasal cavity shape and size in modern humans, though in the opposite direction (smaller in colder, drier environments) compared to what is seen in Neanderthals (large nasal aperture in colder Europe) (Noback et al., 2011). If the shape and/or size of the nasal cavity are important adaptations to particular environmental variables or ecological interactions, other than temperature, alterations of the nasal cavity due to hybridization could have a dramatic impact on the hybrid fitness for better or worse. I also hypothesized that there will be a greater frequency of nonmetric traits in the hybrid nasal cavity, with higher frequencies in the anterior region compared to the posterior region, due to developmental instability caused by the interaction of specialized genes from different parental groups (Ackermann et al., 2006).

Analogue species, *Papio anubis*, olive baboon, and *P. cynocephalus*, yellow baboon, were used to explore the morphological differences due to hybridization because Neanderthal and AMH hybrids cannot be analyzed directly. The baboons in the collection analyzed in this study have been pedigreed to understand their direct ancestry as olive, yellow, or both (hybrid). Therefore, any morphological differences or nonmetric traits found in the hybrid nasal cavity can be attributed to hybridization as Ackermann et al. (2006) concluded after analyzing the external features of baboon skulls from the same collection.

This thesis also analyzed the affect of hybridization on morphometric features. The nasal cavity was measured at various landmarks and then compared between the hybrids and parental baboons (olive and yellow) to identify size and shape difference associated with hybridization. Changes in size reflect alterations in energetic demands (Noback et al., 2011). Shape changes

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indicate alterations in nasal cavity function (Noback et al., 2011). This is the first study, to the best of the author's knowledge, to analyze the affect of hybridization on metric and nonmetric traits in the nasal cavity.

1.5 Public Issues

In addition to the academic interest in hybrids and evolutionary theory, there is also a concern about hybridization in the wild for the conservation of species (Detwiler et al., 2005; Nolte and Tautz, 2010). It is possible for hybridization to lead to the extinction of one of the parental species due to gene swamping (Seehausen, 2004; Detwiler et al., 2005). It is hypothesized that gene swamping may have caused the extinction of Neanderthals (Jolly, 2001; Cartmill and Smith, 2013: 444-447; Zinner et al., 2009; Zinner et al., 2011; Smith, 2013). However, without hybridization and gene flow between small populations, the lack of genetic diversity makes it more difficult for a small population to overcome new diseases, environmental changes, or human disturbance. Conservationists must carefully assess how hybridization can be used as a tool to save species while minimizing the risk of extinction due to gene swamping.

This study analyzes the skeletal remains of baboons that lived in a captive colony at a research centre where they were part of other genetic and dietary studies. There are ethical concerns when using non-human primates in research that solely benefits humans. The public should be aware of how these or any animals are being treated during and after research studies and researchers should attempt to find alternatives or be less invasive if possible.

1.6 Objectives

The main objective of this thesis is to model the effects of hybridization on the nasal cavity using Computed Tomography (CT) scans and visual inspection of the same baboon skeletal collection that was examined by Ackermann et al. (2006). Methodology and discussion for this thesis directly build from the Ackermann et al. (2006) study. Additional objectives include:

Model of Hybridization in the Nasal Cavity: The metric and nonmetric models of hybridization in the nasal cavity, developed in Chapters 4 (metric) and 5 (nonmetric), are used to hypothesize features of the nasal cavity of a Neanderthal and AMH hybrid (Section 6.3).

Model of Baboon and Pleistocene Hominin Hybrid Zones: The structure of the hybrid zone of yellow and olive baboons in Amboseli, Kenya, with an examination of current anthropological evidence, were used to hypothesize, the most parsimonious model of the

Neanderthal and AMH hybrid zone (Section 6.1, Section 6.2). This model accommodates currently known paleoanthropological evidence (Chapter 2, Chapter 3) and trends found from the model of hybridization in the baboon nasal cavity (Chapter 4, Chapter 5).

Re-assess the Baboon Lateral Recess: The definition and function of the "lateral recess" in baboons is re-assessed after trends in the morphometric measurements and nonmetric traits due to hybridization in baboons are evaluated (Section 3.2.2, Section 4.4, Section 5.4).

Identify and discuss public issues: a) Hybridization can lead to the rapid extinction of the smaller population and is a conservation concern for primates (Section 2.1.2, Chapter 6). b) Many ethical issues revolve around research with primates, including issues encountered during the development of this project (Section 3.1).

Chapter 2

Background

Though my project is examining baboon hybrids as a model for identifying Neanderthal and AMH hybrids, my experiment will not be useful unless it is placed into the context of hybrid evolutionary theory. The theory is particularly important for understanding if and how Neanderthals and AMH hybridized. This background is useful for understanding discussions in Section 6.1 and Section 6.2.

In addition, researchers in paleoanthropology are divided by perceptions of Neanderthal and AMH hybrids, with debates about the existence and physical form of hybrids. In this chapter, I present evidence for hybridization as well as arguments against it, introducing the controversy in paleoanthropology and to explain why I am searching for morphological, metric and nonmetric, indicators of hybridization.

2.1 Evolutionary Theory of Hybridization

Hybridization, as an important evolutionary process, has gained recognition as researchers have observed more examples of hybrids in the wild and speculated about their existence and identification in the fossil record.

The outcome of a hybridization event can be the creation of a new species from the hybrid population through reticulate evolution, the merging of the parental taxa, or reinforcement of the separation between the parental taxa (Mallet, 2005). Which outcome occurs depends on many variables in population ecology and genetics. From population ecology, we know that the outcome of two taxa re-encountering each other is determined by population size, effective population size (the number of fertile females), age distribution, sex ratio, and dispersal patterns. From genetics, we know that some important factors affecting the outcome of hybridizationare divergence between populations, adaptation to specific habitats, hybrid viability and hybrid fitness. Neither of the lists of variables in ecology or genetics form a complete list of variables that determine whether or not populations will hybridize and what outcome occurs due to hybridization. For simplification, researchers have distinguished types of hybrid zones: mosaic, intermediate, and bimodal, based on these variables and these are discussed in Section 2.1.1.

Hypotheses concerning the characteristics of the Neanderthal and AMH hybrid zone will be compared to the baboon hybrid zone in Chapter 6, and one scenario will be proposed as the most parsimonious with hybrid theory and archaeological evidence.

Under certain circumstances, such as the immigration of a large invader population into a region where the local population is small, and the populations have developed trait specialization as an adaptation to their environments and they have a long history of species divergence, the process of hybridization can lead to the extinction of the small local population. Hybridization in wild populations is a major conservation issue as habitats are destroyed and fragmented by humans, forcing the diverged, small populations back into contact.

In the discussion that follows, "hybrid" refers to the first generation cross between two genetically isolated populations, F1. When other hybrids are discussed, such as hybrid-hybrid crosses and backcrosses, the generation and genetic history is indicated.

2.1.1 Evolutionary Theory

The perceived importance of hybridization in influencing evolution has greatly changed in recent years. Previously, hybridization was only considered important in plant species, with limited applicability in animals (Arnold, 1992; Dowling and Secor, 1997).

> Pure species have of course their organs of reproduction in a perfect condition, yet when intercrossed they produce either few or no offspring. Hybrids, on the other hand, have their reproductive organs functionally impotent, as may be clearly seen in the state of the male element in both plants and animals. (Darwin, 1859)

However, through observations in the wild, hybridization is beginning to be seen as a very influential process in animals as well (Mallet, 2005; Mallet, 2007; Shurtliff, 2013). Mallet (2005) reviewed the literature for hybridization in animals and found that out of 200 examined European mammalian species, 6% were known to hybridize. Primate taxa are also strongly influenced by hybridization (Arnold and Meyer, 2006; Detwiler et al., 2005; Zinner et al., 2011). Of all the primates that scientists currently recognize, >10% are known to hybridize (Arnold and Meyer, 2006).

Hybridization has been identified in wild primates across all major primate clades through genetic and observational studies, examples include: yellow and olive baboons (Phillips-Conroy and Jolly, 1981; Samuels and Altmann, 1986; Jolly, 2001; Alberts and Altmann, 2001; Jolly et al., 2007; Zinner et al., 2009); gelada baboons and olive baboons (Dunbar and Dunbar, 1974; Zinner et al., 2009); hamadryas and olive baboons (Phillips-Convoy and Jolly, 1981; Phillips-Convoy et al., 1992; Zinner et al., 2009); macaques (Tosi et al., 2000; Evans et al., 2001;

Schillaci and Froehlich, 2001; Tosi et al., 2003; Schillaci et al., 2007); howler monkeys (Cortés-Ortiz et al., 2007; Agostini et al., 2008; Aguiar et al., 2008; Kelaita and Cortés-Ortiz, 2013), tamarins (Cheverud et al., 1993; Cropp et al., 1999; Kohn et al., 2001), marmoset (Tagliaro et al., 1997), lemurs (Wyner et al., 2002; Gligor et al., 2009; Delmore et al., 2011; Delmore et al., 2013); langurs (Choudhury, 2008; Denise et al., 2008); gibbons (Brockelman and Gittins, 1984; Reichard, 2009); orangutans (Xu and Arnason, 1996; Muir et al., 2000; Warren et al., 2001); bonobos and chimps (Kaessmann et al., 1999); gorillas (Ackermann and Bishop, 2009); and hominins (Arnold and Meyer, 2006; Holliday, 2003; Ackermann, 2010; Harvati et al., 2007; Zinner et al., 2011).

Hybrids are often larger or smaller than the parental populations depending on the degree of divergence between the parental populations and the interactions between alleles, genes, and loci. Some anthropologists studying hybridization have attributed larger size with heterosis and smaller size with dysgenesis, though they do not link the size changes to hybrid fitness (Cheverud et al., 1993; Schillaci et al., 2005; Ackermann et al., 2006; Harvati et al., 2007). Schillaci et al. refer to heterosis as hybrid vigor in which "the hybrid phenotype exceeds the midpoint, i.e., midparental average, of the parental taxa" due to increased heterozygostity (2005: 342). Greater heterozygostiy occurs when there is a large difference in the gene frequencies of the two parental populations and when a specific allele has directional dominance (Schillaci et al., 2005). Dysgenesis occurs when "the hybrid phenotypic mean is less than the mean of the parental taxa" resulting from "hybridization between two taxa with different environmental adaptation and coadapted gene complexes" (Schillaci et al., 2005: 342). Ackermann et al. (2006: 2) share similar definitions of heterosis and dysgenesis as Schillaci et al. (2005) as well as the reasoning for why size changes occur. However, Harvati et al. focus only on size, and define heterosis as the "departures of the hybrids toward greater size … than expected based on the phenotypes of the parental taxa," and dysgenesis as departures of the hybrids toward smaller size than expected based on the phenotypes of the parental taxa (2007: 733). This paper will follow these definitions of heterosis and dysgenesis.

Hybrid Zones

A hybrid zone is a geographic region within which isolated populations re-encounter each other and interbreed to produce hybrids (Nolte and Tautz, 2010). In the theoretical literature, there are several identified hybrid zone spatial structures: intermediate or clinal, mosaic or patchy, and bimodal. The underlying genetic compositions of individuals within the hybrid zone determine which spatial structure a particular hybrid zone exhibits (M'Gonigle and FitzJohn, 2009). In

studies of hybrid zones in the wild, descriptions of hybrids are intermediate, mosaic, or parental-like (hybrids are similar to one parent or the other as in bimodal zones), referring to the phenotypes that can be observed by the researchers. The phenotypic descriptions somewhat correspond to the genetic descriptions of hybrid zones, though some researchers argue that the phenotypic observations can fall into other categories due to coarse sampling, which will be discussed (M'Gonigle and FitzJohn, 2009; Nolte and Tautz, 2010).

First, an intermediate hybrid zone refers to a continuous gradient, or cline, of size and shape, or alleles, from one parental population to the other. Intermediate hybrid zones create a unimodal distribution where the intermediate phenotype is most common compared to phenotypes resembling one parent or the other (Jiggins and Mallet, 2000). For example, olive and yellow baboon hybrids are described as having intermediate diagnostic morphology between the parental taxa, in features such as pelage colour, hair growth, body size and the length and posturing of the tail (Alberts and Altmann, 2001; Arnold and Meyer, 2006). Specifically, olive baboons have a short (above the knee), thick tail while yellow baboons have a long (at least to back of knee), and thin tail. Hybrids are intermediate in length and thickness (Alberts and Altmann, 2001).

Second, a mosaic hybrid zone refers to the spatially or temporally separated patches where parental taxa interbreed and each patch may result in a different dominant genetic combination (Dowling and Secore, 1997; Gaubert et al., 2005; Nosil et al., 2005; M'Gonigle and FitzJohn, 2009). The differences between patches are first established by founder effect and then reinforced by adaptive selection due to different environmental pressures in different patches and assortative mating (selection against the hybrid) or immigrant inviability (selection against the immigrant) within each patch (Barton, 2001; Nolte et al., 2005; M'Gonigle and FitzJohn, 2009). The other use of "mosaic" is to describe the combination of genotypes and phenotypes from both parental groups in the individual hybrids, so that they hybrid presents a few morphological traits from one parental group and a few traits from the other parental group (Dowling and Secor, 1997; Gaubert et al., 2005). Mosaic morphology has been observed in female howler monkey hybrids, which showed a pelage coloration pattern that is a combination between parental species, such as having some patches of fur that were the golden colour of *Aloutta caraya* and other patches that were the black colour of *A. clamitans* (Aguiar et al., 2008; Delmore et al., 2013). Potential Neanderthal and AMH hybrids are often described as having a mosaic of features from both parental groups (see Section 2.2.2). Because each patch in a spatially mosaic hybrid zone follows a different evolutionary path due to various selective pressures discussed above, morphologies that are a combination of parental morphologies can be observed in some patches, while

morphologies that resemble one parent or the other parent or intermediate morphologies are observed in other patches (M'Gonigle and FitzJohn, 2009).

Third, hybrids are also found that have phenotypes more similar to one parent or the other in bimodal hybrid zones (Jiggins and Mallet, 2000). For example, hamadryas and olive baboons hybridize to produce hybrids that have phenotypes and genotypes more similar to one or the other parental species (Alberts and Altmann, 2001). Bimodal hybrid zones are very different from intermediate and mosaic hybrid zones. Bimodal hybrid zones are often characterized by positive assortative mating as a prezygotic barrier, so that each parental species will more often mate with a member of their own population or those hybrids who are similar to them, than mate with those who are different from them (Jiggins and Mallet, 2000). Therefore, females will mate with males of their own species or hybrids that resemble their own species rather than mate with a male from a different species or hybrids that resemble a different species. Bimodal hybrid zones often form when the parental species are more diverged and well adapted to their environments, resulting in hybrids that have lower fitness, due to the low probability that a recombination of chromosomes will create a hybrid that is more fit than the parents (Barton, 2001; Ackermann et al., 2006). Therefore, it is improbable that hybrid speciation will occur in bimodal hybrid zones, though introgression, gene flow from one population to another, may occur in one or both parental populations, increasing genetic diversity in the parental populations (Wu, 2001).

Reticulate evolution is the formation of a new species from two or more species through interbreeding, or hybridization (Ackermann, 2010). In a phylogenetic tree, traditional depictions of species relationships present a node, representing the last common ancestor, in the past from which 2 species branch upward to present day. A phylogenetic tree based on reticulate evolution results in complex network-like connections between divergent species (Ackermann, 2010). In reticulate evolution, hybridization takes place many times throughout the history of the diverging taxa and may reoccur if the populations ever re-encounter one another.

Heterozygote Advantage and Hybrid Fitness

In an isolated population, over many generations, chance alone can lead a particular allele to fixation in that population. In an individual, assuming random mating in a population, the probability of having two of the same alleles (homozygote) at a given loci is 1/(2N), where N is population size. Therefore, smaller populations tend to have a greater number of homozygote individuals. This process is called genetic drift, and if uninterrupted over many generations, creates populations that only have one allele at a given loci and all individuals are homozygous. Due to genetic drift, populations prior to interbreeding have more homozygotes than a population

in a hybrid zone. Within a hybrid zone, alleles from a different population are reintroduced to the other population so that an allele at a particular loci is no longer fixed in the gene pool and there are more heterozygote individuals (different alleles at a particular loci).

The increased allelic diversity in hybrid zones is particularly important for population fitness due to heterozygote advantage. Homozygotes can express deleterious alleles by having two of the same alleles (for example aa or AA) with a deleterious mutation (aa produces sickle cell anemia, AA are more vulnerable to malaria). Heterozygotes, on the other hand, can cover the expression of the deleterious allele by a dominant allele (Aa which covers sickle cell anemia, and gives some immunity to malaria). Because hybrid zones create heterozygote hybrids, hybrids may have greater fitness than the parental population due to heterozygote advantage (Aa, rather than aa or AA) (Ackermann, 2010). Increased heterozygosity in the hybrid populations has been related to heterosis, increased trait size (Schillaci et al., 2005; Ackermann et al., 2006).

If the parental populations are not strongly diverged, a hybrid could receive unique advantageous allele combinations resulting in a greater diversity of phenotypes, from which some may be more beneficial in a new or altered environment (Barton, 2001). The more diverged the parental populations, the less probable that the allele combinations will be advantageous (Barton, 2001). Extreme divergence of populations could occur during the fixation of different alleles, which occurs in inbred populations or long-term genetic drift. For hybrids to become established in the population, they must have greater or equal fitness to the parental taxa. Hybrids can have greater fitness if they acquire advantageous allele combinations from the parental taxa, or they have new mutations that increase fitness in the new environment, though advantageous mutations are very rare (Barton, 2001). Such an introduction of new advantageous allele combinations into the hybrid population, which restores alleles lost due to genetic drift or selection, results in greater fitness in the hybrids compared to the parental populations (Ackermann et al., 2006; Ackermann, 2010).

Because hybrids demonstrate novel combinations of alleles, which could potentially be well adapted to a new environment, hybrids may be a mechanism of saving genetic diversity between species. Nolte and Tautz (2010) call this mechanism of hybridization a creative evolutionary force. If the hybrids that are created after the initial re-contact between the parental taxa are able to survive in a habitat in which parental taxa cannot survive, and display reproductive isolation from parental taxa, or show assortative mating with other hybrids, the hybrids may have a greater range of phenotypes than the parental species (Nolte and Tautz, 2010). This process of increasing genetic and phenotypic variation is called transgressive segregation (Seehausen, 2004; Nolte and Tautz, 2010). Forty-five of 58 (78%) studies of

hybridization in wild animals observed transgressive segregation based on an evaluation of 650 phenotypic traits (Rieseberg et al., 1999). Charpentier et al. (2012) also observed transgressive segregation and greater genetic diversity in olive and yellow baboon hybrids. The greater range of genotypes and phenotypes gives hybrids an adaptive advantage over the parental species in novel environments because it is more probable that one of many phenotypes may be beneficial and selected for rather than one of fewer phenotypes (Seehausen, 2004). It may also be possible that females will preferentially mate with males of another species, interbreed, if a hybrid phenotype would survive better in an altered environment, as has been observed in toads (Pfennig, 2007). This mating selection would give hybrids a competitive advantage, higher fitness. If taken to the extreme conclusion, higher fitness in hybrids can result in reticulate evolution in which a new subspecies/species is formed from the hybrids.

However, because the combination of alleles is random during hybridization and often novel, the resulting phenotypes have not undergone natural selection and may be disadvantageous (Barton, 2001). Combinations that are disadvantageous or break down coadapted gene complexes found in parental groups would lower the fitness of hybrids, which can result in dysgenesis, or reduction in the size of features (Ackermann et al., 2006; Ackerman, 2010). Hybridization is therefore similar to the introduction of novel alleles through mutation. Mutation can produce advantageous, neutral, or disadvantageous alleles, which can be lethal. However, deleterious mutations tend to be lethal than new allele combinations developed through hybridization (Jolly, 2001). Disadvantageous combinations occur more often between populations that are diverged more and highly specialized to opposite environments.

Gene swamping

The effective population size of the two parental populations also influences hybrid outcomes (Zinner et al., 2011). Often, hybrid zones form because one parental population is "invading" or migrating into the territory of a resident or local population. If the effective population size is larger in the invading population compared to the local population, such as the migration of the larger AMH population into Europe where the smaller population of Neanderthals is local to the environment in Europe, introgression often occurs in one direction, into the local species (Zinner et al., 2011). Invading species then get an advantage because their gene pool is larger. Therefore, any alleles from the local population that enter into the invader population through hybridization and backcrosses are only a small percentage of all possible alleles in the invader population's gene pool. This effectively dilutes the local alleles in the invader population. The alleles from the local population that introgress into the invader population have a lower probability of

disappearing due to genetic drift because they are now part of a larger growing population that has more allele types (Shurtliff, 2013). For the local population, however, the introgression of invader alleles through hybridization and backcrosses results in a much higher overall percentage of the invader alleles in the gene pool, assuming that the rate of backcrossing in the local population is equal to or greater than the rate of backcrossing in the invader population.

This process is called gene swamping, introgressed alleles from the foreign population overwhelm the smaller gene pool of the local population (Seehausen, 2004; Detwiler et al., 2005). Gene swamping can lead to outbreeding depression in the local population because the foreign invader alleles in its gene pool may not be as well adapted to the local environment (Seehausen, 2004; Detwiler et al., 2005). Gene swamping has also been referred to as "genetic assimilation," "contamination," "infection," "genetic deterioration," "genetic pollution," "genetic takeover," and "genetic aggression" (Rhymer and Simberloff, 1996).

Therefore, there is a real risk of extinction of the smaller population, replaced by either the invader or the hybrid (Rhymer and Simberloff, 1996; Mooney and Cleland, 2001; Levin, 2002; Wolf et al., 2011). Wolf et al. (2011) modeled in plants that such replacement and extinction could take place in as few as five generations. Detwiler et al. (2005) explore the conservation consequences of hybridization in Cercopithecine monkeys, concerned with the risk of extinction of endangered species, which are rare and have small populations, making them vulnerable to gene swamping during reticular events. It is possible that gene swamping took place between Neanderthals and AMH, resulting in the extinction of pure Neanderthal genotypes and the introgression of Neanderthal genes into the AMH gene pool (see Section 6.2) (Jolly, 2001; Cartmill and Smith, 2009).

Conversely, invaders can exhibit "immigrant inviability" in which immigrants are selected against due to reproductive barriers between invaders and native species (Nosil et al., 2005). In this case, the local population has the adaptive advantage in the environment and has higher fitness than the invading population and any hybrids that may be born. In the extreme, invaders, and possibly hybrids, would eventually die out, leaving the local population genetically unchanged.

Haldane's Rule

Hybrids can be constrained by Haldane's rule, that the heterogametic sex will be missing or sterile in the hybrid population (Haldane, 1922). In mammals, the heterogametic sex is male (XY), which means that males are often missing in the hybrid populations. The explanation for Haldane's rule is the same as the explanation for sex-linked disorders, for example colour-

blindness, muscle dystrophy, and hemophilia. The dominance theory states that if the inherited X chromosome in the male contains a harmful recessive allele that cannot be hidden by a dominant allele, as it may be in females by the second X chromosome, the recessive phenotype is expressed and can often lead to sterility or inviability in the male (Turelli and Orr, 1995). Haldane's rule is observed in many mammal taxa (Shurtliff, 2013), and in many primates (Zinner et al., 2011), such as in howler monkeys (Cortes-Ortiz et al., 2007; Aguiar et al., 2008), and gelada and olive baboon hybrids (Jolly et al., 1997).

Wu (2001) states that to understand the outcome of re-encounters between diverged species, researchers must understand the ecology, genetics and reproductive biology of the populations. These factors determine which scenario hybrids and parental species take: extinction, speciation, or further divergence. In the fossil record, researchers have only a limited understanding of the ecological relationship of the parental species to other species. Any information about the ecology of ancient populations is obtained from associated faunal and floral remains found with the species in an archaeological context, such as bones of food remains, other animal remains, pollen, or lake and ice cores and other paleoecological techniques to recreate ancient environments. Nor do researchers often have access to many different individuals from the same population to understand phenotypic and genetic variation, especially since preserved ancient DNA is rare. Hominin reproductive biology is mostly speculative, based upon our own reproduction as modern *H. sapiens* or other modern nonhuman primates, although dispersal patterns and intragroup or intergroup relationships can never be proven definitively.

2.1.2 Public Issue: Conservation Challenges in Hybrid Zones

Through habitat destruction and fragmentation, humans may inadvertently be creating or altering hybrid zones. Many researchers (Bullini, 1994; Rhymer and Simberloff, 1996; Dowling and Secore, 1997; Bynum, 2002; Levin, 2002; Detwiler et al., 2005) recognized human disturbances as a general driver for the creation and destruction of hybrid zones in mammals and specifically primates. For example, the hybrid zone between olive and yellow baboons in Amboseli, Kenya was only identified in 1982 though periodic censuses had been taken since the 1960s (Maples and McKern, 1967; Samuels and Altmann, 1986). Samuels and Altmann (1986) observed male olive baboons immigrating to more southern populations of yellow baboons and successfully mating to create mixed hybrid populations. The males may have begun moving south due to habitat destruction in the original olive baboon territory (Samuels and Altmann, 1991). Alberts and Altmann (2001) suggest that interactions with humans around Mt. Kilimanjaro were the impetus

for male olive baboons to emigrate and end up in yellow territory. They also suggest that if negative interactions between olive baboons and humans continue, the local population of olive baboons might go extinct and the hybrid zone will no longer receive new immigrants with olive genotypes. Eventually, the genes that have introgressed from olive into the yellow population in Amboseli will become a smaller percentage of a hybrid's genotype until little trace of the contemporary hybridization would exist (Alberts and Altmann, 2001).

Similarly, in East Asia, each peninsula is home to several unique species of macaque, with hybrid zones on the borderland of the parental species territory (Watanabe et al., 1991; Evans et al., 2001; Bynum, 2002). Watanabe et al. (1991) suggested that hybridization in macaques might be occurring due to disturbances and loss of habitat by humans, forcing populations to migrate and create overlapping territories. Bynum (2002) specifically identifies the construction of the Tawaeli-Toboli road, a major highway through macaque territory, as a significant factor in future hybridization interactions between two macaque species. Cortés-Ortiz et al. (2003) also hypothesized that human fragmentation of neotropical forests led to the formation of hybrid zones between howler monkeys.

Of course, hybrid zones also occur naturally, though some researchers believe that the incidence of hybrid zone creation may be greater due to human disturbance (Dowling and Secor, 1997; Bynum, 2002). Human disturbance has a potentially severe implication for endangered species. Gene swamping and extinction of rare, endangered species occurs more often in fragmented or smaller habitats, artificially created by humans (Levin, 2002; Detwiler et al., 2005). This is a public issue of which humans are contributing to the creation of hybrid zones and potential extinction of the smaller parental population.

The issue is made more complicated when countries allocate public funds to protect endangered species, regulated through legislature such as the Endangered Species Act in the United States. The Endangered Species Act currently has no established policy for hybrids (Levin, 2002). Should hybrids be protected, such as in cases of human interference through the introduction of an abundant related subspecies or species to hybridize with the endangered species? Is the endangered species still that species or is it now part of the more common species?

These questions are particularly controversial when conservationists decide to hybridize an endangered species with a more abundant related species in order to increase the genetic diversity of the endangered species. For example, when the Florida panther began showing dramatic population declines, partially due to male infertility caused by inbreeding and low genetic diversity, conservationists decided to introduce the Texas puma, a related subspecies, into the range of the Florida panther. The two subspecies readily interbred creating viable hybrids,

which began to increase the number of panthers in Florida, though it could be argued that the hybridization "compromises the Florida panther's very identity as a distinct subspecies" (Levin, 2002: 4-5).

Smaller populations that are endangered tend to have increasingly more homozygote individuals as potential mates become more related to each other, which occurred in the Florida panthers (Levin, 2002). As discussed earlier, homozygosity at loci allow deleterious recessive mutations to be expressed, lowering the fitness of populations with many homozygote individuals. Homozygosity also decreases the genetic diversity in the populations as alleles become fixed due to genetic drift or assortative mating. Lower diversity also lowers the resilience of the population to diseases or environmental disturbances. For example, monocultures, such as the production of rice in China, are an extreme example of low genetic diversity, where all individuals are genetically identical. One of the most persuasive arguments against monocultures is that the lack of diversity makes the entire production of corn vulnerable to a new disease, but when crop diversity is embraced, rates of disease lower, and yields increase (Zhu et al., 2000). Hybridization increases the number of heterozygote individuals in the population (Ackermann, 2010). Therefore, the deleterious recessive alleles are hidden to create a population with higher fitness, due to heterozygote advantage (Barton, 2001; Ackermann, 2010). Also, hybridization increases genetic diversity, so if a disease attacks the population, it may kill off some of the population, but not necessarily the entire population because some individuals have different allele combinations or mutations (Wu, 2001; Seehausen, 2004). Hybridization may sometimes be preferred as a conservation mechanism to save species at the risk of gene swamping leading to the extinction of the small, endangered population (Levin, 2002).

The public, the tax payers, should be aware of how their money is being spent for endangered and hybridized species. If we want to continue conservation efforts to save the many endangered primate species, our closest relatives, we need to take into account these additional complex ecological interactions caused by hybridization.

2.2 Identification of hybrids in the fossil record

Unfortunately, most of the examples of phenotypic differences between parental populations and hybrids are observed on external phenotypes of living animals or in genetic analysis. Very few studies have been conducted on skeletal material of extant primate species, the interest of this thesis (Ackermann et al., 2006; Ackermann and Bishop, 2009), though it is the skeletal material that is examined in the fossil record and used to identify potential hybrids.

Anthropologists can identify hybrids in the fossil record from morphological analysis of the skeletal remains or molecular analysis of ancient DNA. In the sections that follow, skeletal and genetic evidence for and against Neanderthal and AMH hybridization is presented, and it is concluded that hybridization, to some extent, occurred.

These two methods, skeletal and genetic, are fallible and have shortcomings that have led to debates in the literature about the evidence of hybridization, as discussed in Sections 2.2.2 and 2.2.3.

However, technological issues may not be the most contentious issue in hybrid identification. The other major component that must be discussed is the group of assumptions in which different researchers with particular paradigms apply to the analysis of fossils. Particularly in the Neanderthal and AMH taxonomic relationship, two paradigms are at odds with one another (Section 2.2.1). A paradigm is a way of understanding and evaluating the world that are often passed along an academic lineage from teacher to student (Campbell and Rice, 2011). They are unable to meet in common ground due to different initial, uncompromising assumptions (Willermet and Clark, 1995; Smith and Harrold, 1997; Campbell and Rice, 2011).

2.2.1 Paradigms in Paleoanthropology

The two paradigms, the Multiregional paradigm and the Replacement, or Out of Africa, paradigm, primarily differ in the assumptions of species designation, ability to interbreed, and place in recent human evolution as ancestral or sister taxa. Paleoanthropology in general is dominated by two paradigms based on speciation concepts: the lumpers and the splitters. Lumpers tend to group many different specimens into a single species, and splitters tend to categorize the same specimens into many different species (Campbell and Rice, 2011). Generally, the Multiregional scholars would be considered lumpers, while the Replacement scholars would be considered splitters (Campbell and Rice, 2011).

Multiregional scholars consider Neanderthals and AMH as the same species, but different subspecies, while Replacement scholars view Neanderthals as a different species from AMH. These species classifications have arguably biased concepts about interbreeding. Multiregional scholars hypothesized that Neanderthals and AMH interbred to create hybrids that are the ancestors of contemporary humans. Replacement scholars hypothesize that interbreeding did not occur between Neanderthals and AMH or interbreeding is negligible, therefore Neanderthals cannot be ancestral to contemporary humans, but are an extinct branch on the evolutionary tree (Klein, 2000; Wolpoff et al., 2004; Smith et al., 2005; Stringer, 2008; Tattersall and Schwartz, 2008; Cartmill and Smith, 2009). Some researchers have escaped the paradigmatic thinking to

establish other intermediate hypotheses, such as the Assimilation model in which Neanderthals and AMH interbred to some extent and are the ancestors of contemporary humans (Smith et al., 2005, Cartmill and Smith, 2009; Smith, 2013).

The continuous debate between the paradigms often stagnates research and collaboration. Willermet and Clark (1995) have assessed that scholars from both paradigms have only analyzed 11% of the total dataset that paleoanthropology has generated. This means that the hypotheses generated by both paradigms have been essentially based upon fundamentally different evidence that is selected by scholars to support their own theory (Willermet and Clark, 1995), using circular logic. Smith and Harrold (1997) have also found substantial differences between the Replacement and Multiregional views such as differences in definitions, what evidence is analyzed, and which features are emphasized in the analysis. However, Smith and Harrold (1997) propose a more accurate and less polarized view of the paradigm debates that "this dispute is not a clash between incommensurable paradigms, but rather reflects a potential spectrum of views between two poles" (1995: 134), which would include Assimilation as an intermediate theory between Replacement and Multiregional paradigms. The academic paradigm divide is perhaps a greater challenge to research than the limitations of technology and theory.

Discussion of the paradigms is crucial for understanding how the different groups of anthropologists interpret data. Particularly when examining recent human evolution, the public and academic images of a Neanderthal have influenced these interpretations. The Replacement scholars often have an impression of Neanderthals as intelligent and cultured, but not as intelligent and culturally complex as AMH (Smith, 2013). This impression developed from century-old images of Neanderthals as brutish, ape-like, devolved cavemen that cannot possibly be the ancestor to sophisticated contemporary humans (Drell, 2000). The evidence they collect often reflects this view of Neanderthals as non-human, a different species, and unable to interbreed with AMH (Willermet and Clark, 1995). The Multiregional and Assimilasionist image depicts a cultured, intelligent, complex human-like ancestor that has some superficial features that make them appear different, but do not alter behaviour significantly from AMH (Drell, 2000). The evidence they collect often reflects potential hybridization and similarities to AMH and contemporary humans (Willermet and Clark, 1995). Section 2.2.4 examines the social influences on research, using archaeology as an example, which I think tends to influence scholars of both paradigms.

2.2.2 Evidence from Skeletal Remains

The overwhelming academic perception of a hybrid in the fossil record is a specimen displaying a mosaic of features from both parents or intermediate features between both parents (see Harvati et al., 2007). As discussed in Section 2.1.1, extant hybrids exhibit a variety of morphologies that can be mosaic, intermediate, or more similar to one or the other parent depending on the genetic divergence and specialized adaptation of the parent species. The assumption of mosaic features in hominin fossils is therefore not entirely supported, though researchers continue to use this mental construct to identify potential hybrids in the archaeological record. In addition, the initial assumptions of the paradigms, Multiregional, Replacement, and Assimilation, can bias a researcher's interpretation of a specimen. Within paradigm thinking, any evidence is fit into a larger conceptual framework (Willermet and Clark, 1995). Thereby, the evidence cannot exist in the scholar's mind without being placed in the context of paradigmatic thinking (Willermet and Clark, 1995). For example, Laitman et al. (1996) accuse "lumpers", specifically Wolpoff, of paradigmatic thinking:

> This group, often called "lumpers," is primarily comprised of those who view Neanderthals as falling within the range of variation represented by diverse modern human populations (27 [Wolpoff, 1996]). Given their predilection, it *becomes a priori* impossible for them to view Neanderthals as ever being sufficiently different so as to exhibit highly derived respiratory anatomy or specialized respiratory or vocal behaviors. If they are us, then they cannot be fundamentally different. Observations on the difference between Neanderthals and extant populations are routinely dismissed as being within the range of "human" variation. (Laitman et al., 1996: 10544)

Therefore, because Multiregional and Assimilation scholars have hypothesized that hybrids or transitional forms existed, they will interpret skeletal remains as possible hybrids. Replacement scholars do not believe introgression occurred and therefore do not expect to find any hybrids in the fossil record.

For example, in 1998, João Mauríco and Pedro Souto found the skeletal remains of a child's left hand and forearm in Lagar Velho, Portugal (Duarte et al. 1999; Zilhão and Trinkaus, 2002). Further excavation in 1998 and 1999 revealed that the skeleton was an Upper Paleolithic child who had been buried about 24,500-25,000 years ago. Typically, skeletal remains found during this time period have been associated with AMH because it is believed that Neanderthals as a pure species disappeared in Europe about 28,000 years ago to 41,000 years ago depending on location (Cartmill and Smith, 2009: 347).

Duarte et al. (1999) found a mosaic of features in the Upper Paleolithic skeletal remains with AMH traits, such as the development of a strong chin, as well as Neanderthal traits, such as hyperarctic, or cold-adapted, body proportions, molar formation, and features of the mandible and

temporal bones (Zilhão and Trinkaus, 2002). Due to the mosaic of features, they hypothesized that the Lagar Velho 1 skeleton was a descendant of a hybridized population between Neanderthals and AMH. They concluded from the skeletal evidence that Neanderthals and AMH must have interbred (Duarte et al., 1999; Zilhão and Trinkaus, 2002). Tattersall and Schwartz (1999) argued against the hybridization argument. Tattersall and Schwartz (1999) reviewed Duarte et al. (1999) and derived a new conclusion, that the child was not a hybrid skeleton, but had features that are within the variation for early *H. sapiens*. They claim that what Duarte et al. (1999) identified as hyperarctic body proportions associated with Neanderthals is within the expectations of a robust AMH child. Additionally, the traits that Duarte et al. (1999) claimed to be Neanderthal, such as molar formation and mandibular traits, were reassessed by Tattersall and Schwartz (1999) to be typical of AMH. Replacement scholars also suggested that the hyperarctic body proportions may not be associated with Neanderthals, but is an adaptation of AMH to colder climates, parallel evolution (Stringer, 2001; Cartmill and Smith, 2009).

To support the hybrid position, scholars compared the limb/body proportions of the Lagar Velho 1 skeleton to other AMHs, but found that no other AMH has cold-adapted limb proportions, but present tropical adaptations (Zilhão and Trinkaus, 2002; Cartmill and Smith, 2009). Nor are the limb proportions in the Lagar Velho 1 skeleton the result of nutritional influences (Zilhão and Trinkaus, 2002; Cartmill and Smith, 2009). Therefore, they conclude that the limb proportions are indicative of admixture when most of the other traits are those of AMH (Duarte et al., 1999; Zilhão and Trinkaus, 2002)

Since the claim of admixture in Lagar Velho 1, the paradigms maintained the division between Multiregional and Replacement. The Multiregional and Assimilation scholars both cite Duarte et al. (1999) or Zilhão and Trinkaus (2002) as evidence of Neanderthal and AMH hybridization (Wolpoff et al. 2004; Smith et al. 2005). Zilhão and Trinkaus state, "Those who had taken hard-line positions against any Neandertal-modern human continuity rejected the interpretation (of evidence for admixture) without serious consideration" (2002: 26). They also state that Tattersall and Schwartz (1999) misunderstood the evidence, accusing them of misuse of terminology, lack of biomechanical understanding, and misquoting sources, dramatic accusations (Zilhão and Trinkaus, 2002: 26).

In contrast, Stringer (2008), a Replacement scholar, cites Duarte et al. (1999) as an example of evidence that the Multiregionalists depend on, but concludes that the skeleton in question is a robust AMH with shorter limbs as a short-term cold adaptation in AMH, the same conclusions as Tattersall and Schwartz (1999). Klein, a Replacement scholar, also cites Duarte et al. (1999), but remarks that "the anatomical indications are at best ambiguous, and few experts

recognize any hybrids" (2003: 1526), implying that this paper is anomalous in the literature. I also wonder whom Klein recognizes as experts and whom he excludes from expertise status, since many, not a "few", of the Multiregional and Assimilation scholars who were not directly involved with the study do recognize this skeleton as a hybrid.

Though the two investigations disagree about the ancestry of the Lagar Velho skeleton, they both share a conceptualization of a hybrid. Duarte et al. (1999) classify a hybrid as having intermediate features between either parental species or a combination of features from both parental species, a mosaic. Tattersall and Schwartz (1999) agree that this classification of a hybrid may exist in the initial cross between two species, the first and second generations. However, Tattersall and Schwartz (1999) differ from Duarte et al. (1999) in that Duarte et al. (1999) proposed that the Lagar Velho child was a member of a hybridized population that hybridized thousands of years earlier. Tattersall and Schwartz (1999) proposed that the hybrid would not exhibit such distinct features 200 generations after the initial interbreeding, though they do not suggest what such a hybrid would look like.

If this skeleton really is a hybrid many generations after the initial cross, then it would be expected that other primate hybrids would show the same mosaic of features, though such a study has not yet been conducted. The study presented in this thesis is a start, but it only presents a model of the first generation of baboon hybrids, which will help in the identification of only the first generation of Neanderthal and AMH hybrids.

A more recent example of potential hybrid population comes from the Les Rois pre-Gravettian, or Aurignacian, human sample (Ramirez Rozzi et al., 2009; Ahern et al., 2013). The evidence for admixture comes from two mandibles and teeth from Les Rois. One mandible and several isolated teeth are considered to be AMH because morphometric measurements of the teeth are more similar to other AMH samples. The other mandible, with cutmarks, and several isolated teeth are attributed to a Neanderthal because large dental size, perikymata numbers on the teeth, and the nonmetric traits, such as the distal accessory ridge on the canines, and the presence of subvertical grooves at the anterior fovea, were more similar to other Neanderthals. Ramirez Rozzi et al. (2009) have hypothesized three different scenarios to account for the evidence: 1) the Neanderthal child mandible was left over from consumption and/or used symbolically by AMH and only AMH made Aurignacian tools; 2) the population at Les Rois was made up of both AMH and Neanderthals who both made Aurignacian tools (possible hybridization); 3) the population at Les Rois was composed of all AMH that still presented plesiomorphic characters shared with Neanderthals and AMH variation is greater than previously thought.

Trinkaus has expanded on Duarte et al. (1999) and continued to propose a mosaic hypothesis for the form a Neanderthal and AMH hybrid. Trinkaus (2005) describes the Herto and Qafzeh-Skhul remains, identified as early AMH from Africa, as having a "mosaic of archaic African and modern human features." Oase 2 provides an additional example with "parietal bones that exhibit the marked curvature of modern humans but a frontal bone that is exceptionally long and flat" (Trinkaus, 2007: 7368). Trinkaus (2005) also describes the bridging of the mandibular foramena, a Neanderthal trait, in Oase 1, considered a modern human by most authors due to all other derived traits. In addition, Trinkaus (2007) identified that ~18% of AMH, such as Brno 2, Cro-Magnon 3, Dolní Věstonice 11, Pavlov 1, and Předmostí 1, 2, and 7, have occipital buns, a Neanderthal derived trait. Trinkaus argues that the addition of these Neanderthal traits in a mosaic of features of early AMH from Africa is an indication of admixture between the two populations.

In order to evaluate the ancestry of Mladeč 5 and 6, Wolpoff et al. (2001) compared the presence of nonmetric traits in Mladeč 5 and 6 to *Homo erectus* from Java (Ngandong 1, 4, 5, 6, 9, 10, and 11), early AMH in the Levant (Skhul 4, 5, and 9, Qafzeh 6 and 9, Singa), early AMH in Africa (Jebel Irhoud 1 and 2, Laetoli 18, Omo 1 and 2), European Neanderthals (Spy 2, La Chapelle, La Ferrassie, and Guattari), and an early AMH in Australia (WLH-50). Wolpoff et al. (2001) found that Mladeč 5 and 6 contained about equal amounts of nonmetric traits specific to early AMH and Neanderthals, concluding that Mladeč 5 and 6 have AMH and Neanderthal ancestry. Wolpoff et al.'s (2001) conclusions should be taken with caution. Bräuer et al. (2004) propose that Wolpoff et al. (2001) chose specimens that would support their hypothesis, such as a more robust Australian specimen rather than other available specimens that are more gracile. Bräuer et al. (2004) also suggests that more features could have been analyzed, and those that were analyzed are subject to interobserver error and create a phylogeny that contradicts other morphological and genetic data.

Ackermann took a different view. Unlike Trinkaus and Wolpoff and colleagues, Ackermann et al. (2006) did not specify that the nonmetric traits must be derived from ancestral forms, but instead emphasized that some types of nonmetric traits are more prevalent when there is genetic stress (such as inbreeding or hybridization), which creates developmental disturbances. Ackermann (2010) even argues against the concept of nonmetric ancestral traits as hybridization indicators because these nonmetric traits could also be interpreted as retained traits from the last common ancestor. To test the developmental disturbance hypothesis, Ackermann et al. (2006) used baboons as analogue species and found a higher frequency of nonmetric traits, not necessarily an ancestral form, in hybrid baboons compared to parental populations. In gorilla skeletal remains, Ackermann and Bishop (2009) found malar sutures, which are sutures on the

zygomatic bone, and 2 cases of sutures dividing the parietal bones, as well as anomalous dentition in the form of supernumerary teeth, and rotated molars.

Ackermann (2010) argues that the Lagar Velho 1, Peştera Muierii, and Oase 2 remains, which others have argued are hybrids (Trinkaus, 2005; Soficaru et al., 2006), are difficult to assess because the size of the population, from which these specimens belong, are too small to statistically conclude morphological relationships. Ackermann (2010) also identified possible hybrids in the fossil record, such as the Krapina Neanderthals, because they display a high rate (36%) of rotated third molars compared to other Neanderthals and AMH (6%), indicating hybridization between Neanderthals and some yet unidentified archaic human. She also found that Skhul 4, considered an AMH, has rotated premolars (P^4), and Skhul 5, considered an AMH, displays craniofacial asymmetry, an indicator of developmental instability. Qafzeh 6, 8, and 9, considered AMH, have dental crowding and Qafzeh 11, considered AMH, has a rotated left premolar (P_4). Amud 1, considered a Neanderthal, has a reduced right molar (M^3), which is highly unusual in other Neanderthals. Oase 2, considered an AMH, shows the opposite and has very large third molars. Therefore, changes in developmental timing must also be considered in hybridization identification. Ackermann, nor any other scholar that the author knows of, has analyzed the nasal cavity for nonmetric traits that could form from developmental instability resulting from hybridization, which is the subject of this thesis along with metric analysis.

Harvati et al. (2007) has come the closest to a comprehensive analysis of a hybrid in the fossil record by evaluating the mosaic hypothesis (from Trinkaus, Wolpoff, Duarte and their colleagues), the developmental instability nonmetric trait hypothesis (Ackermann), and size differences (Cheverud et al., 1993; Schillaci et al., 2005; Ackermann et al., 2006) in Cioclovina, a possible hybrid between Neanderthals and AMH. Like Wolpoff et al. (2001) above, Harvati et al. (2007) also compared the specimen of interest (Cioclovina) to AMH (from Africa, Levant, and Europe), and Neanderthals (from Europe). Harvati et al. (2007) concluded that Cioclovina is not a hybrid based on the hybrid models presented in each hypothesis. Cioclovina does not have a mosaic of features from Neanderthals and AMH, but all features fall into the range of AMH and contemporary humans. Cioclovina does not show any rare nonmetric traits, specifically sutural traits. Cioclovina does not show either heterosis or dysgenesis in centroid size (the square root of the sum of the squared distances of all landmark to the centroid of the object), though no groups differed in this measure. However, heterosis and dysgenesis can occur in hybrids, but on different features, as Ackermann et al. (2006) found in baboon hybrids. Therefore, by combining the distances of all landmarks to the centroid, the variable heterosis and dysgenesis of different features may be hidden.

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Such an analysis of future skeletal remains should be conducted similarly to Harvati et al. (2007) by taking into account the current hypotheses of hybridization. However, hypotheses of hybrid form will continue changing in the future and methods of identification from skeletal remains must change as well. Combining the different morphological and genetic methods may produce the most comprehensive picture of human evolution (Gaubert et al., 2005; Kelaita and Cortés-Ortiz, 2013), and overcome the assumptions of the paradigms. Such analyses also prompt collaboration between different fields and different paradigms, which should thereby increase the 11% of shared data interpretation within paleoanthropology (Willermet and Clark, 1995).

2.2.3 Evidence from Ancient DNA

The second form of evidence for hybridization in modern paleoanthropology is based on ancient DNA (aDNA). Many aDNA studies have already been alluded to above; however, they merit their own section due to their high status as the conclusive, objective "truth" in paleoanthropology. DNA studies are considered unbiased and removed from the active subjective interpretations of morphology and artifacts. The DNA analysis has altered the debate of whether hybridization occurred between Neanderthals and AMH. Overall, the DNA evidence indicates that at least some minimal hybridization did occur, thereby justifying my search for morphological indicators of hybridization.

In this section, I will demonstrate how these studies are not as objective as they first seem due to the numerous assumptions that must be made to make a conclusive statement, assumptions such as mutation rates, random mating, demographic variables such as populations size, fertility, death, or migration rates. Though technology will continue to improve, allowing us to be more confident in the aDNA results, currently, the assumptions made by aDNA studies have led to several methodological issues that ought to caution readers. I will also outline several instances in which long-standing arguments were reassessed and even swayed by the new aDNA evidence, specifically the pivotal articles Krings et al. (1997) and Green et al. (2010).

First, I will analyze the assumptions of DNA studies in general, and then I will analyze the assumptions and methodological issues of aDNA. The technological revolution that allowed DNA to be segmented, replicated, and examined pair by pair has, among some incredible advancements in research and medicine, led to the development of the phylogenetic species concept based on the differences of DNA sequences between taxa. In an oversimplified explanation, if the DNA sequences of two taxa (A and B) differ by only 1 pair, while the DNA sequences of two different taxa (C and D) differ by 5 pairs, the tenant of the phylogenetic species concept would conclude that taxa A and B are more similar to each other than taxa C and D are

similar to each other (Kimbel, 1991; Jolly, 2001). However, even to make such a seemingly simple conclusion, the researcher must consider what the implications are for choosing a particular part of DNA (technology is progressing to allow us to analyze longer and longer sequences, but there still must be a functional reason to do so), or choosing an outgroup to compare the differences between taxa (for example, taxon E is more distant from A, B, C, and D; for example, if A, B, C, and D are different primate populations, E could be a rodent).

Though the main purpose of phylogenetic studies tends to be the creation of phylogenetic trees, depicting which taxa are related to other taxa, geneticists often also calculate the general date of divergence between taxa. They are able to do this by assuming that the greater difference between pairs in a DNA segment, the longer the taxa have been separated. Researchers then assume a constant substitution rate, specifically the rate that neutral mutations enter the genome, by which they can then multiply the number of differences to estimate when species divergence occurred from the last common ancestor. This process depends on the "molecular clock" which estimates that the substitution rates for a specific clade remains constant for each generation or each year regardless of population size (Bromham and Penny, 2003; Pulquério and Nichols, 2007). However, in many cases, assuming a constant rate of mutation is not accurate. Indeed, there is evidence of mutation rates differing in different clades, differences during time periods (for example, it is estimated that since the Neanderthal and AMH common ancestor, mutation rates increased by 20 times in *H. sapiens*), or different rates in mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) within the same taxon, or different rates at different locations within mtDNA (Pulquério and Nichols, 2007; Endicott et al., 2009). Much of the controversy about the molecular clock in human evolution is the difference between the dates of divergence generated by the molecular clock methods and by the fossil record (Bromham and Penny, 2003; Endicott et al., 2009). Of course, dating using chemical ratios, as in radiocarbon dating, and relative dating based on artifacts and geological layers also have problems and inaccuracies that cannot necessarily confirm or refute the molecular clock dates.

Such dating inconsistencies have been speculated from site mixing, calibration, contamination, or what sample is used for dating. For example, many sites, including late Neanderthal and early AMH sites in Europe, have shown mixing of layers. Therefore, the principles of geology, such as the oldest layer is below newer layers, cannot be applied. Ovchinnikov et al. (2000) had such a site, Mezmaiskaya Cave, where the remains of a Neanderthal infant were found. Instead of trusting the approximate dates of the soil and rocks around the specimen (~45,000 years ago), they used a radiocarbon accelerator using the bone collagen of the specimen itself, providing what they consider a more accurate date for the

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specimen (~29,195 years ago). Unfortunately, many studies relying on radiocarbon dating may be flawed. The recent date for the specimen (~29,195 years ago) was since found to be caused by a contamination issue by modern carbon (Skinner et al., 2005). Skinner et al. (2005) analyzed non-hominin teeth in each archaeological layer using electron spin resonance (ESR) and presented a date of ~40,000 years ago for the same specimen. Subsequent radiocarbon dating of the same specimen presented a date of ~39,700 years (Pinhasi et al., 2011). Levels of carbon in the atmosphere during the last 50,000 years has been recalibrated based on a deep sea sediment core and validated by oxygen isotope ratios from an independent dating of ice cores from Greenland (Mellars, 2006). These recalibrated dates make sites older than we have previously estimated, which may greatly affect interpretation of the Neanderthal and AMH interactions in Europe because temporally overlapping sites may no longer have existed contemporaneously (Mellars, 2006). Cartmill and Smith (2009) suggest that the dates of AMH and Neanderthals may both be recalibrated similarly so that the AMH and Neanderthal ranges overlapped for the same amount of time, but earlier. These discrepancies create greater gulfs between molecular clock methods and radiocarbon methods of dating.

For aDNA in particular, there are issues of retrieving the often degraded DNA from remains without contaminating the sample. Conditions for the preservation of DNA are very difficult to obtain. DNA is naturally broken down by enzymes when cell compartments break down after the organism dies, then it may be subjected to waves of bacteria, fungi, and insects (Pääbo et al., 2004). Researchers attempt to test and control for preservation by adhering to a set of guidelines (Cooper and Poinar, 2000; Gilbert et al., 2005). Researchers check other remains from the same area for preservation as well as contamination. They search for other biomolecules, such as collagen, which would indicate good sample preservation. Researchers are also cautious if they observe long segments of DNA fragments or other unexpected molecular behaviour from DNA because it indicates that the DNA degraded to some degree (Cooper and Poinar, 2000; Gilbert et al., 2005). Smith et al. (2001) is also concerned with the environmental conditions of the sites where the remains are found. For example, the cold temperatures in Mezmaiskaya Cave created a great environment for preservation, from which Ovchinnkov et al. (2000) recovered ancient DNA from Neanderthal remains. Smith et al. (2001) analyzed 39 Neanderthal cave sites, and found only 9 sites that would have the temperature and environmental conditions, such as air and soil humidity, soil pH, and phosphorus content of the soil, for DNA preservation (Ovchinnikov reply to Smith et al. 2001). Even in ideal circumstances, such as rapid desiccation of tissue after death, for example, the method of preservation in Ötzi, the iceman, or when DNA is absorbed into a mineral matrix, the DNA will still slowly continue to degrade. If retrieved

before complete desiccation, polymerase chain reaction (PCR) may amplify the damaged DNA segment to obtain large enough samples to study (Pääbo et al., 2004). However, by extracting the DNA from the sample, bringing it to a lab and analyzing it, researchers might introduce contaminants, which can compromise the results.

Researchers attempt to control for contamination of ancient DNA samples with modern DNA. The cautionary tale for researchers to be particular conscious of potential contamination in ancient DNA comes from the misattribution of "dinosaur" DNA that was re-analyzed as a Y-chromosome from modern humans (Zischler et al., 1995; Green et al., 2000). In general, guidelines for working with ancient DNA recommend researchers to: i) isolate aDNA samples from other projects; ii) use negative control extractions (sample without DNA) and amplifications; iii) reproduce results from multiple PCRs and extractions; iv) clone products to assess damage, contamination, and amplification errors; v) replicate results by independent research groups; vi) quantify the starting templates in the reaction (quantifying the amount of original DNA extracted) (Cooper and Poinar, 2000; Gilbert et al., 2005). For research with Neanderthals and AMH, in particular, extra caution must be taken due to the similarities between genomes. Green et al. (2009) advocate the creation of a library of all possible contaminants in a laboratory, as well as a library of each individual sampled in order to decipher fixed differences in the Neanderthal genome and contemporary humans. While such libraries are created, Green et al. (2009) have proposed additional guidelines for working with aDNA:

> Interim approaches based on mtDNA differences between Neandertals and current humans, detection of male contamination through Y chromosomal sequences, and repeated sequencing from the same fossil to detect autosomal contamination. (Green et al., 2009: 2494)

These precautions are essential for understanding the implications of DNA analysis, especially in studies comparing ancient Neanderthal or AMH data to contemporary humans, where the DNA is very similar (Krings et al., 1997; Ovchinnikov et al., 2000; Green et al., 2010).

To understand the subsequent issues associated with aDNA, it would be useful to employ specific examples from paleoanthropology. There are two major periods of genetic investigation around the Neanderthal question: the era of mitochondrial (mt) DNA since 1997, followed by the first publication of nuclear DNA (nDNA) in 2010. mtDNA provides supportive evidence for the Replacement paradigm, but the nDNA provides supportive evidence for the Multiregional and Assimilation paradigm. When the evidence supported the presupposed paradigm, the scholars of that paradigm celebrated, while scholars of other paradigms developed alternative hypotheses and pointed out methodological flaws. However, the evidence from nDNA has led to a surprising

theoretical shift by a primary scholar of the Replacement paradigm, transitioning the debate from whether or not hybridization occurred, to the extent that it occurred and affected the genome of AMH.

Between 1997 and 2010, genetic evidence in paleoanthropology primarily referred to ancient mtDNA. Because mtDNA is inherited from mother to offspring, it was hypothesized that if Neanderthals interbred with AMH, then some lineages of contemporary humans, where the ranges of Neanderthals and AMH overlapped, would have inherited Neanderthal mtDNA (Serre and Pääbo, 2008). In 1991, Krings and colleagues began working on the extraction, amplification, and sequencing of the first Neanderthal mtDNA from the right humerus of Neandertal 1, the 1856 Neanderthal from Germany. In 1997, Krings et al. (1997) published the pivotal study that sequenced a segment of the Neanderthal mtDNA and compared the sequence to contemporary humans. They concluded that "the Neandertal sequence falls outside the variation of modern humans… this suggests that Neandertals went extinct without contributing mtDNA to modern humans" (Krings et al., 1997: 19).

The conclusions of Krings et al. (1997) set off a wave of publications in response. The Multiregional and Assimilation scholars argued that thousands of years after interbreeding took place, there was selection or genetic drift against the Neanderthal mtDNA lineages after interbreeding, both of which would erase the signature of Neanderthal mtDNA in living humans, but still recognizes the possibility of interbreeding (Nordborg, 1998; Pearson, 2004; Trinkaus, 2005; Hawks, 2008). They also argue that the sample size of ancient Neanderthal and AMH mtDNA is too small to determine if any lineage has survived (Nordborg, 1998). Concluding population level implications from a small sample of the population (in the case of Krings et al. (1997), 1 Neanderthal, 2051 contemporary humans, and 59 chimpanzees) is an inherent problem with aDNA studies (Gilbert et al., 2005). Serre et al. estimated that "under the model of constant population size, about 50 early modern human remains would need to be studied to exclude a Neandertal mtDNA contribution of 10%" (2004: 316). However, Arnold and Meyer (2006) argue that the mtDNA evidence does not conclusively reject hybridization because nuclear introgression can occur between taxa without mtDNA introgression, as observed in chimpanzee subspecies and between chimpanzees and bonobos. The Multiregionalists and Assimilationists also argue against the conclusions from the mtDNA studies because they place more objective weight on the skeletal and archaeological evidence, citing the inherent difficulties of ancient DNA studies (Trinkaus, 2007; Churchill and Smith, 2000): "Despite paleogenetic evidence to the contrary, consideration of certain morphological details evident in the last Neandertals and the earliest modern humans in Europe suggests that this coexistence also entailed a significant degree of

genetic exchange as well" (Churchill and Smith, 2000: 106). Therefore, they argue that interbreeding still took place, but that the mtDNA evidence does not capture this signature of interbreeding.

Meanwhile, further mtDNA studies were being published, confirming the findings of Krings et al. (1997). Ovshinnikov et al. (2000) published the second sequence of Neanderthal mtDNA from two ribs of an infant Neanderthal from Mezmaiskaya Cave. Compared to mtDNA from 5,846 contemporary humans, Ovchinnikov et al. concluded, "Their [Neandertal 1 and the Mezmaiskaya infant] mtDNA types have not contributed to the modern human mtDNA pool. Comparison with modern populations provides no evidence for the multiregional hypothesis of modern human evolution" (2000: 490). Schmitz et al. (2002) sequenced mtDNA from a Neanderthal specimen from Neander Valley (NN1) which was similar (1-4 pairwise differences) to previously published sequences of Neanderthal mtDNA. Caramelli et al. (2003) sequenced the same region of mtDNA that Krings et al. (1997) sequenced, but this time in two AMH (Paglicci-25 and Paglicci-12), finding the AMH mtDNA to be very similar to contemporary humans, but diverged from the available Neanderthal sequences. Serre et al. (2004) analyzed four additional Neanderthals (Vindija 77, Vindija 80, Engis 2, and La Chapelle-aux-Saints) and five additional AMH (Mladeč 25c, Mladeč 2, Cro-Magnon, Abri Pataud, and La Madeleine), but found Neanderthal-like sequences, based on previous studies, only in the Neanderthals, not the AMH. Green et al. (2008) sequenced the first complete mtDNA of a Neanderthal (Vindija 33.16) and came to the same conclusions as earlier studies and estimated a small effective population size for Neanderthals. Then Briggs et al. (2009) published the entire mtDNA sequences of 5 additional Neanderthals (Vindija 33.25, Feldhofer 1 (also known as Neandertal 1), Feldhofer 2, Sidron 1253, and Mezmaiskaya 1) and concluded that the effective population size of Neanderthals must have been less than 3500 females. Ancient DNA evidence seemed to strongly support the Replacement model, for which Replacement scholars were quite excited (Tattersall and Schwartz, 1999; Stringer, 2008; Tattersall and Schwartz, 2008).

However, the weight of evidence shifted with the publication of Green et al. (2010). Green et al. (2010) sequenced segments from three Neanderthal nuclear DNA samples (Vindija 33.16; Vindija 33.25 and Vindija 33.26) to create a draft of the Neanderthal genome, and then compared Neanderthal nDNA to a small sample of modern humans from Europe (n=1), Asia (n=2), and Africa (n=2). They concluded that 1-4% of the genomes of contemporary Europeans and Asians are derived from Neanderthals, indicating that at least minimal inbreeding between Neanderthals and AMH occurred. This DNA evidence supported the Assimilation model and the modern Multiregional model. "I jumped up and down when the Neandertal genome came out,"

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said Fred Smith (Bower, 2012: 24) because Green et al. (2010) provides evidence that supports his model, the Assimilation model, which proposed significant interbreeding between Neanderthalls and AMH. While Hawks (2012) recognizes that the 1-4% of the genome may be caused by polymorphisms between Neanderthals and AMH that existed in both genomes prior to their divergence or result from linkage disequilibrium (Eriksson and Manica, 2012), Hawks (2012) also believes that not all of the genome similarities can be explained without introgression. Yotova et al. (2011) supports the findings of Green et al. (2010) by discovering that 9% of non-African populations have Neanderthal ancestry in X- chromosomes.

The response of the Replacement paradigm was varied. Schwartz and Tattersall (2010) dismissed the evidence as uncorroborated, placing more weight on the skeletal evidence to support their model:

> Whether or not this conclusion will stand as more data come in, it is most likely on the basis of current knowledge both of the fossil record and of the effects of hybridization on morphology that *H. neanderthalensis* made no identifiable morphological contribution to any known fossil (or modern) population of *H. sapiens*. (Schwartz and Tattersall, 2010: 118)

However, many researchers, such as Trinkaus and Smith, would argue that transitional forms, or hybrids, between Neanderthals and AMH exist (see Section 2.2.2). In 2011, in a section about the genetic evidence for hybridization in a broad review of recent human origins, Tattersall cites the mtDNA evidence (Serre and Pääbo, 2008) as proof that interbreeding did not occur, as "there was clearly no biologically significant genetic interchange" (2011: 49). Tattersall (2011) does not acknowledge the Green et al. (2010) article when discussing Neanderthal introgression, even though the 2010 article (Schwartz and Tattersall, 2010), quoted above, makes it clear that he was familiar with the nuclear DNA evidence from Green et al. (2010).

One Replacement scholar, Chris Stringer, altered his view after the publication of Green et al. (2010). Prior to Green et al. (2010), he hypothesized that there was no interbreeding between Neanderthalls and AMH (Stringer, 2008), but after Green et al. (2010), he incorporated into his hypothesis that there may have been some interbreeding (Stringer, 2012). Stringer added that the extent of interbreeding is limited and does not significantly affect or alter the genome of AMH nor contemporary humans, differentiating his view from the Assimilation model (Stringer, 2012). Stringer's modified view is known as the Mostly Out of Africa model, originally developed by Relethford (2001) and is very similar to the model developed by Templeton (2002) (Bower, 2012). However, these models (Relethford, 2001; Templeton, 2002) are specific to genetic evidence, while the Assimilation model accommodates evidence from any method and

was the first to propose interbreeding between Neanderthals and AMH with a strong influence from Africa (Smith et al., 1989).

Combining the results of the mtDNA and nDNA, Neanderthals and AMH probably did interbreed to some extent. Mason and Short (2011) attempted to unite the DNA evidence by suggesting that male Neanderthals must have mated with female AMH in order to introduce Neanderthal nDNA, but not maternally inherited mtDNA into the genomes of contemporary humans. This mating pattern may be consistent with hybrid zone theories, in particular heterozygote advantage, which suggests that females will chose mates from a different population when they enter a new habitat and disassortative mating may potentially give hybrid offspring advantageous alleles (Seehausen, 2004; Pfennig, 2007). For example, it is possible that Neanderthals contributed immunity to Northern diseases to the immigrating population, AMH, which would increase fitness (Mendez et al., 2012).

2.2.4 Archaeological Evidence

The archaeological record preserves the material culture of the Neanderthals and AMH. Binford's middle range theory and Spaulding's view of archaeology classifies archaeologists as ethnographers of the past, interpreting culture from artifacts (Lyman, 2007). The paradigms differ in how they perceive culture in Neanderthals and AMH from artifacts, interpreting Neanderthals as either less or equally sophisticated and complex as AMH culture. Beneath this perception lies the assumption that mate selection is dependent upon recognition of the other taxa as similar enough to mate, both physically and culturally. Therefore, if Neanderthals had a culture and intelligence that AMH could relate to and if AMH viewed Neanderthals as physically similar, and vice versa, Neanderthals and AMH would recognize each other as potential mates, leading to hybridization. Mate recognition is the central argument to the species concept of Recognition (Kimbel, 1991; Tattersall, 1991). Unfortunately, culture, intelligence, and mating preferences are very difficult to impossible to quantify from the incomplete archaeological record.

While interpreting the archaeological record, scholars can be biased by subconscious preconceived assumptions of Neanderthal intelligence based on their paradigm alignment. In particular, the Replacement scholars have a preconception of Neanderthal culture as too simplistic and Neanderthal skeletons as too archaic and distinct to be recent human ancestor. The paradigm thinking removes the possibility of Neanderthals interbreeding with AMH to become ancestors of contemporary humans (Willermet and Clark, 1995). They are rejecting hybridization due to paradigm thinking established by historical academic and public perceptions of Neanderthals. Paradigm thinking also permeates into preconceptions held by Multiregional scholars, who view

Neanderthals as intellectual and cultural equals to AMH and as not so distinct that mating would not occur. For a Multiregional scholar, it would be logical that Neanderthals and AMH interbred, just as throughout history, human populations interbred with foreigners.

Paradigm Thinking in Archaeology

Archaeologists interested in interbreeding between Neanderthals and AMH focus on two temporal periods in Europe, the Middle and Upper Paleolithic, when Neanderthals and AMH may have come into contact. The Middle Paleolithic occurred from ~ 250,000 years ago to, conservatively, ~40,000-50,000 years ago (Klein, 2000) or 28,000-41,000 years ago in central Europe (Churchill and Smith, 2000; Cartmill and Smith, 2009), depending on the sites being dated. The Middle Paleolithic was followed by and, to some extent, overlapped with the Upper Paleolithic which occurred between 50,000 or 30,000 years ago to ~10,000 years ago (Klein, 2000).

The Middle Paleolithic stone tool assemblage, called the Mousterian assemblage, is associated in the archaeological record with Neanderthals in Europe. Neanderthals are assumed to be the toolmakers because Neanderthal skeletal remains have been found alongside Mousterian tools and Neanderthals were also the only known hominins in Europe at this time (Klein, 2000; Smith et al., 2005). The Mousterian tools are considered more advanced and varied compared to the assemblage that existed earlier in association with *Homo erectus*, the Acheulean assemblage (Klein, 2000). The archaeological record shows that at start of the Upper Paleolithic, a new assemblage appeared, the Aurignacian. The Aurignacian is associated with AMH because it coincides with the timing of migration out of Africa and is found with AMH remains. Compared to the Aurignacian assemblage, the Mousterian assemblage is considered to be more homogenous and less complex (Klein 2000; Klein 2003).

In Africa, the Replacement scholars report that *H. sapiens* experienced a major leap in mental capacity between 50,000-70,000 years ago, the start of the Late Stone Age (Klein, 2000; Klein, 2003; Bower, 2012). Prior to this leap, *H. sapiens* tool assemblage in Africa resembled the Mousterian tools, but after the leap, the tool assemblage was more varied and geographically distinct, becoming the Aurignacian assemblage in Europe when *H. sapiens* migrated (Klein, 2000; Klein, 2003). The Replacement advocates, as well as many unassociated scholars, propose a rapid replacement of the Mousterian assemblage by the Aurignacian assemblage after 40,000-50,000 years ago, the same time period that AMH migrated to Europe (Klein, 2000) (See Sextion 1.2 for alternative estimates of dates for AMH arrival in Europe). The Replacement scholars extend the implications that only AMH are associated with the Aurignacian assemblage, making

the claim that only AMH had the mental capacity to create a more complex assemblage with a greater variety of tool types, different materials for the creation of tools, and the beginnings of art (Klein, 2000; Klein, 2003). The Replacement scholars propose that the Neanderthals lacked the mental capacity to create the more complex tool assemblage (Klein, 2000; Klein, 2003; Wolpoff et al., 2004).

Other scholars have disputed the leap in mental capacity. Instead of a sudden change in technology, scholars have found evidence of a gradual shift in Africa over 30,000 years between the Mousterian-like artifacts in the Middle Stone Age, or the Middle Paleolithic in Europe, to the more complex Aurignacian-like assemblage of the Late Stone Age, or Upper Paleolithic in Europe (McBreaty and Brooks, 2000; Cartmill and Smith, 2009). Indeed, stone points from the more complex assemblage began appearing in Europe and Africa prior to when researchers believe AMH moved into Europe. Therefore, Neanderthals would have been making these complex tools in Europe (Lazuén, 2012). The Middle Stone Age technology was also found in association with AMH. McBreaty and Brooks (2000) argue that a leap in mental capacity did not occur because the physical adaptations in skull structure occurred long before the Late Stone Age technology developed. Therefore, the transition was probably not the result of a leap in mental capacity. However, if AMH in Africa were using tools similar to those used by Neanderthals during the Middle Stone Age, or the Middle Paleolithic, then it is possible that the argument that Neanderthals lacked the mental capacity to create more complex tools is inaccurate.

Preconceptions of Neanderthals

Anthropologists, like all people who are exposed to the general media, may hold preconceived notions about human ancestors. The Replacement scholars may hold preconceived notions of Neanderthal and AMH intelligence. Multiregionalist scholars, view Neanderthals as intellectual and cultural equals to AMH. The notion that Neanderthals lacked mental capability may stem from depictions of Neanderthals in the popular media that exclude Neanderthals from the definition of human. These depictions often show the Neanderthals as brutish, non-human, ape-like creatures, which developed rapidly after the initial discoveries of Neanderthals (Drell, 2000; Sommers, 2006). These preconceptions in both paradigms influence how scholars interpret archaeological evidence.

After the publication of Charles Darwin's *On the Origin of Species* in 1859, Neanderthals became the first recognized fossil ancestor, though its place in human ancestry was contested. Evolutionary theory at the time hypothesized the existence of a missing link that contained human-like features, in particular a large brain, and ape-like features in the general body form.

The Neanderthal's image adopted the intermediate features that researchers hypothesized (Moser 1998: 136). The first image of a Neanderthal to the public depicts a brutish Neanderthal and appeared in 1873 in *Harper's Weekly* based on a skeleton from Neander Valley with the accompanying text: "A more ferocious-looking, gorilla-like human being can hardly be imagined" (Moser, 1998: 137; Drell, 2000: 9) (Figure 1a). In 1886, Maximim Lohest reconstructed a Neanderthal based on the Spy 1 Neanderthal anatomy, which he and Julien Fraipont interpreted to have been ape-like, walking with bent knees (Trinkaus and Shipman, 1993; Drell, 2000) (Figure 1b). In 1909, anatomist Marcellin Boule and illustrator Frantisek Kupka reinterpreted the image of the Neanderthal as even more ape-like with a hunched, awkward walk (Figure 1c). Boule provides support for this view by using his authority as an anatomist, by rigorously examining and documenting the La Chapelle-aux-Saints Neanderthal skeleton to create what he believed to be a scientific portrayal (Drell, 2000; Sommer, 2006). Boule compared the skeleton to apes and humans, but emphasized the ape-like features, resulting in a reconstruction of strong prognathism, a thrust forward head, and a hunched back of an ape rather than an upright bipedal spine, moderate prognathism, and modern-like head balance over the spine (Drell, 2000: 6).

Boule considered Neanderthals a missing link, but not a direct ancestor to contemporary humans (Drell, 2000; Sommer, 2006). In the illustration of the La Chapelle-aux-Saints Neanderthal, which has been reprinted many times and remains iconic today, Boule presents a view of Neanderthals as the cultural "other," developing a rift between "us" (contemporary humans) and "them" (Neanderthals) (Sommer, 2006).

> His [Boule's] conclusions were to influence the image of Neanderthals more than any previous deductions; they were scientific, detailed, rigorous and methodologically unimpeachable, but also building upon earlier work. Boule described each part of the skeleton systematically and compared it to other Neanderthal material, apes and humans. (Drell, 2000: 6).

Yet, the well-known image of Boule's Neanderthal is a brutal creature hunched around a cliff, waiting to attack with his primitive club. Because Boule believed that he had scientifically examined the skeleton, though it is apparent now that his reconstructions were flawed, this image was considered an accurate representation that continued to influence scientists' understanding of Neanderthals (Drell, 2000: 9). However, this Neanderthal image is of "an evolutionary failure: a brutish, club-bearing caveman" (Sommer, 2006: 231), which has no claim as a direct ancestor of modern humans.

The image in the minds of Multiregional and Assimilation scholars portrays Neanderthals with modern human-like intelligence, fully capable of being human ancestors. This image appeared about half a century after Neanderthals were originally discovered. In 1911 (Figure 1d) Sir Arthur Keith commissioned a drawing with artist Amadée Forestier of the same La Chapelle-aux-Saints skeleton in response to Boule's depiction in 1909 (Sommer, 2006; Moser, 1998). Keith advocated a human-like rather than an ape-like Neanderthal in order to depict Neanderthals as the ancestors to the oldest AMH skeleton then known, the Galley Hill Man (Sommer, 2006). The drawing, entitled 'Not in the "Gorilla" stage,' in response to Boule's interpretation, portrays a modern human-like ancestor: a groomed, clothed, and adorned pensive man sitting in his cave by a fire and using a stone tool to work bone after a presumably successful hunt (Drell, 2000; Sommer, 2006: 230). However, at the time, there was no evidence to depict this skeleton with the cultural artifacts shown in the drawing. This image is just as biased as Boule's, but in the opposite direction.

In part, the images and paradigms are influenced by concepts of human uniqueness. Since Linnaeus, scientists have been trying to draw a line between humans and animals, often focusing on culture, measures of intelligence, language capability, and, biologically, relative brain size (Cartmill, 1990). Scientists have a tendency to consider humans special and unique from other animals. Therefore, "the stories that we tell about human origins, even if they are true stories, are myths; and the general point of those stories is explaining – and legitimating – human control and domination of nature" (Cartmill, 1990: 178). Many lines have been drawn separating modern humans from pre-modern humans, early human lineage from other ape lineages, and humans from animals.

During the last century, the definition of human was challenged by new fossil findings, such as the australopithecines, and first members of the genus *Homo*. Scientists placed australopithecines in the lineage of modern humans because they had the unique trait of bipedalism, separating them from other apes.

The distinction between *Australopithecus* and *Homo*, is cranial capacity, a proxy for brain size, though not the ability to make tools (Cartmill and Smith, 2009). "It is tempting to think that stone tools are the exclusive hallmark of the genus *Homo*, but that proposition cannot be demonstrated by the archaeological record" (Cartmill and Smith, 2009: 265). Scientists have now witnessed tool use in a variety of species of monkeys, apes, birds, and more. Primatologists and others who study the complex structures of animal life, have found that, in the words of Jane Goodall from her TED talk, "There isn't a sharp line dividing humans from the rest of the animal

kingdom. It's a very wuzzy line. It's getting wuzzier all the time as we find animals doing things that we, in our arrogance, used to think was just human."

Prior to the 1970s, the groups now known as *Homo heidelbergensis*, *Homo sapiens*, and Neanderthals were considered the same species, archaic *Homo sapiens*. They were grouped in the same species designation as contemporary humans because they shared an average brain-size with contemporary humans. However, they were termed "archaic" because they still displayed primitive-looking cranial morphology (Cartmill and Smith, 2009: 292-293).

The differences in anatomy and technology classified Neanderthals as dissimilar to modern humans (being the people who produce agriculture, build cities, and explore space), which, anatomically, the AMH were considered to be. Neanderthals became an "other" to which modern humans can be compared (Sommer, 2006: 209). Some researchers have argued that *H. sapiens* are the only "symbolic" species, as seen in their complex artifacts, and therefore are more intelligent than Neanderthals (Holliday, 2008). Intelligence may be a prezygotic isolating mechanism that prevented mate recognition between AMH and Neanderthals (Holliday, 2008). If it were shown that Neanderthals have equally complex tools and symbolic cultures, would their placement within human history move over the line to accompany modern humans, oe will thye always be the cultural "other"?

Neanderthal Culture

Multiregional and Assimilation paradigms view Neanderthals as containing the mental capacity for complex culture and technology. These paradigms propose that the Aurignacian technology may have been made by both Neanderthals and AMH, because there was a transition from Mousterian technology to Aurignacian technology by region (Wolpoff et al., 2004; Smith et al., 2005). They argue that there is no evidence of precursors to Aurignacian tools outside of Europe, and that the Aurignacian assemblage varies geographically, following Mousterian regional differences (Smith et al., 2005). The archaeological site, Arcy-sur-Cure, which dates 40,000-38,000 years ago, contains a unique assemblage of tools, Châtelperron, which are considered evidence of the transition to a more advanced and varied technology. These tools that are both Mousterian- and Aurignacian-like, also known as transitional tools, were found in association with Neanderthal remains at Arcy-sur-Cure (Churchill and Smith, 2000; Klein, 2000; Smith et al., 2005). Two hypotheses explain this transition: the influence of AMH culture on Neanderthals, who may have the mental capacity to copy more complex and specialized technology, but not to conceptualize it themselves (Klein, 2000); or Neanderthals developed Aurignacian assemblages independently from any external influence (Smith et al., 2005). Transitional tools between the

Middle and Upper Paleolithic have been identified in the fossil record since the late 19th century (Tartar, 2012). There is little evidence to conclude which hypothesis was more probable because Aurignacian assemblages are often not found in association with any skeletal remains. When they are found with skeletal remains, artifacts are often found with isolated teeth, which are difficult to assign to one species or the other (Churchill and Smith, 2000; Smith et al., 2005; Svoboda, 2005; Bailey et al., 2009).

Other Neanderthal culture has also been discovered at Neanderthal sites. At Arcy-sur-Cure, Neanderthals made personal ornamentation and built permanent structures (Churchill and Smith, 2000; Klein, 2000; Smith et al., 2005). They cared for their sick and injured, which let them survive after teeth were lost and heal after traumatic injuries (Hublin, 2009). In addition, evidence from pollen associated with flowers and found with Neanderthal remains even suggested that Neanderthals held burials for their dead (Solecki, 1971). Speculatively, Neanderthals may have had a form of language because they have the FOXP2 gene, which is essential to speech, and appropriate anatomical adaptations (Krause et al., 2007).

The archaeological evidence about the sophistication of Neanderthal culture is inconclusive. Though there is evidence of culture, presented above, a lot of additional evidence has effectively been retracted. For example, the new dating of the personal ornamentations, including an ivory ring, that were found at Arcy-sur-Cure, no longer fall within the Middle Paleolithic, but are probably from the "Proto-Aurignacian" level above, about 35,000 years before present and associated with AMH (Mellars, 2010). However, this proposition has been countered by Caron et al. (2011). Experimental archaeology has found that the famous Mousterian "flute" made of a cave bear femur is probably the result of carnivore activity, though the debate between Neanderthal manufacture or carnivore activity continues (Morely, 2006; Tuniz et al., 2012).

Attempting to identify cultural sophistication from artifacts is a very difficult task that will probably never be conclusive. Even if the two groups, Neanderthals and AMH, recognize the other as physically similar, and they have overlapping territories, culture may still be an effective barrier to reproduction because they may not recognize the other as a potential mate. It would be much more difficult for hybrids to occur in such a context. However, interpretation of artifacts is influenced by the preconceived assumptions, from century old images, about Neanderthal intelligence associated with the paradigm under which that particular scholar was educated and continues to analyze evidence. The cultural potential for hybridization is influenced strongly by paradigm thinking, which may be behind the conclusions that Neanderthals could or could not be the ancestors of contemporary humans from the inconclusive, incomplete archaeological record.

2.2.5 Summary

This chapter summarized the theory behind the outcome after divergent populations come back into contact. Depending on a variety of ecological and demographic factors, populations can go extinct, fuse, create new species, or remain genetically isolated. These outcomes have become a conservation concern for small primate populations that are forced into contact due to habitat destruction and fragmentation by humans. The implications of this theory for Neanderthals and AMH will be discussed in Chapter 6.

Forms of evidence for Neanderthal and AMH hybridization have also been analyzed. Skeletal and genetic evidence has been interpreted as evidence both for and against hybridization, though the latest genetic evidence most strongly supports hybridization. Despite this evidence, researchers associated with opposite paradigms disagree about the cultural potential for hybridization, assuming that Neanderthals are or are not intelligent and sophisticated enough to be the ancestors of contemporary humans based on the archaeological evidence. I can justify the purpose of conducting research to identify trends associated with hybridization through the skeletal and genetic evidence, though I may never be able to convince Replacement scholars that hybrids may have existed because such a possibility lies outside of their paradigm thinking. By explaining the reasoning behind the interpretation of archaeological evidence, I hope to have convinced the reader that hybridization was possible and that the reason for my research is substantiated.

Chapter 3
Research Design

This project employed an analysis of the nasal cavity in analogue species (olive and yellow baboons) to identify morphological, metric and nonmetric, indicators of hybridization. These indicators were applied to the fossil record to identify potential hybrids between Neanderthals and AMH. The choice of studying baboons is discussed in Section 3.1 and the choice of analyzing the internal nasal cavity is discussed in Section 3.2.

3.1 Selection of Analogue Species: Olive and Yellow Baboons

It is not possible to perform a direct analysis of morphometric traits in Neanderthal and AMH hybrids because researchers currently have no way to verify which specimens are hybrids. Any traits discovered on a Middle to Upper Paleolithic specimen thought to be a hybrid can also be argued to be at the extreme end of variability for either species, as Tattersall and Schwartz (1999) stated in response to Duarte et al. (1999). It is also not possible to analyze the skeletons of contemporary *H. sapiens* because all humans living today are the same species, therefore hybrids today do not exist. It would be interesting to study the skeletons of offspring from parents who are both adapted to different environments, such as cold to hot adapted, or high altitude to sea level adapted, humid to dry adapted, etc. However, such collections are rare and the research may be hindered by the politics surrounding race, and ownership of human remains.

Because the species of interest cannot be examined directly, a model of similar species and their hybrids was used to understand morphological changes in hybrids. For this study, baboons, specifically olive baboons (*Papio anubis*), yellow baboons (*Papio cynocephalus*), and their first generation hybrids (*Papio anubis* x *Papio cynocephalus*), were used as analogue species for Neanderthals, AMH, and their hybrids.

Due to similar genetics, anatomy, and physiology, baboons are often used as an analogue species for hominins. Baboon DNA sequence is very similar to humans (Caccone and Powell, 1989), as well as the sequence of genes in the DNA (Rogers and Hixson, 1997), and the placement of loci on chromosomes (Rogers and Hixson, 1997). The divergence of baboons and modern humans, when the last common ancestor lived, was relatively recent. The hominid clade leading to humans and chimpanzees split from the catarrhine clade, the old world monkeys, 25 million years ago compared to 5-6 million years ago when the clade leading to modern humans

split from the clade leading to modern chimpanzees (Page and Goodman, 2001). To put this in perspective, the last common ancestor between all primates existed 55.8-50.3 million years ago, and the last common ancestor between all placental mammals lived about 64.85 million years ago (O'Leary et al., 2013).

3.1.1 Public Issue

Non-human primates are often used as analogue species to examine a wide variety of research questions, from genetics and diseases to possible hominid behaviour and social structure, which cannot be analyzed directly in modern humans due to logistical and ethical limitations. Studying non-human primates also faces ethical issues such as the physical or mental harm to intelligent primates in order to conduct research. Often these types of studies are justified with the argument that the research will ultimately save x number of human lives. Fortunately, in recent years, there has been a movement to scrutinize research involving non-human primates and to provide care in primate sanctuaries after the experiments are completed, rather than euthanasia (Carlsson et al., 2004; Drummond, 2009).

Many primatologists also travel to wild populations of primates to observe their ecology and behaviours (for baboons Maples and McKern, 1967; Dunbar and Dunbar, 1974; Phillips-Conroy and Jolly, 1981; Samuels and Altmann, 1986; Alberts and Altmann, 2001; Charpentier et al., 2012). In order to avoid human interaction, researchers decide to tediously collect and analyze DNA from feces rather than the more easily studied form of blood or tissue, such as in Tung et al. (2008). Research from wild populations provides valuable insights into human ancestry and the evolutionary development of behaviours, communication, residence patterns and other cultural traits that living humans have today. Research on wild populations and primates in protected sanctuaries also benefit the primates directly, leading to the protection of their habitats (Detwiler et al., 2005). Though this form of research also has its ethical issues, such as how or when humans should intervene to save a primate population. For example, should a researcher give medicine or food to the animals they are studying? Is advocating for long-term conservation essentially the same intervention as giving immediate relief of disease or food shortages that may have also been caused by humans? Should primate conservation be a greater priority than the needs and cultures of the people who occupy the same territory as primates, including poachers or farmers who kill them? These are public issues that primatologists turned conservationists and activists struggle with. These are also issues that had to be faced in this study because baboon skeletal remains were used.

3.1.2 Study Sample

The baboons analyzed in this thesis led relatively normal baboon lives at the Southwest National Primate Research Centre (SNPRC) in San Antonio, Texas. The baboons lived in captive colonies, allowing them to interact with one another with little human interference within a large fenced off area (Joganic J, Personal communication). When the animals died of natural causes, the remains were cleaned and curated by Jessica Joganic at the Department of Anatomy and Neurobiology at Washington University (Ackermann et al., 2006; Johanic J, Personal communication).

This study is analyzing the same skull collection as Ackermann et al. (2006) and will be compared to Ackermann et al. (2006) throughout.

This baboon collection is extremely valuable as it is the only collection that the author knows of which contains both parental species and hybrids along with seven generations of pedigree and genetic information. The original yellow and olive populations were captured from the wild from southern and western Kenya more than 30 years ago (Maples and McKern, 1967; Newman et al., 2004). Because they were wild caught, the populations probably experienced founder effect when they entered the captive colony, which created a genetic bottleneck resulting in less genetic diversity. Acknowledging this founder effect, this study cautiously interprets the results in a model of limited genetic diversity. Researchers maintained a purebred population and controlled inbreeding by housing one breeding male with 10-30 females. Only one male was housed with the females to ensure pedigrees and record the parents of each offspring. However, when purebred populations began to shrink, increasing inbreeding and decreasing heterozygosity in the population, the researchers decided that admixing between olive and yellow baboons was preferred over inbreeding to maintain a healthy population. Researchers know the pedigrees and % admixture of the olive x yellow hybrids (Mahaney MC, Personal communication). Only by knowing the pedigree of the baboons, is it possible to associate specific traits with known hybrids.

However, this created a scenario of artificial mating selection, where the researchers chose the male that would be housed with the females rather than the females choosing the males or the males competing for access to the females. Thus, sexual selection was removed from the population conditions. This has implications for the interpretation of male and female differences, especially sexual dimorphism, as discussed in Chapter 4.

Many museum collections do not have information on pedigrees because the specimens were wild caught and thus family histories were unknown, or it was not considered important to distinguish between species or knowledge of interbreeding was unknown at the time of capture. Hopefully, the identification of traits related to both parental species and hybrids, as presented in this study and in Ackermann et al. (2006), will help museum curators correctly identify their

specimens whose species and/or collection location is unknown. Indeed, Ackermann and Bishop (2009) applied this concept to museum specimens of gorillas to identify eastern and western species and their hybrids, with the assumption that hybrids had a higher frequency of nonmetric traits. From the location the specimens were obtained and through analysis of traits, they were able to identify a hybrid zone in gorillas (Ackermann and Bishop, 2009).

3.1.3 Species Concepts

Evolutionary History

Baboon hybrids share a similar evolutionary history as Neanderthal and AMH hybrids. The two species of baboons in this study, *Papio anubis* (olive) and *P. cynocephalus* (yellow) diverged from each other about 160,000 years ago based on mitochondrial genetic evidence (Jolly et al., 1997; Jolly, 2001; Newman et al., 2004). Anthropologists estimate that Neanderthals and AMH diverged 410,000-440,000 years ago (Endicott et al., 2010), or 270,000-440,000 years ago (Green et al., 2010). Holliday (2008) hypothesized that Neanderthals and AMH were not diverged long enough that viable hybrids could not be produced because their divergence time is conservatively half as long ago as the split between Thomson's gazelles and red-footed gazelles, which shows the most rapid onset of postzygotic isolating mechanisms currently known. Though the divergence time differs for the two clades, the baboon species and the Neanderthals and AMH populations would have had enough time to adapt to their environments through natural selection, creating unique features. These are the features that may be altered during hybridization, such as differences in shape, size, and frequency of metric and nonmetric traits in this study.

However, divergence time was not long enough, or divergent selection was not strong enough to create major barriers to reproduction when the olive and yellow baboon species re-encountered one another in Amboseli, Kenya. Researchers were fortunate to record the development of the first hybrid zone between olive and yellow baboons with the migration of the first male olive baboon into a yellow baboon group 50 years ago (Maples and McKern, 1967; Samuels and Altmann, 1986; Jolly, 2001). These and other studies of the Amboseli hybrid zone will be discussed in Section 6.1.

Similarly, Neanderthal and AMH territories may have overlapped for about 14,000 years (see Section 1.2), which would have given Neanderthals and AMH an opportunity to interbreed (Cartmill and Smith, 2009; Smith et al., 1999). However, it is not known when the Neanderthal and AMH hybrid zone began or how it functioned, which is hypothesized in Section 6.2.

Species Classification

Taxonomists examining the genus *Papio*, baboons, have compared the debate of how to classify baboon species or subspecies with how to classify Neanderthals and AMH (Jolly, 2001). Are olive and yellow baboons distinct species due to unique adaptations to different environments though they cannot interbreed, and therefore classified as *P. anubis* and *P. cynocephaus* respectively? Or are olive baboons and yellow baboons the same species because they can interbreed, and therefore be classified as *P. papio anubis* and *P. papio cynocephalus* respectively? Some taxonomists consider them different species (Samuels and Altmann, 1986; Samuels and Altmann, 1991; Detwiler et al., 2005; Arnold and Meyer, 2006), while others consider them subspecies (Zinner et al., 2009). Jolly (2001) avoids the species or subspecies debate by classifying these baboon populations as "allotaxa:" "phylogenetically close, but well-differentiated and diagnosable, geographically replacing forms whose ranges do not overlap, but are either disjunct, adjoining, or separated by comparatively narrow zones in which characters are clinally distributed" (Jolly, 2001: 193-194), "morphologically diagnosable, yet not reproductively isolated" (Jolly, 2001: 177).

Similarly, paleoanthropologists have debated classifying Neanderthals and AMH as different species, *Homo neanderthalensis* and *Homo sapiens*, implying that interbreeding has not taken place, or as subspecies of the same species, *H. sapiens neanderthalensis* and *H. sapiens sapiens* respectively, implying that hybridization could take place. These classification questions have been asked of Neanderthals and AMH since their initial discovery (Sollas, 1908; Hrdlička, 1927; Stringer, 2002; Wolpoff et al., 2004; Smith et al., 2005; Tattersall and Schwartz, 2008; Stringer, 2008; Ahern, 2008). Therefore, it is worth questioning the definition of species.

Species Concepts

Several definitions of species concepts were offered in Chapter 2 during the analysis of skeletal remains, ancient DNA, and artifacts. Often, the definition of species in the literature implies a degree or ability of species to interbreed, referred to as the "biological species concept". Mayr's (1942: 120) definition of the biological species concept is often evoked: "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups," emphasizing reproductive isolation. In terms of AMH and Neanderthals, if they are labeled as different species, then, according to the biological species concept, they could not breed. However, there are many examples of populations that humans have labeled as species that do interbreed, such as the two howler monkeys *Alouatta guariba climatins* and *Alouatta caraya* (Agostini et al., 2008; Aguiar et al., 2008).

The genetics of the olive, yellow, and hybrid populations were studied to deduce both long-term isolation, (Newman et al., 2004) and past hybridization events that influence current distributions (Zinner et al., 2009). Using genetic differences to classify species into related

ancestral clades invokes the phylogenetic species concept. Studies using phylogenetics are considered the gold standard for understanding how species are related through evolution.

> A species exists whether or not we are able to detect its diagnostic character(s), but in order for the species category to be useful in evolutionary analyses of any kind, two species must differ from one another in at least one intrinsic, diagnostic attribute (phenotypic or genotypic). (Kimbel, 1991)

Therefore, the phylogenetic species concept leaves open the opportunity for interbreeding, but is still able to distinguish the parental populations.

> Since both species definitions [biological and phylogenetic] use the same basic attributes of populations (pheno- and zygostructure), merely differing in how to weight them, we should focus on describing these attributes, and shelve indefinitely the largely bogus 'species problem.' (Jolly, 2001: 193)

I tend to agree with Jolly: arguing about whether or not a population falls within a species, subspecies, allotaxa, etc., is not particularly useful ecologically. Species concepts are human constructs of nature, attempting to systematically divide nature into smaller components. However, natural populations often break these rules, for which different species concepts would define them differently. "The question regarding the appropriate taxonomic level is more a matter of philosophy, depending largely on the underlying species concept" (Zinner et al., 2009: 84).

If a population is defined as a species by one concept, it does not mean that it meets the assumptions of any other concept. In the fossil record, scientists can only really classify extinct populations by identifying morphological differences on the skeletal remains. According to the morphological species concept, morphological differences between populations would make them different species (Arnold and Meyers, 2006). As explained in Section 2.2.2, Neanderthals and AMH have many different morphological features that let anthropologists readily identify a cranium as Neanderthal or AMH, which would make them different species according to the morphological species concept. However, we currently do not have enough DNA evidence for the two populations to classify Neanderthals and AMH using the phylogenetic species concept. Nor are we able to observe interbreeding events that would classify them as the same species in the biological species concept. However, if they are separate species according to the morphological species concept, it does not mean that they necessarily cannot interbreed, a conclusion that some authors jump to, such as:

> Yet although it is important to recognize that the numerous autapomorphies of *H. neanderthalensis* [morphological species concept] not only preclude it from the ancestry of any other known hominid species, but also presumably from any successful and

biologically significant hybridization with them [biological species concept]. (Schwartz and Tattersall, 2010: 100-101).

As I have throughout this paper, and following the example of Cartmill and Smith (2009), I will continue to refer to the populations as Neanderthals and Anatomically Modern Humans (AMH), referring to the shared anatomy of this population with contemporary humans.

Implication of Species Designation

There is an interpretative implication for this thesis in using the same species concept to compare the baboons with Neanderthals and AMH. If yellow and olive baboons are at the same taxonomic level as Neanderthals and AMH, then the comparison between the two is more valid. If baboons are separate subspecies while Neanderthals and AMH are different species, then applying baboon trends to recent modern humans will result in an underestimation of hybrid changes. This source of potential error in the thesis cannot be presently removed because there are currently no species concepts that would be able to make such judgments about the relative taxonomic positions of baboons to recent modern humans. Because baboons diverged over a shorter time period (160,000 years (Newman et al., 2004)) than Neanderthals and AMH (410,000-440,000 years ago (Endicott et al., 2010), or 270,000-440,000 years ago (Green et al., 2010)), it is possible that any baboon trends applied to recent modern humans will be an underestimate. An underestimation is preferable for this study than an overestimation of morphological differences in hybrids. Therefore, this study is conservative in applying the effects of hybridization on the nasal cavity of baboons to Neanderthals and AMH.

3.2 The Nasal Cavity

This study focuses on the hybrid morphology of internal structures, specifically the nasal cavity. The nasal cavity consists of two areas in a dry specimen: the bony cavity and the nasopharynx. The bony cavity is defined as the anterior portion below the anterosuperior margin of the nasals to the posterior margin of the hard palate, or the posterior opening called the choana. Posterior to the posterior margin of the hard palate is the nasopharynx (Jone, 2001; Mlynski et al., 2001; Noback et al., 2011) (Figure 2).

3.2.1 Neanderthal Nasal Cavity

The nasal cavity is of particular interest because the Neanderthal nasal cavity has been recognized as particularly different from AMH nasal cavity. The traits are so opposing and possibly environmentally adaptive that there may be developmental instability when the genes from both

parental populations attempt to regulate the same region. Alternatively, the hybrid may exhibit the traits of only one parent rather than an intermediary or mosaic nasal cavity that might compromise function, such as airflow, warming and humidifying air.

For example, Morgan et al. (1991) determined that air mixes in the anterior third of the nasal cavity, or the anterior bony cavity. The nasopharynx does not play a role in airflow other than to direct the airflow downwards towards the lungs. Noback et al. (2011) found further functional differences between the bony cavity, which is responsible for warming the incoming air, and the nasopharynx, which is responsible for humidifying. Further, the nasal cavity functions in olfaction; sensation of chemicals, such as ammonia; immunology since the nasal cavity contains immunoglobulin's; mucociliary clearance to remove foreign objects such as pathogens; and filtration of particles larger than 30 μm (Mygind and Dahl, 1998; Jone, 2001). The functional differences within the nasal cavity make it an interesting and complex area to study in a hybrid whose parental populations had very different nasal cavity shapes and sizes, such as in Neanderthals and AMH.

Preservation of Nasal Cavities

Unfortunately, the nasal cavity is rarely preserved, though the unique Neanderthal morphology has been confirmed in the few Neanderthals that have complete or nearly complete nasal cavities: Gibraltar, La Ferraissie 1, La Chappelle-aux-Saints, Forbes' Quarry Neanderthal FQ1, Shanidar 1, Saccopastore 1, Engis 2, Pech de l'Azé, Roc de Marsal, St. Césair (used in comparative studies by: Schwartz and Tattersall, 1996; Franciscus, 1999; Friess et al., 2002; Bruner and Manzi, 2008; Schwartz et al., 2008; Rae et al., 2011). Most authors agree that the Neanderthal nasal cavity is generally large, with a wide anterior nasal aperture described very early in the literature (Sollas, 1908) that sets them morphologically apart from Pleistocene AMH and modern humans.

Neanderthal Nasal Cavity Comparison to AMH

A lot of focus has been placed on the anterior nasal cavity, just within the anterior nasal aperture. The internal ridge in Neanderthals, posterior to the anterior nasal aperture, is described as having vertically oriented "conchal crest", rather than a horizontally oriented conchal crest as seen in Pleistocene AMH and modern *H. sapiens*, which forms a "medial projection" about a third of the way superior to the palate that bulges medially into the nasal cavity (Engis, Gibraltar, Krapina, La Chapelle-aux-Saints, La Ferrassie, La Quina, Pech de l'Azé, Roc de Marsal, Subalyuk) (For photographs of this feature, see Schwartz and Tattersall, 1996; and Schwartz et al., 2008). Schwartz et al. (2008) concluded that the medial projection is a growth of the maxillary frontal

process in Neanderthals. Franciscus (1999), however, referred to the medial projection as "crista turbinalis," according to Gower, which occurs in about 10% of living modern humans in Europe, Asia, or Africa, and in 65% of examined Neanderthals that have preserved nasal cavities. In Neanderthal specimens that were not subject to reconstruction, which can alter the nasal region, the conchal crests were slanted or horizontal as they are in modern humans (Franciscus, 1999), not vertical, as Schwartz and Tattersall (1996) described. The conchal crest anatomy has been used to make inferences about the inferior nasal conchae, such as unusual bulging and movement back into the nasal cavity, though no Neanderthal inferior conchae have been found (Schwartz and Tattersall, 1996; Schwartz et al., 2008).

The posterior nasal cavity in Neanderthals has been described as both wider than Pleistocene AMH and modern humans with swelling from the lateral wall (Schwartz and Tattersall, 1996) and narrower than Pleistocene AMH, though not different from modern humans (Franciscus, 1999). As an aside, Schwartz and Tattersall have consistently argued in the literature for a separate species designation for Neanderthals without hybridization (see Section 2.2) while Franciscus has consistently considered Neanderthals to be within the variation of *H. sapiens* (Franciscus, 1999; Franciscus, 2003). This debate is yet another manifestation of the paradigm divide in paleoanthropology.

Another example of an unique Neanderthal trait from the nasal cavity that has since been found not to be unique is the bi-level nasal floor. The bi-level nasal floor has often been cited as a distinctive Neanderthal trait, compared to the sloping or level nasal floor found in early modern humans. Wu et al. (2012) found that amongst a sample of archaic *Homo* (Sangiran 4, Chaoxian 1, Xujiayao 1, and Chang- yang 1), three of the four had bi-level nasal floors. Wu et al. (2012) concludes that the bi-level floor is not distinctive in Neanderthals.

Studies have also hypothesized that growth rates for various traits are different in Neanderthals compared to modern humans, basing age estimation on teeth (Williams, 2013). The nasal cavity is no exception. It has been hypothesized that the bony palate grows at a faster rate, but for a shorter duration in Neanderthals due to the late closure of the premaxillry suture, and the wide nasal aperture can be explained by an extended period of growth compared to modern humans (Maureille and Bar, 1999; Williams, 2013). Developmental timing, duration of growth, and growth rates are the characteristics that can substantially change in response to hybridization due to contradictory genes attempting to regulate the same area (Ackermann et al., 2010).

Conclusions Drawn from Neanderthal Nasal Cavity

From the morphological differences between Neanderthals and AMH, authors have hypothesized potential physiological implications. Laitman et al. (1996) suggest that the large anterior nasal cavity and paranasal sinuses are evidence that Neanderthals depended more heavily on nasal respiration than oral, which would lead to differences in their range of sound production. Laitman et al. (1996) also suggest that the large maxillary sinuses play a part in warming and humidifying cold, dry air, implying cold-climate adaptation. Franciscus (1999) finds these hypotheses problematic due to the contradictory or scarce skeletal evidence for these claims, as pointed out above.

Cold adaptation has since been attributed to Neanderthal features beyond the nasal cavity and paranasal sinuses by many authors, including the example from Duarte et al. (1999) in Section 2.2.2 that Neanderthal body proportions are hyperarctic (Churchill, 1998; Friess et al., 2002; Hublin, 2002; Steegmann et al., 2002). Not to imply that all of the features cited above as cold-adapted are disputed, but focusing on the nasal cavity and paranasal sinuses, many authors are now questioning the underlying assumption of cold-adaptation. If the Neanderthal nasal cavity and maxillary sinuses were associated to cold climate, we would expect smaller, not larger, maxillary sinuses and narrower and taller anterior nasal apertures, as experimental studies suggest (Rae et al., 2003; Rae et al., 2006; Marquez and Laitman, 2008; Noback et al., 2011; Rae et al., 2011).

For example, Rae et al. (2006) found that in an experimental study in which rats were reared in environments with different temperatures, the ones raised in colder environments had smaller maxillary sinuses, and nasal cavities. Other hypotheses have been proposed, such as larger paranasal sinuses and broader nasal cavity are the result of the pronounced prognathism in Neanderthal faces, suggesting that the paranasal sinuses and nasal cavity were not under selection (Holton and Franciscus, 2008). Larger sinuses and nasal cavities in Neanderthals may not be understood until the function of the paranasal sinuses is understood (Blaney, 1990).

3.2.2 Baboon Nasal Cavity

Unfortunately, the maxillary sinuses cannot be analyzed in the baboon model because baboons [*Papio*], unlike Neanderthals and AMH, do not have maxillary sinuses. Instead, baboons exhibit a pneumatization of maxillae extending laterally in the nasal cavity, named the lateral recess (Lund, 1988; Koppe and Ohkawa, 1999; Rae and Koppe, 2003; Rossie, 2006). This differentiation between Neanderthals and baboons gives this thesis an opportunity to contribute to the literature on the lateral recess. Section 4.4 and Section 5.4 discuss the affect of hybridization and sex on the lateral recess.

Lateral Recess

Morphometric definitions of the lateral recess are varied and not consistent in the literature (Rae and Koppe, 2003). Lund (1988) suggested that the lateral recess begins at the plane of the root of the canine and extends to the back of the nasal cavity. Koppe and Ohkawa (1999: 80) defined the lateral recess as beginning at the 3rd molar and extending into a "small" lateral recess that bulges into the medioinferior walls of the orbit. An early study of airflow through baboons by Parta et al. (1959), labeled the anterior limit of lateral recess around the same location, the 3rd molar, as Koppe and Ohkawa. Parta et al. (1959) also found that it was a unique functional area of high turbulence and long residence time.

Through preliminary examination of the baboon CT scans, the definition presented by Koppe and Ohkawa seems to be more applicable. During initial assessment of the baboon CT scans, I have also observed significant expansion of the lateral nasal walls occurring posterior of the choana. Further discussion of the definition of the lateral recess appears in Section 4.4. If this definition is accepted, developmental similarity may exist between the lateral recess and the maxillary recess, which also begins at the 3rd molar then expands into a sinus moving posteriorly (Rossie, 2006).

However, the relationship between the maxillary sinus and lateral recess is uncertain in literature. One hypothesis is that baboons, and all cercopithecoids, lost or repressed the maxillary sinus, which was subsequently replaced by the lateral recess (Rae and Koppe, 2003; Rae, 2008; Rossie, 2008). Indeed, the term lateral "recess" can potentially be adding to the misconception because recess traditionally refers to the space during ontogenesis, the folding of the embryonic cartilage, which later develops into the sinus (Rossie, 2006). Specifically, the space that develops into the maxillary sinus is called *recessus lateralis* during development, which divides into the *recessus maxillaris* and *recessus frontalis* to develop into the maxillary sinus and frontal sinus, respectively (Rossie, 2006). Rae and Koppe (2003) even argue that the term "lateral recess" be abandoned because it has been used to denote very different regions in the nasal cavity: the inferior recess next to the canine roots, the space beneath the attachment of the inferior nasal conchae to the walls of the middle nasal cavity, or, most problematically, the maxillary sinus.

It is difficult to determine the relative functions of the maxillary sinus and the lateral recess because it is not yet understood what the purpose of the paranasal sinuses are and why some groups have them while others do not (Blaney, 1990). For example, it is believed that macaques developed maxillary sinuses after separating from the last common ancestor that they share with baboons in *Cercopithecoidea*, which had lost maxillary sinuses (Rae and Koppe, 2003). However, as of yet, there seems to be no obvious environmental or ecological explanation

for macaques to have developed a sinus (Rae and Koppe, 2003; Rae, 2008). Koppe and Nagai (1997) concluded that the maxillary sinus in macaques does not serve a structural purpose, such as reducing weight or maximizing strength for mastication, but serves some, as of yet, unclear purpose in air conditioning or respiration. Rae (2008) hypothesizes that a selective pressure may have acted on a separate trait that also influences maxillary sinus development, or a developmental constraint appeared in the last common ancestor. Subsequently, the selective pressure or the developmental constraints were removed in macaques.

This study will contribute to the literature on the lateral recess by adding sex and taxa differences in *Papio* to help better understand the variation in the morphology of the lateral recess.

3.2.3 Experimental Hypotheses

Generally, studies of internal structures and their relationship with external changes are rare in the literature. Studying Neanderthals, Bookstein et al. (1999) discovered that the internal structure of the frontal bone is conserved in the hominin line though the external anatomy dramatically changes with the expansion and/or reduction of the supraorbital torus/ridge, frontal eminence, and frontal height. This conclusion implies that internal and external structures of the same bone are performing different functions and are therefore subjected to different selective pressures. It also implies that internal structures, in this case the interior frontal bone which comes into contact with the vessels that supply the brain, are more conserved due to their more critical role in survival. If the internal anatomy changes in a suboptimal way, which is more often the result of most mutations or new gene combinations, brain function might be compromised. Therefore, I hypothesize that internal structures may be more stable during development because they are more critical for fitness.

However, can this hypothesis be applied to other internal structures such as the nasal cavity?

Metric Analysis

Ackermann et al. (2006) found that different regions of the baboon skull show heterosis while other regions show dysgenesis, resulting in a change in skull shape in the hybrid baboon. Dysgenesis only occurred at the zygomatics, while other cranial traits demonstrated heterosis. Ackermann et al. (2006) found significant heterosis between the nasion and the posterior nasal spine (almost parallel to the choana) and between the nasion and the bregma. Therefore, I hypothesize that height and length of the choana may show heterosis internally.

Ackermann et al. (2006) did not find significant length differences between taxa in the anterior area of the nasal cavity. However, Bastir and Rosas (2013), studying the nasal cavity in humans, found that the anterior nasal cavity size is correlated with the size of the facial region of the external maxillae. Bastir and Rosas (2013) also found that the posterior (choana) and the anterior openings of nasal cavity act as independent units and therefore respond differently to external size differences.

Because the posterior region did not correlate to alterations of the external maxillae, I hypothesize that the posterior nasal cavity may be more conservative and resistant to genetic changes than the anterior nasal cavity. Ackermann et al. (2006) did not detect regional differences in the nasal cavity, though this is probably due to sparse sampling in this area. However, Ackermann et al. (2006) did acknowledge that there are qualitative changes in this area, such as a "boxy" appearance. Morphometric analysis of the nasal cavity is presented in Chapter 4.

Nonmetric Analysis

In addition to morphometric features, the nasal cavity also exhibits a variety of nonmetric traits or morphologies. Nonmetric traits in the nasal cavity include deviated septum and intrusion of dentition from the alveolus. Further traits were identified during the study and are presented in Chapter 5.

I hypothesize that nonmetric trait variability should have less functional impact on the external anatomy compared to the internal anatomy. For example, an abscess around the roots of a molar contained in the alveolus can cause pain and sensitivity while eating. However, if the roots of that molar enter the nasal cavity, a nonmetric trait, the severity of the pathology increases because the abscess also enters the nasal cavity, spreading the infection to the soft tissues. Severe dental abscesses in humans can lead to infection of the sinuses and soft tissue which can become widespread, deep or necrotizing (flesh-eating), leading to death (Wong, 1999).

Certain nonmetric traits in the nasal cavity are common in people living today. For example, Holton et al. (2012) reported a high incidence of deviated septums in European and African populations, of which nearly all of the 70 human subjects exhibited some degree of deviation. Jone (2001) also found that 30% of humans have concha bullosa, in which one of the middle nasal conchae is enlarged. Stallman et al. (2004) found that patients with concha bullosa often have an associated deviated septum, but that having concha bullosa does not increase chances of nasal inflammation. Therefore, I expect baboons to show a similar high frequency of deviated septum regardless of taxa.

Similarly, I expect baboons will have low frequencies of nonmetric traits that are also rare in humans, except in hybrids. For example, ectopic teeth occur at a rate of 1% in humans and they are extremely rare in the nasal cavity (de Oliveira et al., 2008). The ectopic tooth is the nonmetric trait, but pathologies can result from it if certain circumstances occur. Cysts or minerals can form around ectopic teeth that can cause midline deviations. These cysts, dermoids, epidermoids, ecephaloceles, or gliomas, provide pressure in fetal and infant nasal cavities, resulting in malformations that can block the nasal passage or lead to inflammation (Schlosser et al., 2002). Chen et al. (2009) found that airflow is significantly affected by the presence of a deviated septum, which can potentially impair warming, filtering, and olfactory functions.

The etymology of these nonmetric traits is not entirely clear, though they are often congenital.

Nonmetric Traits in Baboons

Ackermann et al. (2006) focused on anomalies that are generally not associated with additional pathologies. They found higher frequencies of nonmetric traits, what they refer to as anomalies, in hybrid baboons compared to parental species. From the variety of traits examined in the skull, only 5 traits were significant: zygomaxillary suture formation, retention of metopic suture, tooth crowding, supernumerary teeth, and robusticity of the snout region creating a "boxy" appearance. Ackerman et al. (2006) hypothesized that these traits were significantly more frequent in hybrids because:

> We expect their hybrids to display other qualitative morphological signatures of evolutionary distinctiveness, caused by small differences in the rate or timing of development in the parental populations, the subsequent failure of specific developmental interactions in their hybrids and resultant developmental instability, or other epigenetic phenomena. (Ackermann et al., 2006: 11)

Because this study is using the same collection, such changes in developmental timing and genetic interactions could also affect the hybrid baboon nasal cavity. However, if internal structures are more developmentally stable, as hypothesized at the beginning of Section 3.2.3, then the frequency of nonmetric traits should not differ between the hybrids and the parental species. Alternatively, if I do find that the nasal cavities are significantly different in the hybrids compared to either parental species, then examination of internal structures may be a robust indicator of hybridization as Ackermann et al. (2006) concluded for external anomalies.

I also hypothesize that there may be a difference in the frequency of morphometric traits in the anterior and posterior nasal cavities due to the different functions that each area performs. Ackermann et al. (2006) found heterosis at the level of the orbits in the frontal bone and the

zygomatic bones. The nasal cavity spans from the bony palate into the plane of the eye orbit and thus might reveal more subtle changes in this region of the skull that Ackermann et al. (2006) did not detect.

Chapter 4

Morphometric Analysis

Size and shape of skeletal features are determined by a combination of genetic and environmental factors (Section 3.2). This controls for many environmental factors because the specimens originate from a controlled captive colony where environmental influences were similar for all animals. Therefore, this study of morphometric analysis is designed to explore the genetic factors. Measurements of morphometric traits are taken to examine the concepts of heterosis, which will result in larger measurements of the nasal cavity in hybrids, and dysgenesis, which will result in smaller measurements of the nasal cavity in hybrids. Heterosis and dysgenesis in hybrids occur in comparison to measurements in the parental populations.

I hypothesized that measurements of the anterior nasal cavity (bony cavity) will show heterosis and a greater difference between the hybrids and the parental species compared to the posterior nasal cavity (nasopharynx). In the posterior nasal cavity, I hypothesized that generally, as compared to the anterior region, the posterior region will be more resistant to size and shape changes in order to conserve critical functions of this area. Due to Akermann et al.'s (2006) measurements from the nasion that indicated heterosis, I also expect that the choana will have height and width heterosis in the hybrid.

This chapter presents the rationale for the methods and details all the steps for morphometric analysis, including statistical methods within its own section (4.2). At the end of Section 4.2, abbreviations and notation for the statistical analysis are defined. The results are presented in Section 4.3, organized by each type of analysis repeated for each group of baboons tested. Section 4.4 summarizes the main conclusions from the results and places them in context of nasal cavity physiology in baboons. The morphometric results are referenced again in Section 6.3 in order to relate the baboon nasal cavity model to a potential Neanderthal and AMH hybrid nasal cavity.

4.1 Methods

In this project, I assess the morphometric differences of the nasal cavity using computed tomography (CT) scans on the parental baboon species, olive (*Papio anubis*) and yellow (*P. cynocephalus*) baboons, and the first generation hybrid (*P. anubis* x *cynocephalus*). All baboon skulls are from the SNRPC collection at Washington University (see Section 3.1.2). The sample

of olive baboons (*n*=79) contained 52 females and 27 males. The 52 females are a subset of the total olive baboon skulls in the collection, while the 27 males were all of the olive males in the collection. The sample of yellow baboons (*n*=5) contained 4 females and only 1 male, which were the only yellow baboon skulls available the collection. The sample of hybrids (*n*=54) contained 41 females and 13 males, which were all the hybrid skulls available from the collection.

The cleaned and dried skulls were CT scanned at the Center for Clinical Imaging Research (CCIR) at Washington University. All CT scans have a resolution of 512 x 512 pixels and a slice thickness of 0.75 mm or smaller, suitable for measuring at the mm level.

Because volume can act as a general indication of overall differences between the three baboon groups, I measured the volume of the nasal cavity for each specimen from coronally sliced CT scans using the imaging software OsiriX (Rosset et al., 2004). Volume is calculated as the addition of all the voxels within the segmented region of interest (ROI) in each slice. A voxel is defined as the area of a pixel within the CT image multiplied by the thickness of the scan. The area of a pixel, A, is obtained from the scanner resolution matrix, M, and the display field of view, d. Let $M(i,:)$, equal the ith row in matrix M and $M(:,j)$, equal the jth column in matrix M.

$$A = \frac{d^2}{M(i,:) \times M(:,j)} \qquad \text{Equation 1}$$

Segmentation indicates to OsiriX the number of voxels within the nasal cavity on each scan. Each CT scan of the nasal cavity was manually segmented by the author over three months, selecting each pixel to be included in the final ROI of the nasal cavity and the analyzed slices.

For the purposes of this study, the first scan of nasal cavity was defined as the anterosuperior margin of the nasals, at which point the nasal cavity is enclosed by the maxillae on the sides, the maxillary palatine process from below, and the nasals from above. Segmentation continued through to the posterior margin of the palate, the choana. Posterior to the choana, the palate no longer encases the nasal cavity inferiorly. Therefore, I established an artificial inferior margin located tangential to the inferior aspect of the attachment of the inferior nasal conchae to the nasal walls at the posterior margin of the palate. This artificial inferior margin was used to segment the remaining scans of the nasal cavity. The final scan of the nasal cavity was established as the last scan before the space occupying the orbital fissure descends from the orbit and enters into the nasal cavity space. Through the inferior orbital fissure, the infraorbital artery and the zygomatic branch of the maxillary nerve pass on their way through the infraorbital canal and out of the infraorbital foramina. The area of segmentation of the nasal cavity is shown in Figure 3i, ii.

In each CT scan, the nasal cavity was outlined during segmentation. Therefore, internal nasal cavity bones, inferior nasal conchae, vomer, and ethmoid, were not distinguished from the internal nasal cavity space. This methodology is derived from Holton et al. (2013) in which the nasal cavity and maxillary sinuses were segmented in the CT scans of living human subjects.

I was also interested in more detailed shape differences between the three baboon groups. Therefore, the nasal cavity was sampled at five coronally sectioned CT scans for each specimen. Figure 3 shows the location of the slices within the nasal cavity. The first measured slice was the first CT scan of the nasal cavity segmentation, and has already been defined above. The third slice measured was the last slice containing the posterior margin of the bony palate, the choana. The area between the first and third slices is the bony cavity (Noback et al., 2011). The second slice is located midway between the first and third slices, the midbony cavity. The fifth slice, the posterior nasopharynx, is the last slice in the nasal cavity segmentation and has already been defined above. The area between the third and fifth slices is the nasopharynx. The fourth slice is midway between the third and fifth slices, mid-nasopharynx.

Landmarks were located on each of the five slices in order to approximate nasal cavity shape. These landmarks were used to generate groups of linear distances that can approximate the form of a specimen and be used in univariate statistics or multivariate statistics (Lele and Richtsmeier, 2001: 17). This study used traditional type landmarks and constructed landmarks or semi-landmarks. Traditional landmarks are defined as "precisely delineated points corresponding to the location of features of some biological significance" (Lele and Richtsmeier, 2001: 19-20), such as nasal crest. Constructed landmarks are defined as "points corresponding to locations that are defined using a combination of traditional landmarks and geometric information" (Lele and Richtsmeier, 2001: 22-24), such as the width of the nasal cavity tangential to the nasal crest. Landmarks and linear distance measurements are defined in Table 1 and shown in Figure 3.

4.2 Morphometric Statistical Analysis

The data in this study is composed of linear measurements, for example, from the rhinion to the nasal crest, as well as total area of each slice, and volume of the entire nasal cavity.

4.2.1 Clustering Methods

To illustrate group differences, clustering methods were used, principle components analysis (PCA) (Zelditch et al., 2004: 155-179) and canonical discriminant analysis (CDA) (Zelditch et al., 2004: 155-179).

PCAs were employed to determine the combination of measurements that best explains the variation between individual specimens and potentially observe group differentiation assuming that species designation was not known a priori (Zelditch et al., 2004: 155-179). However, because the baboons used in this study have known pedigrees, taxon designation was known a priori. Therefore, CDAs were used to identify which combination of measurements best differentiates known groups, the parental and hybrid groups (Zelditch et al., 2004: 155-179). CDA maximizes the differences between groups, rather than between individuals as PCA does. CDA therefore maximizes the ratio of between group differences to within group differences when creating the canonical scores.

PCAs and CDAs were performed in R (R, 2013). PCA employed the standard R functions *cov*(), to calculate the covariance matrix, and *prcomp*() to calculate the standard deviations, eigenvalues, and proportion of variance explained for each principal component. CDA employed the function *lda*() from the package "MASS" (Ripley et al., 2013) which returns the percentage of separation between groups achieved by each discriminant function, the coefficient of discrimination for each measurement, and the canonical scores for each specimen calculated from the discriminant functions (Coghlan, 2013).

4.2.2 Statistical Tests

To test the differences between groups, multivariate, Wilk's Λ in multivariate analysis of variance (MANOVA) (Zeldith et al, 2004: 209-223) and univariate, analysis of variance (ANOVA) (Samuels and Witmer, 2003: 463-475), statistics were used followed by various forms of t-tests (independent samples student t-test (Samuels and Witmer, 2003: 234-238) and Welch's t-test (Samuels and Witmer, 2003: 227) and the *post hoc* test, Dunnett's C (Dunnett, 1980).

MANOVA, ANOVA, and Dunnett's C post hoc tests were analyzed in SPSS (IBM, 2010) and were used to statistically analyze one measurement at a time to determine which measurements influenced group differences.

4.2.3 Preprocessing data

Prior to statistical analysis, the data were preprocessed. Because volume is a summary of complex 3-dimensional data into a single number measured in cubic units (Lele and Richtsmeier, 2001: 18), volume comparisons between parental and hybrid groups can be treated similarly to linear distance measurements. To make the volumetric values comparable to the other linear measurements and less statistically dominating, volume was cube rooted to represent it in a linear model. Similarly, slice areas, computed as squared centimeters, were square rooted so they could be comparable to linear measurements.

4.2.4 Testing Assumptions

Levene's test for homogeneity and Shapiro-Wilk test for normality, were used to test assumptions for further analysis (Levene, 1960; Razali and Wah, 2011). Levene's tests and Shapiro-Wilk tests were performed in SPSS (IBM, 2010).

Levene's test, summarized in Table 2, revealed that many variables do not have homogeneity of variance. Therefore, tests strictly assuming homogeneity were not performed.

The Shapiro-Wilk normality tests, summarized in Table 3 and Table 4, were used to evaluate if the feature fits a normal distribution. Shapiro-Wilk is considered the most powerful test of normality currently available, however, the power is very low for testing small samples sizes, such as the yellow baboons (Razali and Wah, 2011). Several features were found to not follow a normal distribution for one of the three groups (olive, hybrid, and yellow) (Table 3). Non-sensitive parametric tests were employed for this study because not all of the groups for any feature showed deviance from the normal distribution.

Shapiro-Wilk was also performed on all taxa combined (Table 4). In addition, quantile-quantile (Q-Q) plots were analyzed for normal distribution of each feature, though no Q-Q plot showed substantial deviation from the expected normal values (Figure 4).

Box plots of the nasal cavity illustrate variance and distribution for each of the 45 features of the nasal in Figure 5.

4.2.5 Notation

This section presents notation used in the statistical analyses in Section 4.3.

Statistical notation

p: p-value: the probability, computed under the condition that the null hypothesis is true, of the test statistic being at least as extreme as the value of the test statistic that was actually obtained (Samuels and Witmer, 2003: 238)

α: the threshold value of the test; if the $p \leq \alpha$, the null hypothesis is rejected (Samuels and Witmer, 2003: 238)

α_B: the Bonfferoni corrected threshold value of the test to accommodate greater uncertainty of additional tests based on the significance of a previous test while maintaining family-wise significance level

n: the number of specimens in a sample

n_B: the number of additional tests that will be performed, in Bonfferoni adjustment

d.f.: degrees of freedom: the number of specimens in a sample, *n* minus the number of defined
variables; typically *n-1* unless otherwise defined (Zelditch et al., 2004: 414)

χ^2: test statistic for the chi-square distribution

t: test statistic for the student's *t*-distribution

μ_M: mean of male group

μ_F: mean of female group

sd: standard deviation: calculation of data variance within a group

4.3 Results

This section presents results in the logical order of procedure, so that tests logically follow the result of the previous test. First, Wilk's Λ MANOVA found broad differences between the three baboon groups, olive, hybrid, and yellow, as well as between males and females (Section 4.3.1). Sexual dimorphism was then tested directly using index of sexual dimorphism developed by Simpson et al. (1960) and Welch's t-test (Section 4.3.2). In Section 4.3.3, sexual dimorphism is corrected for in the data.

PCA was then used to cluster the data by finding individual differences, prior to and after the correction for sexual dimorphism (Section 4.3.4). PCA was analyzed in males only, females only, all groups prior to the correction for sexual dimorphism, and groups with males and females combined after the correction. None of the PCAs clustered the groups particularly well by taxa, though males and females were clearly separated in the analysis of all the groups, indicating sexual dimorphism, prior to the correction for sexual dimorphism.

CDA was used to cluster the data by maximizing group differences, prior to and after the correction for sexual dimorphism (Section 4.3.5). CDA was analyzed in males only (with and without solitary yellow male), females only, all groups prior to correction, and groups with males and females combined after the correction. All groups were separated by taxa using CDA with no to moderate overlap of group distributions. Sexual dimorphism was also observed with clear separation of males and females in the CDA of all the groups prior to the correction for sexual dimorphism.

Hypothesis testing then compared all of the baboon groups to test the significance of the observed separation (Section 4.3.6).

Abbreviations and notation for statistical analysis are in Section 4.2.5.

4.3.1 Differences by Taxa and Sex

In order to get an initial impression of parental and hybrid group differences, a Wilk's Λ MANOVA was performed on the 45 measurements found in Table 5. MANOVA was used to test the hypothesis that the differences in shape between the parental groups and the hybrid group are not due to chance alone (Zelditch et al., 2004: 58). Wilk's Λ multivariate test was chosen because it can be applied to more than two groups (Zelditch et al., 2004: 58).

Wilk's Λ concluded that across olive, yellow, and hybrid groups, shape differences are not due to chance alone ($\alpha = 0.05$, $d.f. = 88$, $\chi^2 = 0.328$, $p = 0.011$). However, Wilk's Λ test also found significant differences in shape across sex (male or female) alone ($\alpha = 0.05$, $d.f. = 44$, $\chi^2 = 0.237$, $p < 0.005$), indicating that these baboon samples exhibit considerable sexual dimorphism, as Ackermann et al. (2006) found in the external baboon skull measurements of the same specimens.

4.3.2 Sexual dimorphism

Two tests were used to analyze sexual dimorphism correctly, the index of sexual dimorphism and Welch's t-test. The results contradicted one another, though Wilk's Λ MANOVA and, later, the PCA and CDA in Sections (4.3.4, and 4.3.5) visually confirmed sexual dimorphism. Comparisons of methods, ISD and Welch's t-test, are discussed in Section 4.4.

Index of Sexual Dimorphism

Sexual dimorphism was first analyzed using the method developed by Simpson et al. (1960) and utilized by Phillips-Conroy and Jolly (1981) to analyze the degree of sexual dimorphism in hamadryas baboons, olive baboons and their hybrids.

For each group, olives and hybrids, an index of sexual dimorphism, *ISD*, was calculated:

$$ISD = \frac{\mu_M}{\mu_F} \qquad \text{Equation 2}$$

Yellow baboons were not analyzed due to small sample size. Then a 90% confidence interval for *ISD* was calculated, derived from the 95% confidence intervals for males and for females. To calculate the lower and upper limit of the 90% confidence interval for *ISD*, L_{ISD}, U_{ISD}, respectively: let L_M and L_F equal the lower limit of the 95% confidence interval for the male group and female group, respectively; and let U_M and U_F equal the upper limit of the 95% confidence interval for the male group and female group, respectively:

$$L_{ISD} = \frac{L_M}{U_F}$$ Equation 3

$$U_{ISD} = \frac{U_M}{L_F}$$ Equation 4

Sexual dimorphism between the groups is considered significant if the 90% confidence intervals do not overlap (Simpson et al., 1960).

Figure 6 illustrates the confidence intervals between olive baboons and hybrids for this study. Because the confidence intervals for all of the measurements were overlapping, no features were found to be sexually dimorphic using this method. Phillips-Conroy and Jolly (1981) also did not find significant differences using this method. However, this result contradicts the MANOVA in Section 4.3.1 that indicated sexual dimorphism.

Student t-tests and Welch's t-test

A second set of tests was conducted to analyze sexual dimorphism between groups. A Bonfferoni adjustment was applied to the family-wise α, where $\alpha = 0.05$ and $n_B = 45$, making the level of significance threshold, α_B, smaller to accommodate greater uncertainty of additional tests based on the significance of MANOVA (Section 4.3.1) (Samuels and Witmer, 2003):

$$\alpha_B = \frac{\alpha}{n_B}$$ Equation 5

Therefore, $\alpha_B = 0.0011$ for the remaining tests in this section.

In student t-tests between male and female olive baboons, 18 of the 45 measurements of the nasal cavity were found to be significantly different, with males having larger measurements in all 18 features (Table 5). In hybrid baboons, 32 of 45 of the nasal cavity measurements were found to be significantly different between male and female hybrid baboons, with males having larger measurements in all 32 features.

The degree of sexual dimorphism, *DSD*,

$$DSD = \mu_M - \mu_F$$ Equation 6

was then compared between olive and hybrid baboons to test the hypothesis that hybrids have a greater degree of sexual dimorphism using Welch's t-test. Welch's t-test is designed to compare two populations with unequal sample sizes and unequal variances, (see Table 2 for results from Levene's test). The mean, μ_W, for each group,

$$\mu_W = \mu_M - \mu_F \qquad\qquad \text{Equation 7}$$

and standard deviations for each group, *sd,*

$$sd = \sqrt{\frac{sd_M^2}{n_M} + \frac{sd_F^2}{n_F}} \qquad\qquad \text{Equation 8}$$

must be calculated to calculate the test statistic, *t*:

$$t = \frac{\mu_{olive} - \mu_{hybrid}}{sd_W} \qquad\qquad \text{Equation 9}$$

where *sd*$_W$ is

$$sd_W = \mu_{olive} - \mu_{hybrid} = \sqrt{\frac{sd_{olive}^2}{n_{olive}} + \frac{sd_{hybrid}^2}{n_{hybrid}}} \qquad\qquad \text{Equation 10}$$

and degrees of freedom, *d.f.*$_W$,

$$d.f._W = \left(\frac{sd_{olive}^2}{n_{olive}} + \frac{sd_{hybrid}^2}{n_{hybrid}}\right)^2 \left(\frac{sd_{olive}^4}{n_{olive}^4(n_{olive}-1)} + \frac{sd_{hybrid}^4}{n_{hybrid}^4(n_{hybrid}-1)}\right)^{-1} \qquad \text{Equation 11}$$

Of the 45 features of the nasal cavity, 17 had significantly different degrees of sexual dimorphism between olive and hybrid baboons, with hybrids having a larger degree of sexual dimorphism in 15 of the 17 significant features, and olives having a larger degree of sexual dimorphism in 1 of the 17 features, the height to width ratio in slice 2 (Table 5).

One feature, the height from the artificial inferior margin to the alae of the vomer in slice 4 (defined in Table 1 and illustrated in Figure 3), was significant for Welch's t-test, though not significant for the independent samples student t-tests, because the difference between olive males and females is slightly positive (males are larger), and the difference between hybrid males and females is slightly negative (females are larger).

Figure 7a visually summarizes the significantly sexually dimorphic features and areas of the nasal cavity.

4.3.3 Correction for Sexual Dimorphism

Because significant sexual dimorphism was found in Wilk's Λ MANOVA, and the Welch's t-test, the variable of sex was removed from the data through a correction for sexual dimorphism.

Sexual dimorphism transformed the male data, where x_a is the original male value obtained from the original measurements, x_b is the new adjusted male value, μ_F is the female mean, and μ_M is the male mean:

$$x_b = x_a + (\mu_F - \mu_M)$$ Equation 12

The correction for sexual dimorphism was performed separately for each taxa, olives, yellows, and hybrids. This correction has been applied in other studies to remove the influence of male and female differences across different groups (Cheverud et al., 1993; Kohn et al., 2001; Ackermann et al., 2006).

4.3.4 Principle Components Analysis

PCA was performed to determine if any combination of measurements might organically organize the specimens into the correct groups (parental and hybrid groups) by finding the greatest difference between individual specimens (Zelditch et al., 2004).

PCA was applied to 31 of 45 measurements of the nasal cavity. The 14 measurements that were removed give estimates of total nasal cavity measurements (volume, areas, height to width ratios, length of nasal cavity, bony cavity and nasopharynx), where as this study is interested in the detailed analysis of the measurements within the five CT scans.

PCA rotation recombines the morphometric traits into generated variables called principle components (PC). Each specimen receives a PC score, or a new value combined from different weights of the original values, corresponding to each PC. Scores from two PCs, where, for example, PC 1 corresponds to the x-axis, and PC 2 corresponds to the y-axis, can be graphed together on bioplots with vectors showing the weight of each original morphometric measurement and the contribution of that trait to the PC (Zelditch et al., 2004).

A loading, or weight is the contribution from the original measurement to a particular PC, and changes for each PC. Loadings that are greater than 2.5 or less than -2.5 separate influential vectors from vectors that contribute little to the PC. Only these vectors are labeled on the biplots.

PCA in Males

Male olives, male yellow, and male hybrids were clustered according to PCA (Table 6). Together, the first four principle components explain 61.3% of the variation between samples, with each subsequent PC explaining less than 7% of the variation in the data as seen in the scree plot (Figure 8a). Eigenvalues for the first four principle components are also quite low: 1.2, 0.8, 0.5, and 0.4, respectively.

PC 1 explains 25.7% of the variation between samples. Male olives and male hybrids are moderately separated along this axis, with much overlap between the groups. The yellow male was not separated from any other group. PC 2 explains an additional 16.0% of variation between samples, though it visually does not separate the groups (Figure 8a). PC 3 and PC 4 explained an additional 11.4% and 8.2%, respectively (Figure 8b). However, they visually do not separate the groups any further.

According to the Kaiser criterion, which states that eigenvalues below 1 do not significantly contribute to explaining the sample variance, PC 2, PC 3, and PC 4 do not contribute to the understanding of group separation (Kaiser, 1960). Therefore, PC 1 should be the only PC explaining significant variation in the data.

There is minimal separation of males using PCA.

PCA in Females

Female olives, female yellows, and female hybrids were also clustered using PCA (Figure 9). Similar results were observed for females as for males. Together, the first four principle components explain 50.8% of the variation between samples, with each subsequent PC explaining less than 8% of the variation in the data as seen in the scree plot (Figure 9a). The eigenvalues for the first three principle components are also small: 0.8, 0.5, and 0.4.

PC 1 explains 24.2% of the variation and separated female olives on the right and female hybrids on the left, though separation is minimal and female yellows are not separated at all. PC 2 explains 15.7%, but does not visually separate the groups. PC 3 explains an additional 10.9% though does not further separate the groups (Figure 9b).

There seems to be minimal ability of the PCA to separate females.

PCA in Males and Females Prior to Correction for Sexual Dimorphism

Male olives, female olives, male hybrids, female hybrids, male yellow, and female yellows were clustered using PCA before applying the correction for sexual dimorphism (Figure 10). Cumulatively, PC 1 and PC 2 explain 60.7% of variation in the data with each subsequent PC explaining less than 7% of the variation in the data as seen in the scree plot (Figure 10a). The eigenvalue of PC 1 is quite large: 3.2. The eigenvalue of PC 2 is small: 0.7.

PC 1 explains 51.5% of the variation in the samples and separates the samples into males on the right and females on the left (Figure 10b). PC 2 explains 9.2% of the variation though no pattern of group separation was detected.

PCA reinforces the earlier results from MANOVA and Welch's t-test, that the nasal cavity is sexually dimorphic in baboons.

PCA in Males and Females Combined After Correction for Sexual Dimorphism

For each taxa, males and females were combined after the correction for sexual dimorphism was applied. Therefore, PCA was applied to 3 groups: olive, hybrid, and yellow baboons. Cumulatively, PC 1, PC 2, and PC 3 explain 46.9% of variation in the data with each subsequent PC explaining less than 8% of the variation in the data as seen in the scree plot (Figure 11a). The eigenvalues of the first three PCs were similar again small: 0.8, 0.5, and 0.3, respectively.

PC 1 explains 22.6% of sample variation, PC 2 explains 15.2% (Figure 11a), and PC 3 explains 9.1% (Figure 11b).

No patterns of group separation were detected in the first three principal components, with The sexual dimorphism correction removed the trend seen in PC 1 of the PCA prior to the correction (Figure 10), which separated males and females. This result appears more similar to the PCA of all the males (Figure 8) and the PCA of all the females (Figure 9).

Summary of PCA

Neither the PCA prior nor after the sexual dimorphism correction were very useful in explaining differences between the parental and hybrid groups. As expected of a biological morphometric sample, many of the measurements have high covariance, making it difficult for the PCA to construct specific variables from a combination of measurements that influence the differences between specimens. Unfortunately, the rotations provided by the PCAs also do not explain a large amount of the variation in the sample (male comparison: 61.3%, female comparison: 50.8%, before correction: 60.7%, after correction: 46.9%). In addition, expected clustering of the known taxa were not observed to a great extent in any of the PCAs.

4.3.5 Canonical Discriminant Analysis

CDA analyzes which combinations or rotations of measurements explain the differences between known groups, the parental and hybrid groups. CDA was applied to the same 31 features that were analyzed in PCA.

CDA creates rotations that maximize differences between each cluster it creates, rather than rotations based on differences between individuals as in PCA (Zelditch et al., 2004). The new axes, called the canonical discriminant functions (CD), are scaled to accommodate the patterns of within-group variance identified by CDA. Like the PCA, new scores are assigned to each specimen based on the CDs. These are plotted to visualize group clustering.

Clustering locations are discussed as above or below 0, as a visually reference on the CDA graphs.

CDA in Males

Male olives, male hybrids and the male yellow were clustered using CDA (Figure 12a). CD 1 substantially separated the three groups with yellow on the left, olive in the middle and hybrid on the right. CD 2 further separated yellow below 0 and olive and hybrids around 0. The histograms of CD 1 and CD 2 present an alternative view of the separations (Figure 12b).

CDA was performed again on males, but without the yellow male (Figure 13). The number of canonical discriminant functions that can be calculated equals the number of groups minus 1. Therefore, only 1 CD was created when analyzing olive and hybrid males (Figure 13). To be able to see all of the scores, the CD 1 scores were distributed along the y-axis in the order of the specimens. The y-axis does not have any bearing on interpretation of this CDA.

CD 1 neatly separates male olives on the left and male hybrids on the right (Figure 13a), as confirmed by the histogram of CD 1 (Figure 13b).

CDA in Females

CDA was also performed on female olives, female yellows, and female hybrids.

CD 1 separated the three groups with olive on the left, hybrids in the middle and yellows on the right. CD 2 further separated female yellows, which appear at the top of the graph, while olive and hybrid females appear around 0 (Figure 14a).

The histograms of CD 1 and CD 2 show that there is still substantial overlap between groups (Figure 14b).

PCA in Males and Females Prior to Correction for Sexual Dimorphism

The CDA performed before sexual dimorphism correction analyzed six baboon groups divided by species designation and sex (female olive, male olive, female hybrid, male hybrid, female yellow, male yellow).

The first and second discriminant functions were analyzed because together they explain 95.29% (87.99% by first discriminant function, 7.3% by second discriminant function) of the separation between groups. The remaining discriminant functions add negligible information about group differences (3rd: 3.28%, 4th: 1.42%) and were therefore not analyzed further.

The plot of the first two discriminant functions reveals two main groupings CD 1 with female olives, female hybrids, and female yellows grouped together on the left and male olives,

and male hybrids grouped together on the right (Figure 15a). This pattern is also seen in the stacked histogram in Figure 15b.

Similar to the PCA analysis, the CDA reveals strong sexual dimorphism that overpowers species differences.

Unlike the PCA, however, the y-axis, CD 2, seems to somewhat separate the hybrids (with values greater than 0) and the olives (with values less than 0). However, the histogram of CD 2 shows that there is still a lot of overlapping between parental and hybrid groups.

PCA in Males and Females After Correction for Sexual Dimorphism

CDA was performed again after sexual dimorphism was corrected for, shown in Figure 16. The same 31 features were analyzed. However, the groups were reduced to 3, combining males and females together into their species designations (olive, hybrid, and yellow). Therefore, only 2 discriminant functions were generated.

Along CD 1, olives are moderately separated from hybrids and yellow, which have values greater than 0. Along CD 2, olives and hybrids are not separated, though yellows seem to cluster alone in the upper right corner.

If the sample size were bigger, perhaps yellow baboons would be more strongly distinguished. These patterns are verified in the histograms (Figure 16b).

Based on the loadings, several features stand out as influencing taxa separation. Specifically, the first discriminant function is strongly influenced by a combination of the width of the middle meatus in slice 1 (loading: -3.26), the width of the inferior margin in slice 4 (-2.99), the height of the right inferior nasal concha in slice 1 (2.25), the width of the lateral recess in slice 5 (-2.03), the height from the nasal crest in slice 2 (1.90), and the height of the left inferior nasal concha in slice 2 (-1.78).

The second discriminant function is influenced by the height of the right inferior nasal concha in slice 3 (-3.59), and the height of the right inferior nasal concha in slice 2 (1.87). Opposite loading signs indicate that the variables are contrasted (Coghlan, 2013), and therefore might be more strongly associated with one group or the other.

Summary of CDA

CDA successfully separated the baboon groups with no or minimal overlap between the group distributions. The strongest separation was observed between the male baboon groups. The female groups were moderately separated with some overlap of group distributions. Comparing

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males and females, it seems as though the differences between males are driving the significant difference in degree of sexual dimorphism (Section 4.3.2).

The greatest influence on group separation when all six baboon groups were compared was size difference between males and females, or sexual dimorphism. Prior to the correction, CDA separated sex, but only minimally separated groups. Correction for sexual dimorphism successfully separated taxa with minimal overlap.

However, neither in PCA nor CDA was significance tested. Therefore, multivariate and univariate techniques were employed in Section 4.3.6.

4.3.6 Hypothesis Testing

Hypothesis testing compared baboon groups to discover if any traits are significantly different. Each trait is then analyzed for size, and in comparison between traits, shape can be analyzed between baboon groups.

Male olive and male hybrid baboon traits were compared using an independent samples student t-test. Male hybrids have heterosis and shape differences throughout the nasal cavity.

Independent Samples Student t-test between Olive and Hybrid Males

An independent samples student t-test for males was conducted to analyze the mean differences between morphometric traits in male olives and male hybrids (Table 6). Of the 45 features analyzed, 16 were significant at $\alpha = 0.05$. The significant features are highlighted in Figure 7b. Male hybrids were larger than male olives for all 16 traits, including overall volume, indicating heterosis at these locations.

Of the 16 features, 10 are attributed to the anterior bony cavity, including area and all traits but the ratio of height to width. Therefore, the anterior bony cavity was significantly larger in male hybrids, indicating heterosis, but shape was not affected.

Shape difference was observed at the choana, mid-nasopharynx, and posterior nasopharynx. The larger area of the choana in hybrids is influenced by the greater height from the nasal crest at the choana in hybrids. The greater area of the mid-nasopharynx in hybrids is also influenced by greater height (height at inferior margin). The width of the lateral recess was also greater in hybrids at the posterior margin of the nasopharynx, though the area of the slice was not affected.

Therefore, size and shape of the nasal cavity in males are affected by hybridization, achieved through heterosis.

ANOVA and Dunnett's C tests between Olive, Hybrid, and Yellow Females

The one-way ANOVA and subsequent post-hoc Dunnett's C tests revealed a similar trend between female olives, female hybrids, and female yellows (Table 7). Not all of variables show homogeneity of variance, (Levene's test, results in Table 2) and most, but not all, variables are normally distributed (Kolmogrov-Smimov and Shapiro-Wilk tests of normality, results shown in Table 3 and Table 4). Therefore, the Dunnett's C was an appropriate post-hoc test that compares multiple groups to each other (Dunnett, 1980).

Of the 45 traits analyzed, 19 traits were significant at $\alpha = 0.05$. Of the 19 traits, the Dunnett's C tests identified pairwise differences in 12 traits. Greater mean values for female hybrids were identified in 7 of the 12 traits, demonstrating heterosis, and greater mean values for female olives in 5 of the 12 traits, demonstrating dysgenesis (Figure 7c).

Heterosis in female hybrids was demonstrated in the areas of the anterior nasal cavity, choana, and mid-nasopharynx. Throughout the nasal cavity, the anterior bony cavity, the choana, the mid- and posterior nasopharynx, female hybrids have a narrower inferior meatus, indicating heterosis. Therefore, shape and size have been altered in female hybrids.

Therefore, size and shape also influence females during hybridization, though it is achieved through both heterosis and dysgenesis.

Hypothesis Testing in Combined Olive, Hybrid, and Yellow Baboons

After analyzing the traits of the nasal cavity in each sex, males and females were combined into three groups: olive, hybrid, and yellow baboons. The traits were then analyzed hierarchically, from a multivariate analysis including all traits across the three baboon groups using Wilk's Λ, then an analysis of each trait in a series of ANOVAs, followed by the Dunnett's C post hoc tests for any significant ANOVA traits to find significant pairwise comparisons.

MANOVA in Olive, Hybrid, and Yellow Baboons

A MANOVA was performed after the sexual dimorphism correction was applied to the male specimen values, removing any confounding effects of sexual dimorphism on size and shape differences. This MANOVA tests the hypothesis that the nasal cavity shape is different between the three groups (olive, hybrid, and yellow).

Using Wilk's Λ, it was found that the nasal cavity size and shape of the parental and hybrid groups is significantly different ($\alpha = 0.05$, $d.f. = 88$, $\chi^2 = 1.509$, $p = 0.011$).

ANOVA and Dunnett's C in Olive, Hybrid, and Yellow Baboons

To determine which features of the nasal cavity are driving the size and shape differences between parental and hybrid groups, ANOVAs were performed on all of the 45 measurements. Of

the 45 measurements, five showed significant differences between parental and hybrid groups at α_B = 0.0011 (Table 8).

Each of these traits was then analyzed using the Dunnett's C post-hoc test. Figure 7d visually summarizes these statistics by highlighting the significant measurements and colour-coded by the group with the largest measurement for that variable.

Of the five traits identified as significant by ANOVA, two did no show pairwise differences: the height to width ratio at the choana and the width of the inferior margin of the mid-nasopharynx. An ANOVA can be significant for a trait, but not be significant in the post hoc tests because the post hoc tests have a lower significance threshold than ANOVA.

The Dunnett's C tests identified three measurements that were significantly different between the three groups (Table 8). Hybrids were wider at the nasal crest and in the inferior meatus in the anterior bony cavity, demonstrating heterosis. Hybrids also had a greater height to width ratio at the mid-nasopharynx because hybrids were taller, but narrower at the inferior margin, showing a shape change in this area.

Summary of Hypothesis Testing

The hypothesis tests comparing all males, and all females both revealed regional heterosis and shape differences throughout the nasal cavity in hybrids compared to parental taxa. The female hybrids also had significant dysgenesis of the inferior meatus.

However, only two traits were found to be significantly larger in the combined hybrid group, the width of the inferior meatus and width at the nasal crest in the anterior nasal cavity. The all male and all female results were hidden when males and females were combined in groups, even though sexual dimorphism, primarily size, was removed. Therefore, male and female hybrids respond differently to hybridization not only in size, but also in shape.

4.3.7 Intra-observer Error

Consistency of the linear measurements was tested with intra-observer error. After repeatedly measuring all of the morphometric measurements of the nasal cavity used for this study of a single specimen (W984) at five different times, the standard deviation for all measurements was less than 0.1 mm, except for two measurements, width at nasal crest in mid-bony cavity, and width at alae of vomer of the posterior nasopharynx, which were less than 1 cm (Table 9). The standard deviation from the error is only larger than the sample standard deviation in these two variables, neither of which is statistically significant between sex or taxa.

4.4 Conclusions

I hypothesized that height and length of the posterior bony cavity, the choana, may show some heterosis internally and that the posterior nasal cavity, generally may be more conservative and resistant changes than the anterior nasal cavity. Therefore, I expected greater alterations of size and shape in the anterior dimensions.

Posterior Region

The results were surprising in that the hybrid posterior region, from the choana through the nasopharynx, exhibited many size and shape differences, both in heterosis and dysgenesis. Instead of being a highly conserved and unchanging area as hypothesized, this region is instead a dynamically changing area with different responses at different measurements. Measurements of the posterior region were not consistent within the hybrid group because males showed a different pattern than females. Males became wider inferiorly, while females became narrower compared to parental taxa. The differences in this area are so great that the PCA rotations were primarily differentiating the individual specimens through measurements of the nasopharynx width in conjunction with the anterior bony cavity. The opposing responses in males and females may also explain the greater sexual dimorphism compared to the parental taxa.

Specifically, the posterior nasopharynx seems to be a region of evolutionary conservation. This section of the nasopharynx expands beneath the orbits and is contained laterally by the sphenoid. Selection for shape or size change in the functionally simple nasopharynx may not alter the structures responsible for sight or basicranium stabilization, among many other critical functions. In this study, the posterior nasopharynx was not different between the taxa. The only linear measurement in the posterior nasopharynx that showed significant heterosis in hybrids was the width of the lateral recess.

I suspect that the changes are related to physiological function, though not in the way I originally hypothesized. The mid-nasopharynx is mainly responsible for the redirection of air during respiration (Morgan et al., 2001). Perhaps, due to the more simplified function of the mid-nasopharynx, the exact shape was not as critical to respiration and was less strictly regulated by genes, allowing new allele combinations to form in the hybrids. Ultimately, natural selection would establish which combinations provide the greater fitness advantage or the size and shape of the nasopharynx might be neutral, resulting from adaptations elsewhere. However, size and shape may be constrained by extremes so that they do not affect fitness.

Climate influences may also influence size and shape of the nasal cavity. In a study of the nasal cavity and maxillary sinuses in two different species of macaques, each adapted to a

different temperature environment, the choanal width was associated with colder environments (Marquez and Laitman, 2008).

Anterior Region

Although my hypothesis expected greater differences in the anterior bony cavity, I observed regional differences within the nasal cavity beyond simply anterior (bony cavity) versus posterior (nasopharynx). As expected the anterior region of the hybrids, at the rhinion, exhibited greater inferior width in the overall species comparison, indicating a change in shape in hybrids. Male and female hybrids showed overall heterosis, while female hybrids also show shape change in the inferior meatus of the anterior bony cavity.

However, the mid-bony cavity revealed no difference between any of the taxa, though there was a difference between males and females, which will be addressed below. Unexpectedly, it seems as though this is the region of greatest functional significance in the nasal cavity, where the size and shape are conserved even between the parental taxa. It is the bony cavity, specifically the area where air turbulence slows while flowing through the nasal conchae, that is responsible for more critical functions such as the warming, humidifying and filtering of the incoming air (Mygind and Dahl, 1998; Jone, 2001; Noback et al., 2011). The greatest turbulence occurs in the anterior third of the nasal cavity, then slows, which would correspond to the mid-bony cavity as defined in this study (Morgan et al., 1991). Therefore, shared ancestry or convergent adaptive selection may have optimized the mid-nasopharynx in the yellow and olive baboons, which was maintained in the hybrids.

Differences in Size and Shape

Though I discussed shape and size differences when reviewing the conclusions of the posterior and anterior nasal cavity, the distinction between shape and size is functionally important. Noback et al. (2011) found that size is correlated with energetics, to allow greater volumes of air through the nasal cavity during inspiration, while shape has functional significance for physiology, such as warming and humidifying the air.

Heterosis in the nasal cavity may give hybrids an advantage in energetics by increasing the space through which air can pass. However, Bastir and Rosas (2013) caution against concluding too much from the skeletal anatomy because subtle changes in the soft tissue can strongly influence respiration. Charpentier et al. (2012) referenced a submitted article in which the authors observed greater consortship (mate guarding) in hybrid males within a yellow and olive baboon colony, which will result in a greater number of hybrid offspring and higher hybrid

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fitness. Future studies might attempt to examine hybrid respiration in more detail, such as respiratory volume or respiratory rate, to determine if the greater size in the nasal cavity of hybrids gives them energetic advantage.

Shape changes in the first one third of the bony cavity, such as a wider inferior meatus at the rhinion, may reflect differences in airflow. Morgan et al. (1991) found that the first one third of the bony cavity has the greatest airflow velocity and is the location where air streams are separated and sent to various locations for processing. Hybrids may exhibit further physiological changes, suggested for future studies.

Lateral Recess

According to Lund (1988) the lateral recess begins at the plane of the root of the canine and extends to the back of the nasal cavity. I believe that Lund's definition includes the inferior meatus or perhaps the cavities created by the canines that sometimes extend back into the nasal cavity, which was observed in a number of baboon specimens in this study. However, within the bony cavity, I did not observe any areas that expanded more laterally than any other area along the lateral nasal walls of the bony cavity.

The lateral expansions that I did observe began posterior to the choana, into the nasopharynx. This observation best matches the definition of lateral recess by Koppe and Ohkawa (1999: 80): the lateral recess begins at the third molar (M^3) and extends into a "small" lateral recess that bulges into the medioinferior walls of the orbit. This bulging into the orbits was observed on the skull and in CT scans in 44% of all specimens with different degrees of expansion, though there was no difference between taxa, discussed in Chapter 5.

The width of the lateral recess is greater in hybrids when comparing all males or all females. This observation is very interesting in comparison to my argument above about the conservation of the posterior nasopharynx in order to maintain physiological function outside of the nasal cavity. The lateral recess, which expands laterally into the walls of the orbits, does not follow this trend, which may indicate a different function of the area. Whether this is of advantage or disadvantage to the hybrids cannot be determined from the current study. Future work should explore the physiology of this area.

Differences in Sex

The strongest influence on the nasal cavity was sex, which had to be corrected for in order to see differences in taxa. For nearly all the measurements, males, regardless of taxa, were larger.

Hybrid males and females also present different shape responses to hybridization in the nasal cavity, after difference in size is removed by the correction for sexual dimorphism. It would be valuable to study baboon ontogeny and developmental timing of different traits to discern the reasoning behind shape differences between males and females.

One remarkable similarity between males and females is the similarity in nasopharynx length (from choana to posterior nasopharynx), but they differ in bony cavity (anterior bony cavity to choana) length. Therefore, it is the bony cavity length that is greater in males. Though I concluded above that the mid-nasopharynx has the evolutionary experiment with freedom to different shapes and sizes, perhaps length is an important function to maintain. Future research should explore the different morphologies.

Many studies have found that the basicranium responds to facial size and vice versa (Lieberman et al., 2000; Bastir et al., 2010). Because the hybrid males are much larger and longer in the bony cavity, future studies might also consider exploring different aspects of the basicranium in order to possibly detect structural compensation.

Sexual Dimorphism

Both hybrid and olive taxa had significant differences between males and females, sexual dimorphism, at most morphometric features. Significant sexual dimorphism was expected and has been found in many primates, including baboons, in the literature (Phillips-Conroy and Jolly, 1981; Leigh and Cheverud, 1991; Mitani et al., 1996; Ackermann et al., 2006; Schillaci et al., 2007).

However, when comparing sexual dimorphism between hybrids and olives, the two methods employed contradicted each other, the index of sexual dimorphism and the degree of sexual dimorphism. The index of sexual dimorphism method, also used by Phillips-Conroy and Jolly (1981), revealed no differences in the degree of sexual dimorphism for any trait. If the confidence intervals do not overlap, the test suggests that the groups have significantly different degrees of sexual dimorphism. However, this test does not quantify the difference between the 90% confidence intervals between olive and hybrid baboons.

However, I also developed my own method of identifying differences in the degree of sexual dimorphism. This method begins with student t-tests to test for initial sexual dimorphism in olives and in hybrids, followed by a Welch's t-test that compares the differences between olive males and olive females to the difference between hybrid males and hybrid females for each trait. The Welch's t-test is designed to compare differences between groups. The main advantage of the

Welch's t-test is that the analysis outputs a test statistic and *p*-value, which allows the researcher to establish different significant threshold levels.

Other methods, MANOVA, PCAs, CDAs, and even simple bargraphs, all identified significant or dramatic differences between sex. It is less probable that these methods and the Welch's t-tests are all incorrect, especially when so many other studies have also found sexual dimorphism in primates, including baboons. Therefore, this study favors the results from the Welch's t-test rather than the Simpsons et al. (1960) method. (See Section 4.3.2 for calculations).

I conclude that hybrids had a greater degree of sexual dimorphism compared to olives in nearly all morphometric traits. If hybrids were isolated as a population, having a greater difference between males and females would indicate greater sexual selection and mate competition (Mitani et al., 1996). However, hybrids, olives, and yellows live sympatrically, within the same region. Therefore, if hybrids have greater sexual dimorphism and have larger overall size found in this study and Ackermann et al. (2006), male hybrids now have an advantage in a more competitive environment, which is discussed further in Section 6.1.

However, conclusions about sexual selection are made cautiously because the sample population is captive (Phillips-Conroy and Jolly, 1981). Male baboons were artificially selected by researchers to mate with females rather than female mate selection or male-male competition, so sexual selection would not have been reinforced in the captive populations. Therefore, hybrids may have different features of sexual dimorphism in the wild than in captivity.

Summary

In conclusion, the model of the nasal cavity used in this study successfully identified differences between hybrids and parental taxa. The nasal cavity displayed unique regional differences, reflecting different physiological functions that revealed evolutionary constraints in the mid-bony cavity, and posterior nasopharynx, and morphological flexibility to respond to differences in the anterior bony cavity, choana, and mid-nasopharynx. Greater sexual dimorphism in hybrids along with larger size and shape differences may reflect greater sexual selection and hybrid advantage. Discussion about how this model might be useful for the identification of Neanderthal and AMH hybrids is in Chapter 6.

4.5 Study Limitations

Unfortunately, this study was severely limited by the small sample size of yellow baboons. Wild yellow and olive hybrid zones exhibit characteristics of an intermediate hybrid zone, it would have been ideal to be able to compare hybrids more extensively to both parental taxa.

Unfortunately, the colony no longer houses any purebred yellow baboons due to generations of regulated breeding that attempted to minimize heterozygote deficit due to inbreeding (Mahaney MC, Personal communication).

A single yellow male also potentially compromised the sexual dimorphism correction in Section 4.3.3. Because there is only one male yellow baboon, the sample mean was not reflective of the population mean. Fortunately, only a single data point in the study, the yellow male, is affected and it was not used in most statistical analyses.

Measurements for this study were taken between one landmark to another as defined in Table 1. However, these linear measurements were not made between each landmark to create a coordinate system to model the nasal cavity. If the methods were altered to create a coordinate system, more detailed morphometric statistical analysis and visualizations, such as reconstructions, overlays, superimpositions, or warping, could have been applied to the nasal cavity model (Lele and Reichtsmeier, 2001). Though this study was able to analyze shape and size differences using linear statistics, which other studies have successfully used (Spoor and Zonneveld, 1995; Spoor et al., 2003; Ackermann et al., 2006), the advantage of the coordinate system provides the opportunity to explore the data more extensively.

In addition, the linear measurements were not tested for inter-observer error. Because the measurements were designed for this study, definitions should be corroborated through an interobserver study.

The sample sizes for this study were large, except for the yellow baboons. However, it would be difficult to apply the techniques used in this study to fossil species with small sample sizes, often $n - 1$. It may be applied to Neanderthals and AMH because researchers have discovered many remains that we are able to estimate population parameters. However, population estimates are still difficult to obtain in Neanderthals and AMH because the specimens are often fragmentary, and therefore all measurements cannot be calculated, and the remains researchers have found are spread across Europe in subpopulations and through time. Therefore, I caution that such models are most useful only at a population level understanding of a taxa in order to recognize outlier individuals with heterosis or dysgenesis.

This study is also simplified to examine first generation hybrids, though hybrid zones are often very complicated in the wild with multiple generations of hybrids, backcrosses, and purebred individuals living sympatrically (Barton, 2001). The collection examined in this study also contains skulls of backcrosses with olive baboons, which should be considered for analysis in the future. Analysis of backcrosses and many generations later is particularly important to inform the debate between Duarte et al. (1999) and Tattersall and Schwartz (1999), who disagreed on the

traits of a Neanderthal and AMH hybrid that lived in a population that had hybridized many generations before.

Chapter 5
Nonmetric Analysis

Nonmetric traits are often congenital or developmental. Scoring nonmetric traits has been useful in tracing family lines, since family members often have the same variation of a nonmetric trait due to inheritance (Brasili et al., 1999). Nonmetric traits have also been useful in identifying different taxa, such as the occipital bun or supraorbital torus to identify Neanderthals.

Nonmetric traits can be inherited or result from developmental stress, possibly due to the merging of unrelated genomes during hybridization, including those involved in developmental timing. The developmental stress affects the timing of growth from fetus to adulthood, causing extra bone growth in hyperstoic features or failures to fuse in hypostoic features (Buikstra and Ubelaker, 1994).

In the baboon skulls, Ackermann et al. (2006) examined both hyperstoic, such as supernumerary teeth extrasutural bones or sutures, and hypostoic features, such as residual metopic sutures. They also examined additional features that do not fit nicely into either hyperstoic or hypostoic, such as rotated molars or tooth crowding. Ackermann et al. (2006) found that a higher percentage of nonmetric traits on external features of the skull is correlated with hybridization. If the hypothesis in Ackermann et al. (2006) holds true for internal structures of the nasal cavity, then hybrids will show significantly higher frequencies of nonmetric traits in the nasal cavity compared to the parental species.

However, I hypothesized that internal physiology of the nasal cavity is more sensitive to changes in structure compared to external anatomy, including variation in nonmetric traits. In addition, due to the physiological differences between the bony cavity and the nasopharynx, I hypothesized that because of its location closer to the critical areas of the major vessels, basicranium, and structures of the eye, the nasopharynx will have no difference in frequency of nonmetric traits between the parental baboon groups and the hybrid group. Thus, because the bony cavity has less stringent genetic controls, more nonmetric traits might form in hybrids due to developmental instability and increased developmental stress.

5.1 Methods
During the segmentation process, nonmetric traits were visually identified in the nasal cavity from the CT scans. A list was kept of each such trait encountered, with the discovery of ten

different traits in baboon nasal cavities: tooth roots that enter the nasal cavity, ectopic teeth in the nasal cavity, deviated septum, divided greater palatine canals, spur on greater palatine canals, bony growth within greater palatine canals, bony growth within lacrimal canals, relative size of the lateral recess, the attachment of the inferior nasal conchae at slice 3, and the presence of the alae of the vomer in slice 4. The last two traits in the list, the attachment of the inferior nasal conchae at slice 3, and the presence of the alae of the vomer in slice 4, were only observable on the CT scans.

All other traits are observable on the skulls and on the CT scans. Each specimen (n=175) was then re-examined on the CT scans and a subset of 65 specimens across the taxa, both males and females, out of the 175 specimens were examined on the dry skulls to determine the presence or absence of all ten traits. Only a subset of specimens was analyzed on the skulls due to time constraints.

Ackermann et al. (2006) found that hybrids had higher frequencies of nonmetric traits in the dentition and the sutures, specifically supernumerary teeth, tooth crowding, zygomaxillary suture abnormalities, extreme facial size/robustness, and residual metopic suture. However, Ackermann et al. (2006) also searched for other external traits, such as ossicles at lambda and asterion, bregmatic bones, coronal ossicles, epipteric bones, and parietal-notch bones, but they were not present. Ackerman and Bishop (2009) found extra sutures in the zygomaxillary region, ossicles in the zygomaxillary region, supernumerary teeth, rotated teeth, anterior dental crowding, and posterior dental crowding in suspected gorilla hybrids from various museum collections. However, ossicles at lambda and asterion, bregmatic bones, coronal ossicles, epipteric bones, and parietal notch bones were not present (Ackermann and Bishop, 2009). As with Ackermann and colleagues, I examined many potential nonmetric traits in the nasal cavity because it was not certain which or any nonmetric traits would indicate hybridization.

Visual analysis of the dry skulls revealed that several traits seen on the CT scan were not nonmetric traits. For example, what looked like bony obstructions in the lacrimal canals and the greater palatine canals on the CT scans were found to be dried tissue that had not been thoroughly cleaned off the skull. Therefore, these traits were removed from the analysis. This illustrates the value of examining the physical skulls in addition to the CT scans.

Likewise, re-analysis of the specimens using the CT scans showed that a trait identified on the skull could not be reliably located in the scan. The division of the greater palatine canal extended inferiorly in some specimens to create a spur on the palate. However, even in specimens that were identified on the skull as having spurs, the spurs were difficult to locate and quantify on

the CT scans. In addition, this trait did not directly involve the nasal cavity. Therefore, this trait was removed from the analysis.

The final seven nonmetric traits that were compared between parental species and hybrids are defined in Table 10. To quantify the nonmetric traits between baboon groups, a system of scoring was designed with higher scores indicating the presence of the trait or that the trait is larger or obstructs the nasal cavity. A score of 0 to indicates that the trait was not present (Table 10). Figure 17 illustrates examples of each nonmetric trait in the various forms identified, and labeled with the associated score.

5.2 Nonmetric Statistical Analysis

The list of nonmetric traits creates categorical data. Therefore, data analysis required the use of non-parametric statistics such as the Fisher's Exact test (Samuel and Witmer, 2003: 422-431). The Fisher's Exact test is appropriate in this situation where the counts can be very small, especially when comparing the yellow baboons. It was originally designed to be applied to contingency tables of 2x2. A contingency table gives the percent per cell by dividing the count for that cell by the total count for the column and multiplying by 100. To complete a Fisher's Exact test, the categories must be transformed into frequency data in an $r \times k$ contingency table, where r refers to the number of rows (for this study: scores), and k refers to the number of columns (baboon groups) (Table 11). In each test, two groups were compared at a time: olive to yellow, parental (olive and yellow) to hybrid, male parental to male hybrid, female parental to female hybrid, and all females to all males. All tests were performed at $\alpha=0.05$.

The statistical tests were performed to test the hypotheses: 1) the frequency of nonmetric traits in hybrids is different from the frequency of nonmetric traits in the parental species, and 2) there is a difference between the frequencies of nonmetric traits between males and females.

5.3 Results

Analysis of the nonmetric traits in the nasal cavity was conducted using a series of Fisher's Exact tests. Frequencies of each score value for each nonmetric trait are presented in bargraphs in Figure 18. The two parental groups, olive and yellow baboons, were tested for a difference in the frequency of each identified trait. Of the seven traits, none were found to be significantly different between the parental groups (Table 11). Therefore, in the remaining tests, the olive and yellow baboon groups were combined into one group, the parental group, to be compared against the hybrid group.

The frequencies of each nonmetric trait were then examined between: parental and hybrid groups, male parental and male hybrids, and female parental and female hybrids. None of the nonmetric traits occurred at significantly different frequencies between the parental and hybrid groups (Table 11).

Next, the specimens were divided into males and females and tested for each trait. Between the male parental group and the male hybrid group, no significant differences in trait frequency were found for any nonmetric trait (Table 11). Similarly, between the female parental group and the female hybrid group, no significant differences in trait frequency were found for any nonmetric trait at α=0.05 (Table 11).

However, there were several features, deviated septum, lateral recess, and attachment of inferior nasal conchae by the choana, that would be significant at α=0.10.

First, the deviated septum tends to be more deviated in male hybrids compared to male parental baboons (p=0.10). This trend is hidden in the test comparing all parental baboons to all hybrid baboons due to the influence of females (p=0.644).

Second, the lateral recess of hybrids protrudes further into the walls of the orbits compared to parental baboons with p=0.075. This result is consistent with the wider lateral recess found in the hybrids (Section 4.3.6).

Third, the inferior nasal conchae are attached by the choana more frequently in female parental baboons compared to female hybrids at p=0.073. This trait could also be examined as a metric trait by measuring the location of the posterior margin of the inferior nasal conchae in comparison to other features, such as the posterior margin of the palate (choana), which was examined here.

In several tests, there were no counts for a particular score, which has implications for how the Fisher's Exact test functions. For the ectopic teeth, three tests had values of 0 for both groups: score 3 between olive and yellow; score 2 between male parental and male hybrid; scores 3 and 4 between female parental and female hybrid. Neither the male parental nor male hybrids had scores of 3, severe, for the deviated septum. These values are marked with an asterix in Table 11. The Fisher's Exact test cannot calculate a statistic if all the observed values in a row are 0. Therefore, these rows were removed from analysis and the Fisher's Exact test continued at a lower degree of freedom.

A final test regrouped the specimens into a) olive, hybrid, and yellow females, and b) olive, hybrid, and yellow males. These Fisher's Exact tests found that 6 of the 7 tested nonmetric traits, tooth roots in the nasal cavity, ectopic teeth, deviated septum, lateral recess in orbit, attachment of inferior nasal conchae in slice 3, and the presence of the alae of the vomer in slice

4, were significantly different between males and females, with males having higher frequencies at α=0.05 (Table 11). Therefore, there is a sexual bias towards males in the frequency of nonmetric traits.

5.4 Conclusions

From Ackermann et al.'s (2006) work, and because the nasal cavity is functionally divided, I expected that hybrids might have a higher percentage of nonmetric traits in the anterior, but not posterior nasal cavity. However, as hypothesized, this study did not find any significant differences between taxa, and hybrids had the same percentage of nonmetric traits in the anterior nasal cavity, which includes tooth roots, ectopic teeth, deviated septum, and division of greater palatine canal, or the posterior nasal cavity, which includes the lateral recess in the orbits, the attachment of the inferior nasal conchae at the choana, and the presence of the alae of the vomer near the middle of the nasopharynx.

In hybrids, three traits were found in higher frequencies, and significant at α=0.10, but not at α=0.05: greater deviation of the septum, unattached inferior nasal conchae at the choana, and greater bulging of the lateral recess into the nasal cavity.

Roots of Teeth in Nasal Cavity

Because Ackermann et al.'s (2006) studies found dentition to be a significant indicator of hybridization, I included two nonmetric traits related to the impact of dentition on the nasal cavity: tooth roots in the nasal cavity, and ectopic teeth in the nasal cavity.

There was no difference in the frequency of the roots entering the nasal cavity between taxa, though there is between sex. Overall, 25% (43 of 171) of all specimens had at least one root enter the nasal cavity. Abscesses entering into the nasal cavity occurred in 47% (20 of 43) of cases of roots entering the nasal cavity. The large quantity of associated abscesses possibly formed due to the diet containing more sugars given to the baboons in the captive colony. The pathological occurrence of abscesses is more frequent in males and might reflect female behavioural differences, such as selective eating or processing that would reduce dental pathology, or possibly some physiological or structural advantage that prevents dental pathologies.

Ectopic Teeth

Ectopic teeth, which are rare (1% in modern humans) and extremely rare in the nasal complex, most commonly form due to problems during embryological development (Castillo, 1994; de

Oliveira et al., 2008; Ramanojam et al., 2013). The ectopic teeth can become encased by cysts, or covered by salts to create a rhinolith, and may be accompanied by pain, such as throbbing in the region, localized pain, or headaches, and other symptoms, such as nasal discharge, epistaxis, deformity of the external nose, or deviated septum, or be asymptomatic (Şenkal et al., 2006; de Oliveira et al., 2008; Ramanojam et al., 2013). In clinical cases, the ectopic tooth is almost always removed surgically, even when asymptomatic, in order to prevent future infections and complications (Şenkal et al., 2006; de Oliveira et al., 2008; Ramanojam et al., 2013).

I hypothesized that the occurrence of ectopic teeth would be similar to the occurrence of supernumerary teeth found by Ackermann et al. (2006). Ectopic teeth often are supernumerary teeth, but they fail to erupt and remain in the nasal cavity or become malformed in the nasal cavity. Ackermann et al. (2006) found supernumerary teeth in 8% (14/169) in all taxa, of which 25% (10/40) were hybrids; of which 4.5% (1/22) were female hybrids, and 50% (9/18) were male hybrids. Though no baboon taxon showed a greater frequency of ectopic teeth in the nasal cavity than any other, the overall frequency (8%) matches with Ackermann et al.'s (2006) study 10%, though it is much greater than the <1% occurrence in humans (de Oliveira et al., 2008). It is possible that the high frequency may be a result of captivity, though rates of ectopic teeth would need to be recorded in the wild for confirmation.

Deviated Septum

Some degree of a deviated septum was observed in 44% of all the specimens. However, there was no difference in rates between taxa and the high rate is not surprising because high rates are also recorded in humans (Holton et al., 2012). Holton et al. (2012) found that nearly all of their human subjects exhibited some degree of deviated septum.

There was a slight difference between the occurrence of deviated septum between male parental and male hybrids, though not significant. Male hybrids exhibit more deviation than male parental baboons. This may be an indication of hybridization in males due to developmental instability.

The occurrence of the concha bolussa, in which one inferior nasal concha is larger than the other, is associated with septal deviation (Stallman et al., 2004). Though concha bolussa was not recorded, I suspect that this was one of the primary reasons for septal deviation and should be investigated in the future. Trauma can also cause a deviated septum though a history of trauma for each specimen would be needed to determine if trauma was the cause.

Greater Palatine Canal

The division of the greater palatine canal had an overall frequency of 33% and was also not found to be significantly different between taxa. In literature on human nonmetric traits and baboon nonmetric traits, there is no mention of such a division in the greater palatine canal. Certainly further studies of this trait in more extensive collections are recommended to discern the occurrence of this trait.

Lateral Recess in the Orbits

The visual expansion of the lateral recess occurred in 44% of specimens. Further discussion of the lateral recess is given in Section 4.4.

A difference was observed in the degree of expansion of the lateral recess. The lateral recess of hybrids protrudes further into the walls of the orbits compared to parental baboons with $p=0.075$. The morphometric measurement of the lateral recess was taken anterior to the orbits, while the nonmetric trait for the lateral recess was observed in the orbits. Koppe and Ohkawa (1999) labeled the lateral expansion in the orbits the "small" lateral recess, which was differentiated form the general lateral recess posterior to the third molar and in the nasopharynx. The observation of expansion in both of these areas in hybrids supports the two definitions of the lateral recess. Future research should test if there is correlation between the two types of lateral recess, or continuity connecting them as the same structure.

Future studies should also morphometrically measure this trait as morphometric traits are generally much more accurate in recording these types of size differences, lowering inter- and intra-observer error.

This study provides a new perspective on the occurrence of the lateral recess in baboons. There is a wide range of expression of this trait, though it is not present in the majority of individuals. In order to identify the purpose of the lateral recess, future studies should further examine potential respiratory differences in individuals with the lateral recess in the orbits, posterior to the 3rd molar, and those without.

Inferior Nasal Conchae Attachment

The attachment of the inferior nasal conchae at the choana occurred more often in females than in males. I suspect that this observation may not be a true nonmetric trait, but a morphometric side affect of the difference in length of the bony cavity in males and females, as discussed in Section 4.3.6.

The male inferior nasal conchae extend beyond the choana into the nasopharynx though the female inferior nasal conchae attaches before or at the choana. Because the inferior nasal

conchae affect airflow, the airflow between males and females might be different as well. Future studies should analyze the physiological functions of this morphological observation.

Similar implications might be applied to female parental and female hybrid baboons. The inferior nasal conchae is attached by slice 3 more frequently in female parental baboons compared to female hybrids at p=0.073. Again, this observation may be an affect of bony cavity length differences, which were significantly different between female taxa (Section 4.3.6).

Anterior Location of Alae

Similarily, I suspect that the presence of the alae of the vomer is caused by length differences between males and females. As described in Chapter 4, the bony cavity is longer in males, though the nasopharynx is the same length. Therefore, the midpoint of the nasopharynx in males (slice 4) is shifted more anteriorly, making it seem as though the alae of the vomer begins more posteriorly. Future studies might examine whether the total anatomy of the nasal cavity is not changing, or if the vomer is similar between males and females, but the length of the nasal cavity alters the location of the alae.

Summary of Nonmetric Traits

Overall, males demonstrated a greater frequency of all nonmetric traits. This trend is also seen in some human traits, such as auditory exostosis, parietal notch bones, and asterionic bones, though certainly not in all (Brasili et al., 1999; Hanihara and Ishida, 2001). The male biased occurrence of nonmetric traits is also considered variable depending upon the population being studied (Brasili et al., 1999; Hanihara and Ishida, 2001). Therefore, the male bias in baboons is an anomaly for all the traits tested and deserves future study.

Ackerman et al. (2006) also examined the same baboon collection that was used in this study and found a greater frequency of nonmetric traits in the external skull of hybrids. Because the rate of nonmetric traits did not significantly differ between taxa, nonmetric traits of the nasal cavity cannot help in the identification of hybrids in the fossil record. There were no differences in the frequency of nonmetric traits in the nasal cavity indicating that the developmental timing of the nasal cavity may not be disturbed, though Ackermann et al. (2006) cites developmental instability as the cause for a greater frequency of nonmetric traits on the external morphology of hybrids.

Therefore, there may be less selectively neutral traits in the nasal cavity compared to other locations of the skull, or I may have selected nonmetric traits that are not useful in hybrid identification.

Chapter 6

Implication of Baboon Hybridization for Pleistocene Hominins

In this chapter, the baboon hybrid model of the nasal cavity and hybrid zone is used to infer the form of the nasal cavity in Neanderthal and AMH hybrids and a Neanderthal and AMH hybrid zone. I examined the baboon hybrid zone and assessed the independent variables important in determining the outcome of hybridization. The model of the baboon hybrid zone then served as a comparison to a potential hybrid zone between Neanderthals and AMH. Considering the available skeletal, genetic, and archaeological evidence, I hypothesized that hybridization occurred between Neanderthals and AMH, followed by the gene swamping of Neanderthal genes by AMH genes, leaving only a small introgression marker of Neanderthal nDNA in contemporary human genomes. Finally, I applied the baboon hybrid nasal cavity model to propose a hypothesized Neanderthal and AMH hybrid nasal cavity.

6.1 Olive and Yellow Baboon Hybrid Zone

The baboon model of the hybrid zone provides insight into which factors influence the formation and maintenance of hybrid zones, and what genetic and morphological evidence is helpful in identifying characteristics of hybrid zones. Unfortunately, the Neanderthal and AMH populations cannot be directly observed in a hybrid zone, but a hypothesized hybrid zone between Neanderthals and AMH can be proposed after understanding the baboon hybrid zone. The literature describes the hybrid zone between yellow and olive baboons in Amboseli, Kenya as unimodal intermediate, with an invader population (olive baboons) immigrating into the territory of yellow baboons.

Samuels and Altmann (1986) describe some of the first hybrids in Amboseli. Samuels and Altmann (1986) discovered juvenile hybrids in the groups of yellow baboons that they were studying. They suspected that these juveniles were the offspring of female yellows and male olives because they were "yellow in colouration, but had *anubis*[olive]-like features (e.g. stocky builds and *anubis*-shaped tails and faces)" (Samuels and Altmann, 1986: 133).

Alberts and Altmann (2001) later formulized the process of identifying hybrids in the field by observing specific "intermediate" traits, such as intermediate body shape, hair length, head shape, tail length and thickness, and tail bend. These traits are scored from 0 (pure yellow) to 2 (pure olive), where 1 is intermediate, 0.5 is "more yellow" and 1.5 is "more olive". This

system of identification of phenotypic characters is designed to capture a unimodal distribution, which is what was observed in July 2000, though it was skewed towards yellow: 77% yellow (scores of 0-025), 10% ambiguous (0.26-0.49), 13% hybrid (0.5-1.54) and less than 0.5% anubis (1.5-2). Alberts and Altmann (2001) hypothesized that the ambiguous phenotypes were hybrids with distant olive ancestors, perhaps one grandparent, or are yellow outliers. Alberts and Altmann (2001) also contrasted the yellow and olive hybrid zone with the more bimodally distributed hamadryas and olive hybrid zone, in which the phenotypes tend to present as either hamadryas-like or olive-like, with no "intermediate" phenotypes.

The baboon population in Amboseli is predominantly composed of yellow baboons, though the percentage of hybrids, both phenotypically and genetically, continues to rise (Alberts and Altmann, 2001; Tung et al., 2008). Alberts and Altmann (2001) reviewed demographic trends and found that births of hybrids increased from 0% in the 1960s and 1970s, to 10% in the 1990s. Tung et al. (2008) analyzed the genetics of baboons in Amboseli from 1968 to 2004 and found that olive genetic ancestry in the population has increased from 0% in 1968-1979, to 12.8% in 1980s, to 25.1% in 1990s, and to 31.3% in 2000-2004.

The rise in olive ancestry is the result of successful hybridization followed by those hybrids successfully mating with yellows and other hybrids. The greater percentage of hybrids in the population, the greater percentage of olive-ancestry, and the successful hybridization might indicate hybrid advantage. Hybrid fertility and high hybrid fitness have been observed in Amboseli. In the 1960s and 1970s, no hybrid births were recorded. Samuels and Altmann (1986) recorded the first births of hybrids by an olive male and a female yellow. From observations of copulation, the olive male probably fathered five conceptions (two of which survived the first year of life). Alberts and Altmann (2001) found evidence of male hybrids emigrating from their natal groups earlier than their purebred yellow counterparts. Early dispersal has been linked with the timing of other important reproductive events, such as age of maturation and the first mate-guarding episode (Tung et al., 2008). Indeed, Charpentier et al. (2012) cited a submitted study that has observed olive-like male hybrids participating in more mate-guarding events, which are associated with successful reproduction and higher fitness. Charpentier et al. (2012) also observed transgressive segregation, greater genetic diversity in olive and yellow baboon hybrids, which gives hybrids an advantage in novel or changing environments and in circumstances in which new pathologies might exist.

It is remarkable how much genetic and phenotypic change has occurred in Amboseli considering that Alberts and Altmann (2001) observed only five purebred male olives and eleven male olive and yellow hybrids immigrate into Amboseli since 1971. Therefore, all of the first

generation (F1) hybrids were derived from a male olive and female yellow. This observation is not surprising because in both yellow and olive baboons, it is the male that disperses from the natal group.

However, the evidence from the mitochondrial DNA (mtDNA) is more complicated. Newman et al. (2004) were not able to differentiate loci from mtDNA that were sampled from three yellow baboons from the hybrid zone in Kenya, six olive baboons from the hybrid zone in Kenya, and four olive baboons near the hybrid zone in Kenya. Newman et al. (2004) hypothesize that the mtDNA is not differentiable because the mtDNA contains traces of past hybridization (not related to the contemporary hybrid zone documented by Samuels and Altman (1986)) between olive and yellow baboons. However, it is uncertain which taxon had the original mtDNA that has since spread to olive and yellow baboons around the hybrid zone. This past hybridization event would have created the contemporary yellow baboon population in Kenya (Newman et al., 2004).

The baboons that Newman et al. (2004) sampled and labeled as from the hybrid zone in Kenya are from the SNPRC colony (the same used in this study) and are more accurately described as the descendants of the wild-caught baboons from Kenya. There is a contradiction in how the colony founders are classified. Newman et al. (2004) suggest that the baboons are yellows and olives from the hybrid zone, which implies that their populations may have experienced recent introgression. However, Dr. Mahaney at SNPRC (Personal communication) informed me that the founders of the colony were pure yellow and pure olive, and were wild-caught prior to known hybrid zones between olive and yellow baboons. Either way, Newman et al.'s (2004) study would still show evidence of a past hybridization event, and suggests that hybrid zones are not stable over time.

In Amboseli, the hybrid zone between yellow and olive baboons is also not stable. Alberts and Altmann (2001) hypothesize that if immigration of male olives ceases due to the local extinction of the natal populations around Mt. Kilimanjaro, the olive genes that have introgressed into the yellow population in Amboseli will become a decreasing percentage of any individual hybrid's genotype in successive generations until little trace of hybridization remains. This would occur because the yellow genes would gene swamp the introgressed olive genes if the supply of olive genes stopped. Tung et al. (2008) may have documented the beginning of this process because hybrids in 2000-2004 have a smaller percentage of olive genes compared to hybrids in 1968-1979. They explain this conflicting evidence by hypothesizing that hybrid males have a selective advantage over yellow and olive males, while there has also been a decrease in the immigration of olive males. If hybrid males did have the highest fitness, the hybrid zone would be

maintained at a study state with intermediate level of olive ancestry, while the hybrids backcrossed with yellows or mated with other hybrids. In addition, fewer olive males are dispersing into yellow territory, so that the overall percentage of olive genes in the Amboseli gene pool remains steady, but new hybrids have a smaller proportion.

Knowing the form of the hybrid zone (unimodal, bimodal, mosaic) and the variables that determine how the hybrid zone changes, it is possible to deduce the general morphology of the hybrid, in this case, a gradient of intermediate morphologies. The language used to describe yellow and olive hybrids in Tung et al. (2008) and Charpentier et al. (2012) returned to the use of the term "anubis-like," or olive-like, hybrids, originally used by Samuels and Altmann (1986). The term "anubis-like" is used to refer both to the phenotype (Charpentier et al., 2012) and the genotype (Tung et al., 2008). The authors have never explicitly described the "anubis-like" features, and I find it interesting that no hybrids have been described as "cynocephalus (yellow)-like."

Perhaps, this is a historical precedent. Since the population was originally pure yellow, any new phenotype or genotype introduced by olive males would look more olive-like. However, from the recent descriptions, I am uncertain how or if the gradient of phenotypes described by Alberts and Altmann (2001) has changed through time. Of course, Charpentier et al. (2012) and Tung et al. (2008) were not attempting to study phenotype variation in hybrids, which I am interested in because I want to find a morphological indicator of hybridization. However, the difference in the application of the hybrid terminology (yellow-like, olive-like), mirrors the literature on hybrids between Neanderthals and AMH. Authors describe mosaic, intermediate, and features more like one or the other parent in potential Neanderthal and AMH hybrids (Section 2.2.2). However, the morphology of a hybrid is somewhat dependent on the type of hybrid zones and how those zones are created (Section 2.1.1). The hybrid morphology is also dependent on the form and function of the two parental taxa, as shown in Chapters 4 and 5. Therefore, it would be useful if a more precise terminology for describing hybrids could be developed to compare hybrid zones and the resultant hybrid morphology.

In summary, the main features of the Amboseli hybrid zone between olive and yellow baboons are as followed. The hybrid zone is unimodal with intermediate genotypes and phenotypes observed in the hybrids. The population genetics are changing over time with a greater percentage of olive genetic ancestry in the baboon population due to the immigration of male olives and the success of hybrids in mating. However, if the olive males cease immigrating, due to the destruction of their natal habitat and extinction of natal groups, the average percentage

of olive ancestry in each individual's genome will begin to decrease over generations. This would create a genetic scenario of mostly yellow genes with a small percentage of olive genes.

6.2 Hybrid Zones of Neanderthal and Anatomically Modern Human

From Wu's (2001) work, we know that demographic features of the populations, ecological interaction, and reproductive biology and behaviour influence hybrid zones. These variables are difficult to determine in populations that cannot be observed directly, only inferred from archaeological sites. However, there is some evidence from skeletal morphology, genetics, and archaeology that can be used to hypothesize a potential hybrid zone between Neanderthals and AMH. The model of the hybrid zone between yellow and olive baboons helps to fill in the gaps in the archaeological record by comparing the evidence between the baboons and the Pleistocene hominins.

6.2.1 Neanderthal Population Variables

The first important variable that influences hybrid zones and hybrid viability is divergence. Divergence between populations refers to the great number of differences in genotype and phenotype due to specialized adaptations since the last common ancestor. Greater divergence is indicated by a greater number of differences. When the populations re-encounter each other, greater divergence between them may result in greater developmental instability due to incompatible allele combinations because the genes were specialized for a specific environment. Incompatible allele combinations can cause changes in developmental timing that alter the shape and size of nonmetric traits and overall structures (Ackermann et al., 2006; Ackermann, 2010). Severe developmental problems act as postzygotic barriers that prevent the hybrid from surviving and reinforce taxa divergence. Less divergence increases the likelihood that hybridization will generate unique advantageous allele combinations in the hybrid, giving the hybrid an advantage in a new environment (Barton, 2001).

Many researchers have used the molecular clock, which assumes a steady rate of mutations in the DNA over time, to estimate the divergence time of Neanderthal and AMH. Estimates for the divergence time of Neanderthals and AMH range between 500,000 to 270,000 years ago, depending on which segments and type of DNA are being analyzed and other assumptions in the applications of the molecular clock (Krings et al., 2000; Ovchinnikov et al., 2000; Endicott et al., 2010; Green et al., 2010) (Section 2.2.3). Such a long divergence time and the migration of Neanderthal ancestors northward would have allowed each population to develop adaptive traits specific to those environments, which is hypothesized to be the method that led to

the development of the "classic" Neanderthal traits (Dean et al., 1998; Hublin, 2002; Harvati et al., 2010).

Species divergence is an important factor in hybrid viability, however, time apart does not necessarily determine to what extent the two groups diverged in terms of behaviour or ecology. Similarities in nDNA and mtDNA evidence suggest strong similarity between the Neanderthal and AMH groups as sister taxa at the species or subspecies level. Researchers have also identified unique differences in mtDNA that allow them to distinguish one population from the other (Krings et al., 1997; Ovchinnikov et al., 2000; Scholz et al., 2000; Serre et al., 2004; Serre and Pääbo, 2008; Green et al., 2010). Further, Holliday (2008) suggests that hybrids between Neanderthals and AMH would be viable because the divergence time is less than half of the divergence time between the two species that have the earliest known postzygotic barriers.

In comparison to the baboon model, olive and yellow genotypes and phenotypes are very similar, probably more similar than they were between Neanderthals and AMH. Olive and yellow baboons can successfully hybridize in hybrid zones, with viable offspring to maintain gene introgression into the yellow population. A different nonhuman model with more distant divergent times may be a better model for Neanderthal and AMH hybrids. A comparable hybrid zone with an equal divergent time would be difficult to find. This is one of the unique traits of the hybrid zone between Neanderthals and AMH, because of the advanced ability for Pleistocene humans to migrate long distances, the two populations came back into contact. Other populations that have equivalent divergent times may be geographically separate and would not be able to naturally re-encounter each other in the wild.

The next demographic characteristics important in the establishment and maintenance of a hybrid zone are population size and density. These variables contribute to determining the extent of gene flow between populations and potential gene swamping. Larger populations tend to have more diversity and larger gene pools, which gives them more resilience to new alleles added through immigration (Shurtliff, 2013). Therefore, new alleles from another population will consist of only a small percentage of the gene pool and may not replace the alleles already established at high percentages. Smaller populations are more at risk of genetic drift and gene swamping, thus losing their unique alleles in the enlarged gene pool that includes the alleles from the larger population as well (Detwiler et al., 2005; Shurtliff, 2013).

From the archaeological record, researchers believe that Neanderthals had smaller group sizes compared to AMH. Smaller group sizes are hypothesized because large remains of tortoises and shellfish are found at Neanderthal archaeological sites, implying that Neanderthal populations were small enough not to apply strong hunting pressures against prey species (Klein, 2000).

Greater hunting pressure selectively removes the preferred prey type, which in the case of tortoises and shellfish, larger is preferred. In contrast, smaller tortoise and shellfish were found at the AMH sites, implying larger AMH group sizes with greater hunting pressure on prey animals (Klein, 2000). Archaeologists also argue that AMH had greater population growth and expansion because the technology associated with AMH, Aurignacian lithic industry, became more diverse and rapidly spread across Europe (Klein, 2000). There are also more Aurignacian sites closer together, with high site density, implying larger AMH populations and growth (Svoboda, 2005). Mellars and French (2011) estimated a smaller Neanderthal population size because there were much fewer Mousterian and Châtelperrion tools and smaller occupation areas associated with Neanderthals, than the many Aurignacian tools and large occupation areas associated with AMH (Smith, 2013). These demographic characters are broad generalizations for Neanderthals and AMH across Europe.

When populations interacted locally, I suspect that group sizes varied widely between Neanderthals and AMH. Some interactions may have been between some small Neanderthal groups and large AMH groups, or vice versa, and medium group sizes. Researchers often examine different demographic scenarios to take into account the local variability and uncertainty of the many assumptions, such as migration rates, population sizes, birth rates, and death rates, to estimate rates of introgression (Currat and Excoffier, 2011; Sørenson, 2011). Sørenson (2011) modeled possible population sizes of Neanderthals and AMH between 260,000 years ago to present, varying overall fertility, temperature, and geographic location, divided as Northern, Middle, and Southern Europe. Sørenson calibrated the model by including climate variation, which effected migration rates, birth rates and death rates due to various pressures associated with living in a very cold environment such as starvation, cold-exposure, predator deaths during glacial periods. His model estimate that between 35,000-30,000 years ago, AMH populations would have been equal to Neanderthal populations (around 5,000 individuals in Southern Europe), though AMH continued to expand after entering Europe ~40,000 to 34,000 years ago, while Neanderthal populations suddenly declined (Ahern et al., 2013). Recognizing low diversity of mtDNA in sampled Neanderthals, Briggs et al. (2009) estimated that Neanderthals must have had a small effective population size, related to the number of fertile females, around 1,476 females, throughout their existence in Europe. In total, researchers estimate that at any time, there were about 5,000 Neanderthals of all age and sex categories with a population density of less than 0.025 individuals/km^2 (Briggs et al., 2006; Sørenson, 2011).

In the baboon model, yellow baboons have the larger population size, while there are only a few (16 known) olive or hybrid immigrants. The median size of baboon groups in

Amboseli is 39 baboons, composed of seven adult males, two subadult males, twelve adult females, nine juveniles, and eight yearlings/infants (Samuels and Altmann, 1991). Combining all eleven baboon groups recorded, there were 138 adult females out of 223 baboons (1.62 adult females for each adult male), with a density of 1.15 baboons/km^2. Therefore, if the baboon and hominin population sizes were standardized, yellow baboons have a greater proportion of females compared to Neanderthals (yellow baboons with migrants: 138/223 * 100 = 62% females, Neanderthals: 1,476/5,000 * 100 = 30% females). A higher proportion of females can give an allele in that population a lower chance of disappearing due to genetic drift, and thus gene swamping. The small overall population size and small effective population size in Neanderthals leaves them vulnerable to gene swamping (Alberts and Altmann, 2001; Detwiler et al., 2005).

According to Sørenson's (2011) model, in Southern Europe around 30,000 years ago, the immigrant AMH population was greater than the local Neanderthal populations. These demographic conditions suggest that AMH may have had invader advantage through larger populations. On a grand scale of the entire Neanderthal and AMH population gene pool in Europe, Neanderthal genes would make up only a small fraction and have little effect on phenotypes. If the two populations were to interbreed on this scale, and hybrids had hybrid fitness equal to at least one parent species, introgression would take place in both directions, called reciprocal hybridization, and hybrids would assimilate into the populations (Huxel, 1999; Wirtz, 1999). If the populations were of equal size, interbreeding might eventually result in the merging of the two taxa into one with equal ancestry from both Neanderthals and AMH, resulting in reticulate evolution.

However, because Neanderthals have a smaller overall population, they are at risk of gene swamping and extinction (Huxel, 1999; Seehausen, 2004; Detwiler et al., 2005; Wolf et al., 2001). Over generations, as the hybrids mate with purebred Neanderthals and purebred AMH, more AMH backcrosses would be born assuming random mating, because AMH populations are larger. Eventually, as the percentage of AMH alleles continue to increase in the gene pool, decreasing the percentage of Neanderthal alleles, and thus gene swamping the Neanderthal alleles, pure-form Neanderthals would become extinct. Only a small amount of Neanderthal DNA would have introgressed into the largely phenotypic AMH population through the backcrosses carrying some Neanderthal DNA into the AMH gene pool (Jolly, 2001; Cartmill and Smith, 2013: 444-447; Zinner et al., 2009; Zinner et al., 2011; Smith, 2013).

However, even in models of low immigrant density and slightly higher immigrant fitness, genetic displacement occurs rapidly (Huxel, 1999). This scenario is illustrated in baboons by the increasing percentage of olive ancestry in an originally yellow population. Even though the

yellow population is larger, olive alleles, originating from the immigration of only five purebred males and eleven male olive and yellow hybrids (low immigrant density) who successfully mated (high immigrant fitness), entered the yellow gene pool at high rates (Alberts and Altmann, 2001; Tung et al., 2008).

6.2.2 Most Parsimonious Introgression Scenario

If Neanderthals have a smaller population size than AMH, as hypothesized above, and interbreeding occurred in both directions, with hybrids having equal or greater fitness than parental taxa, eventually, the new gene pool of the post-hybridization population would consist primarily of AMH alleles and a few Neanderthal alleles. Eventually, the pure-form of Neanderthals would go extinct, as would the pure-form of AMH, though this is less noticeable since most of the alleles would still be AMH and many phenotypes may still resemble the original AMH form. The Neanderthal alleles that would survive in the long-term would be those that are advantageous or are hidden in a recessive form and are thus not being selected against (Jolly, 2001).

In the long term, this scenario would result in predictable evidence in the morphological, genetic and archaeological data. Evidence that would support the scenario of gene swamping would be the sudden disappearance of the Neanderthal phenotypes in the fossil record, replaced by AMH populations carrying traces of Neanderthal DNA. Contemporary human populations, descendants of the hybridized population, should have both Neanderthal and AMH mtDNA to reflect maternal lineages due to the introgression of both male and female Neanderthal genes into AMH. The archaeological record would show similar replacement of Mousterian to Aurignacian industries (Klein, 2000), or Neanderthal acculturation and adoption of AMH technology (Smith et al., 2005; Hublin, 2013).

There would be a transitional period during hybridization, when F1 hybrids with 50% Neanderthal and 50% AMH alleles would exist along side pure Neanderthals, pure AMH, and backcrosses to both parental taxa and crosses between hybrids. Hybrids may initially show intermediate traits, then become more and more AMH-like as each individual over the generations has less Neanderthal ancestry. The hybrids with intermediate traits would only exist in the fossil record for a relatively short time period, before gene swamping would eliminate most of the Neanderthal phenotypes (Jolly, 2001). The only Nenaderthal genotypes that would remain in the AMH population would be adaptively beneficial or linked to a trait that is adaptively beneficial, such as the haplotype at *STAT2*, which is functionally important in immunity, and in contemporary humans, may be derived from Neanderthal introgression (Mendez et al., 2001). For

example, if male olive baboons stop migrating into the yellow and hybrid baboon population, the yellow and hybrid baboons will fuse into one taxon, and due to the greater number of yellow baboons, result in yellow-type baboons with some unexpressed or very little expressed olive DNA (Tung et al., 2008).

The morphological change can take place very quickly, as was observed over only three decades during which only five purebred olive males and eleven hybrid males entered the yellow population, which now consists of 33.2% of baboons with recent olive ancestry (Alberts and Altmann, 2001). Wolf et al. (2001) found that extinction of the smaller, local population often takes place in less than five generations. The likelihood of finding hybrid skeletal morphology that existed for only several centuries, to be very generous, will be extremely small when the archaeological record discerns between several hundred years at best. However, if such a skeleton is ever found, perhaps the model of the baboon hybrid nasal cavity produced in this study may be helpful in identifying a hybrid.

6.2.3 Supporting and Contradictory Evidence

The currently available skeletal, genetic, and archaeological evidence can be interpreted to support the above scenario.

Many researchers agree that the pure-form of Neanderthals died out during the Upper Paleolithic (Smith et al., 1999; Finlayson et al., 2006; Mellars, 2006). However, some Neanderthal derived traits, autapomorphies, may have survived in Upper Paleolithic AMH (Smith et al., 2005; Ahern, 2008; Wu et al., 2012). In particular, Neanderthal traits such as the anterior mastoid tubercle, asymmetrical mandibular notch, horizontal-oval mandibular foramen, occipital bun, retromolar space, suprainiac fossa and large occipitomastoid crest, were found to occur at the same frequency in Neanderthals as in Upper Paleolithic AMH, which can be interpreted as evidence for admixture (Ahern, 2008). Researchers have also identified "transitional" forms between Neanderthal and AMH (Duarte et al., 1999; Zilhão and Trinkaus, 2002; Trinkaus, 2005; Soficaru et al., 2006; Trinkaus, 2007; Ramirez Rozzi et al., 2009) (Section 2.2.2), which would indicate admixture. However, these traits are widely debated, and some authors assert that AMH do not have these traits in any form outside of normal variation (Tattersall and Schwartz, 1999; Harvati et al., 2007; Stringer, 2008; Hublin, 2013).

The genetic evidence presented by the nDNA and X-chromosomes suggest admixture (Mendez et al., 2001; Green et al., 2010; Yotova et al., 2011). Currently, no Neanderthal mtDNA has been found in contemporary humans (Krings et al., 1997; Ovchinnikov et al., 2000; Scholz et al., 2000; Stringer, 2002; Serre et al., 2004; Hawks, 2008; Serre and Pääbo, 2008).

Anthropologists argue that Neanderthal mtDNA may have introgressed into the AMH population, but later a selective sweep against those lineages of mtDNA occurred, removing the Neanderthal mtDNA from the population (Nordborg, 1998), or there may not have been enough samples of Neanderthal mtDNA to locate the lineages that survived.

The "transitional" tool assemblage may indicate contact and sharing of technology between Neanderthals and AMH, regardless of who was the original creator of this assemblage, which establishes the parameters for hybridization (Wolpoff et al., 2004; Smith et al., 2005). To more definitively confirm this scenario, researchers would need to find sites with the mixture of Neanderthal, AMH, and hybrid remains, and possibly a mixture of lithic industries. Such sites would be very rare in the archaeological record.

6.2.4 Alternative Scenarios

Alternatively, researchers hypothesize that Neanderthal mtDNA never introgressed into AMH populations, either because no hybridization occurred, or hybrid offspring of female Neanderthals did not survive or exist.

If no hybridization occurred, "transitional" morphologies would be interpreted as more extreme forms of AMH (Tattersall and Schwartz, 1999; Harvati et al., 2007; Stringer, 2008; Hublin, 2013). The mtDNA would support a sole AMH ancestry, while the results of nDNA could be explained as linkage disequilibrium rather than admixture (Eriksson and Manica, 2012), or an as yet, uncorroborated study in the literature (Klein, 2003). The tools made by Neanderthals, even if they became more advanced such as the Châtelperrion, would have been independent from the Aurignacian of the AMH (Klein, 2000; Klein, 2003; Hublin, 2013).

Although unlikely, it is also possible that only Neanderthal males mated with AMH females, thereby introducing Neanderthal nDNA, but the mtDNA would always be AMH, which supports the current mtDNA and nDNA genetic evidence (Wirtz, 1999; Mason and Short, 2011). The mtDNA would be introduced through male introgression through a variety of scenarios, one of which may be that there were a small number of available AMH males to mate with, in which case the AMH females would accept Neanderthal males as mates (Wirtz, 1999). Wirtz (1999) surveyed the literature and found that interbreeding usually occurs between the females of a rare species and the males of a common species, but not vice versa, due to females often preferring mates more similar to themselves, such as in the same culture or species. But in circumstances when females cannot access males similar to themselves, they may find mates in less similar males (Wirtz, 1999), as observed in toads (Pfennig, 2007).

I suspect that a variety of scenarios occurred at a small scale in different regions, such as admixture of male and female Neanderthals and AMH followed by gene swamping and Neanderthal extinction (the most parsimonious scenario), no hybridization, or only introgression of Neanderthal male genes into AMH populations. There are many other scenarios that are not discussed here.

The most parsimonious scenario, with supporting evidence, corroborates the Assimilation model, which suggests that Upper Paleolithic AMH would express traits that are overwhelmingly African with some persistence of Neanderthal regional features (Smith et al., 1989; Smith et al., 2005; Ahern et al., 2013). I think that it is either only a matter of more sampling until Neanderthal mtDNA is found in contemporary humans, or a selective sweep has occurred after introgression, which erased the Neanderthal mtDNA from human lineages (Nordborg, 1998).

6.3 Nasal Cavity of Neanderthal and Anatomically Modern Human Hybrid

The study of the hybrid baboon nasal cavity can speculate on the shape and size of a Neanderthal and AMH hybrid nasal cavity.

Specifically, this model can apply to the first generation of hybrids. The features of hybrids after the first generation display different degrees of heterosis or dysgenesis, as Ackermann et al. (2006) found in the external features of backcrossed baboons skulls, though backcrosses were not examined in this study. In particular, nonmetric traits may only be present in the earlier generations of hybrids. Because nonmetric traits are neutral and tend not to affect physiology, after many generations, they could eventually be removed from the population by genetic drift (Jolly, 2001). This explanation may explain why Upper Paleolithic AMHs in Europe do not show Neanderthal autapomorphies (Hublin, 2013). Therefore, this baboon model can only suggest the morphological patterns in the first generation of hybrids.

This study illustrates that in the first generation of baboon hybrids, the nasal cavity responded to hybridization differently in each region within the nasal cavity. The areas of most dynamic change in the baboons were the anterior bony cavity, the choana and the mid-nasopharynx. The area that did not differ between the hybrids and the parental taxa was the middle bony cavity. The area that appeared more similar to one parental taxon than the other was the posterior nasopharynx.

I suggest that first generation Neanderthal and AMH hybrids might have shown a similar pattern as observed in hybrid baboons. Currently, no middle bony cavity of a Neanderthal has been found. Due to the functional importance of this section, it is possible that structures in this

region may be conserved from the last common ancestor and would be similar in Neanderthals and AMH, as observed in olive and yellow baboons. Then, applying the hybrid baboon model, the mid-bony cavity may be unchanged in the Neanderthal and AMH hybrid. It would be useful to compare the nasal cavities from many different hominin fossils to discover if this area is conserved. As a proxy, the nasal cavities of extant non-human primates can be examined, though it must be with caution because the structure of the nasal cavity changes in response to changes in the external maxillae. Extant nonhuman primates have specialized dentition and prognathism that also affect nasal cavity shape. Similarity, it would be useful to note how much variation in the mid-bony cavity is observed in contemporary humans from various populations to begin setting an expectation of variance for the study of earlier hominins.

The anterior nasal cavity may show heterosis as it did in olive and yellow hybrids, possibly accompanied by a shape change. Neanderthal and AMH anterior nasal cavities have been documented as unique in size and shape and potentially specialized to different environments (though not to temperature). These adaptations are extreme compared to the much more subtle differences between baboon taxa. Hamadryas and olive hybrids may provide better insight into more extreme adaptations to different environments and could be investigated in future studies.

The width of the inferior meatus in the anterior bony cavity was the only trait that was significantly different between parental populations in olive and yellow baboons. The hybrid morphology responded with heterosis in that trait (though statistically insignificant), significant heterosis of the anterior nasal cavity (larger area), and significant shape change. However, when yellow and olive baboons displayed different shapes in the nasopharynx, yellow hybrids had a more oblong mid-nasopharynx, the hybrids adopted the olive shape instead of the yellow shape. Therefore, in significantly different areas such as the anterior bony cavity between Neanderthals and AMH, I suspect that the features may show heterosis and shape change in Neanderthal and AMH hybrids or take on the features of one or the other parental taxa. Further investigation in more divergent populations that hybridize would be useful in determining which of these outcomes is more probable.

The choanae of Neanderthal and AMH hybrids may possibly have heterosis and shape change as they did in baboon hybrids. The choana has relatively simple physiological functions that do not require extreme constraints on form to function properly and thus may be able to function with different sizes and shapes without negative consequences. A larger choana, a result of heterosis, may even be beneficial in hybrids by increasing airflow (Noback et al., 2011).

This baboon model of the nasal cavity, and the skull in general (Ackermann et al., 2006), describes the expected features of a hybrid, which do not correspond to the mosaic model in the Neanderthal and AMH hybridization literature. The general mosaic concept proposed by many authors discussed in Section 2.2.2, such as Duarte et al. (1999), Tattersall and Schwartz (1999), and Trinkaus (2005; 2007), suggests that a hybrid would have a combination of traits from both AMH and Neanderthals. However, the baboon model of hybrids suggests that most features will show heterosis or dysgenesis and the areas that are significantly different between populations, such as the nasopharynx shape in baboons or, potentially, the anterior bony cavity in Neanderthals and AMH, will present with the trait of one or the other parental group. Generations beyond F1 may show different patterns.

Ackermann et al. (2006) found that nonmetric traits were more frequent in baboon hybrids and proposed that nonmetric traits could be used as an indicator for hybridization in the fossil record. Unlike the usefulness of nonmetric traits on the external skull for identifying hybridization in baboons and possibly between Neanderthals and AMH (Ackermann et al., 2006), frequencies of nonmetric traits in the nasal cavity may not assist in the identification of a hybrid because none of the nonmetric traits examined were more frequent in the baboon hybrids.

To address the issue of the frequency of nonmetric traits multiple generations after hybridization, Ahern (2008) compared nonmetric traits of Neanderthal and Upper Paleolithic AMH (from a time period after potential interbreeding) to nonmetric traits of pre-contact Native Americans and contemporary descendants of Native Americans and Europeans. He found that differences in trait frequency were no different between Native Americans to Europeans and Neanderthals to Upper Paleolithic AMH. This observation implies that Neanderthal features persist into the Upper Paleolithic AMH due to admixture. Which traits that would be retained into later populations would need to be determined based on their adaptive advantage or linkage to other traits that are advantageous.

This model of a Neanderthal and AMH hybrid is based upon work in baboons. Much further analysis with other extant non-human primates and careful examination of the Neanderthal and AMH skeletal remains is required to determine the accuracy of this model.

Therefore, though there is still much research to be done on the nasal cavity in other extant primates, different contemporary human populations, and past populations, the hybrid baboon nasal cavity model can help researchers to hypothesize the features of a Neanderthal and AMH hybrid.

6.4 Transitional Forms

Scientific and religious interpretations of recent evolution vary dramatically. One main point of contention is the observation in the fossil record that there are no or few transitional forms between species. Explained another way, the fossil record is comprised of long periods of the existence of a particular species assemblage, then a sudden disappearance of that species assemblage, replaced by new, and morphologically distinct species. Scientists and creationists both recognize this phenomenon, but they disagree about what this evidence might mean for explaining evolutionary theory.

Creationists are skeptical of scientists because creationists believe that the known fossil evidence only shows species stasis over thousands of years, what they call data, "Where there are good data, we see no evolution. Where the data are scanty, evolutionists can tell a story" (Morris, 1996). The debate between creationists and scientists occurs "where the data are scanty." The creationist view is that "the lack of transitions between species in the fossil record is what would be expected if life was created [opposed to evolved]" (Institute for Creation Research (ICR), 2014).

Scientists have developed two general theories about how evolution occurs. Darwin proposed gradualism, "the principle that species have been evolved by very small steps" (Darwin, 1859). Gradualism explained the lack of transitional forms in the fossil record:

> The sudden appearance of new and distinct forms of life in our geological formations supports at first sight the belief in abrupt development [creationist theory]. But the value of this evidence depends entirely on the perfection of the geological record, in relation to periods remote in the history of the world. If the record is as fragmentary as many geologists strenuously assert, there is nothing strange in new forms appearing as if suddenly developed. (Darwin, 1859)

Darwin proposed that transitional forms are not seen because there are still many gaps in the fossil record. Instead of relying on the fossil record for evidence of species evolution, Darwin referred to embryological development. "The embryo is thus left almost unaffected, and serves as a record of the past condition of the species" (Darwin, 1859). Modern scientists have found that Darwin's explanation is not quite true. His explanation reflects another theory being developed contemporaneously by Ernest Haeckel, "ontogeny recapitulates phylogeny" or the growth and development of an individual organism passes through the various evolutionary stages of that organism (Gould, 1977). Now, it is recognized that similarities in developmental stages may support a common ancestry between many different organisms, but not that there is a development between primitive to advanced or movement between stages.

Gould and Eldridge proposed a different explanation for the lack of transitional forms, punctuated equilibrium. They viewed stasis not as the absence of evolution, but as data in its own right.

"[P]aleontologists never wrote papers on the absence of change in lineages before punctuated equilibrium granted the subject some theoretical space. And, even worse, as paleontologists didn't discuss stasis, most evolutionary biologists assumed continual change as a norm, and didn't even know that stability dominates the fossil record." (Gould and Eldridge, 1993: 223)

They proposed that there were no gaps in the fossil record, but that speciation events occur so rapidly that the likelihood of detecting these changes in the fossil record would be difficult. "The punctuated equilibrium model depicts evolution as long periods of no evolutionary change followed by rapid periods of change" (Saylo et al., 2011).

The results of this thesis also suggest that speciation, through hybridization, reticulate evolution or gene swamping, occurs rapidly as well. After one generation of crosses between yellow and olive baboons, the baboon nasal cavity was distinctly different in the hybrids compared to the parental groups. If crossing continued, as is the current case in Amboseli, a new morphology would exist in that population, developed over only several decades. If the environment remained stable in Amboseli, and no new hybridizations occurred, the new species formed by the cross between yellow and olive could persist relatively unchanged for thousands of years. The probability of finding fossils that existed in the small time period of several decades is infinitesimal compared to finding a fossil of a species in stasis that existed for thousands of years.

Transitional forms are rarely found in the fossil record not because they do not exist as creationists propose, or that the changes are so miniscule between each evolutionary step as Darwin proposed, but that the transition occurs rapidly. The "lack of transitions" is the result of the probability of preservation and finding the transitional forms that existed for only a short amount of time.

Chapter 7

Conclusions

A model of a hybrid in which to compare potential Neanderthal and AMH hybrid skeletal morphology is lacking in paleoanthropology. Researchers refer to hybrids as having a mosaic of features from both parental taxa, though the few studies of hybrid external skeletal morphology in comparative species, (baboons: Ackermann et al., 2006; gorillas: Ackermann and Bishop, 2008), suggest that hybrids tend to show heterosis or dysgenesis at different measurements of the skull, not necessarily a mosaic of features.

This study examined morphometric measurements and nonmetric traits of the interior nasal cavity of two species of baboons (olive and yellow) and their first generation hybrids to determine how hybridization affects the internal anatomy of the nasal cavity. The nasal cavity was chosen because the nasal cavity in Neanderthals and AMH are recognized as uniquely different in size and shape. Therefore, hybrids would not be able to take a form that is the same in both taxa, but would need to change in shape and or size, or adopt the form of only one parental taxon. The nasal cavity is also a critically functioning area for any mammal, as it is responsible for respiration, olfaction, and disease prevention, in addition to other functions.

The collection used for this study was composed of pedigreed olive, yellow, and olive and yellow hybrid baboon skulls in the physical dry form and as computed tomography (CT) scans. The morphmetric measurements were evaluated using clustering methods (PCAs and CDAs), and hypothesis testing (Wilk's Λ MANOVAs, index of sexual dimorphism, Welch's t-tests, ANOVAs, Dunnett's Cs, and independent samples student t-tests). The nonmetric traits were analyzed using Fisher's exact tests. I found that there are significant size and shape differences in the hybrid nasal cavity compared to the parental baboon groups, but no difference in the occurrence of nonmetric traits.

The regions that differed morphometrically between hybrids and parental baboons occurred throughout the nasal cavity and were related to physiological function. The greatest shape and size differences occurred in regions of relatively simple function, where air currents are redirected to the next location, such as the anterior bony cavity at the rhinion, the choana, and the mid-nasopharynx. Little or no shape or size change occurred in regions that have more complex functions, where air is humidified, warmed, and filtered, such as the mid-bony cavity. The posterior nasopharynx also showed little shape or size change, though it performs little air

conditioning. I hypothesize that the posterior nasopharynx was little changed in the hybrid because the area interacts with components of the basicranium, digestive tract, and organs of vision. There are possibly more selective pressures from these other functions that constrain the size and shape of the posterior nasopharynx.

The nasal cavity of male hybrids followed a different trend in response to hybridization compared to the female hybrids, possibly due to differences in the timing of development during ontogeny. In female hybrids, the nasal cavity tended to narrow inferiorly, an expression of dysgenesis. In male hybrids, the nasal cavity widened, indicating heterosis. Males may have an energetic or physiological advantage due to the greater size of the inferior meatus, which directs the most airflow. Hybrids also show greater sexual dimorphism compared to olive baboons, possibly also giving male baboons an advantage in mate guarding due to greater size.

The occurrence of nonmetric traits was not significantly different between taxa (olive, yellow, or hybrid baboons) or regions of the nasal cavity at the 95% significance level. However, at a lower significance level (90%), several traits were significantly different between taxa: greater septal deviation in male hybrids, more protruding lateral recess into the orbits in hybrids, and the extension of the inferior nasal conchae into the nasopharynx in female hybrids. Physiological significance could not be determined from the current study, though future studies may explore the physiology and ontogeny of the taxa to determine if hybrids may have higher fitness than the parental taxa as hypothesized.

The hybrid baboon model of the nasal cavity, and the recorded hybrid zone between olive and yellow baboons were used to hypothesize the form of a Neanderthal and AMH hybrid nasal cavity, and the structure of a hybrid zone between Neanderthals and AMH.

Based on the hybrid baboon model, I hypothesized that the regions of most size and shape change in Neanderthal and AMH hybrid nasal cavity may occur at the anterior bony cavity, the choana, and the mid-nasopharynx. In particular, the anterior bony cavity, the piriform aperture, of a Neanderthal and AMH hybrid may adopt the form of one or the other parental taxon because the Neanderthal and AMH anterior nasal cavities have been recorded as unique in both size and shape. As observed in the hybrid baboon model, I hypothesized that the mid-bony cavity and the posterior nasopharynx may be unchanged between the hybrid and both parental taxa, or the hybrid would assume the trait from one parental taxon.

The baboon model of the hybrid zone provides insight into which factors influence the formation and maintenance of hybrid zones, and what genetic and morphological evidence indicates features of the hybrid zone. From the examination of existing morphological, genetic, and archaeological data of Neanderthal and AMH populations, supplemented with an

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understanding of the baboon hybrid zone, several scenarios using hybrid zones were hypothesized to explain how the two populations may have interacted. It was concluded that the most parsimonious hybrid scenario would be reciprocal hybridization between male and female Neanderthal and AMH populations. Because AMH populations were probably larger than Neanderthal populations, the Neanderthal population may have experienced gene swamping. The resulting population many generations later would be composed of hybrids that contain mostly AMH genes, with a small percentage of Neanderthal genes. Neanderthals and AMH, in their pure genetic forms, would have both gone extinct in Europe.

Further research should be dedicated to comparative models of the affect of hybridization on skeletal morphology, as well as what size and shape changes may mean physiologically. As research continues, it seems that the evidence supports the Assimilation model, which argues that some hybridization occurred between Neanderthals and AMH. This and future studies may help with the identification of these hybrids in the fossil record.

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Appendix A: Tables

Table 1 Definitions of the 45 features of the nasal cavity analyzed in this study.

	Measurement	Definition
Vol	Volume $(cm^3)^{-3}$	Total volume of segmented nasal cavity, transformed by cube-rooting
1A	Area slice 1 $(cm^2)^{-2}$	Area of segmentation in Slice 1, transformed by square-rooting
2A	Area slice 2 $(cm^2)^{-2}$	Area of segmentation in Slice 2, transformed by square-rooting
3A	Area slice 3 $(cm^2)^{-2}$	Area of segmentation in Slice 3, transformed by square-rooting
4A	Area slice 4 $(cm^2)^{-2}$	Area of segmentation in Slice 4, transformed by square-rooting
5A	Area slice 5 $(cm^2)^{-2}$	Area of segmentation in Slice 5, transformed by square-rooting
BCL	Bony cavity length (cm)	Distance between Slice 1 and Slice 3
NCL	Total nasal cavity length (cm)	Distance between Slice 1 and Slice 5
NpL	Nasopharynx length (cm)	Distance between Slice 3 and Slice 5
	Slice 1	
1Hnc	Height at nasal crest (cm)	Vertical measurement from the centre of the nasal crest to the roof of the nasal cavity
1Himr	Height of right inferior meatus (cm)	Maximum vertical height from the hard palate (floor of the nasal cavity) lateral to the right inferior concha
1Himl	Height of left inferior meatus (cm)	Maximum vertical height from the hard palate (floor of the nasal cavity) lateral to the left inferior concha
1Hicr	Height of right inferior conchae (cm)	Minimum vertical height from the hard palate (floor of the nasal cavity) to the most inferior portion of the right inferior concha
1Hicl	Height of left inferior conchae (cm)	Minimum vertical height from the hard palate (floor of the nasal cavity) to the most inferior portion of the lefts inferior concha

Table 1 (continued)

	Measurement	Definition
1Wnc	Width at nasal crest (cm)	Maximum width tangential to the superior portion of the nasal crest
1Wim	Width of inferior meatus (cm)	Maximum width below the inferior conchae
1Wic	Width between inferior conchae (cm)	Minimum width between the inferior conchae
1Wmm	Width of middle meatus (cm)	Maximum width above the inferior conchae
1R	(Height at nasal crest/Width of inferior meatus)	Ratio of height to width
	Slice 2	
2Hnc	Height at nasal crest (cm)	Vertical measurement from the centre of the nasal crest to the roof of the nasal cavity
2Hicr	Height of right inferior conchae (cm)	Minimum vertical height from the hard palate (floor of the nasal cavity) to the most inferior portion of the right inferior concha
2Hicl	Height of left inferior conchae (cm)	Minimum vertical height from the hard palate (floor of the nasal cavity) to the most inferior portion of the lefts inferior concha
2Wnc	Width at nasal crest (cm)	Maximum width tangential to the superior portion of the nasal crest
2Wmm	Width of middle meatus (cm)	Maximum width of the upper half of the middle meatus
2Wic	Width between inferior conchae (cm)	Minimum width between the inferior conchae
2R	(Height at nasal crest/Width at nasal crest)	Ratio of height to width
	Slice 3	
3Hnc	Height at nasal crest (cm)	Vertical measurement from the centre of the nasal crest to the roof of the nasal cavity

Table 1 (continued)

	Measurement	Definition
3Wnc	Width at nasal crest (cm)	Maximum width tangential to the superior portion of the nasal crest
3Wic	Width between inferior conchae (cm)	Minimum width between the inferior conchae

Table 1 (continued)

	Measurement	Definition
3Hicr	Height of right inferior conchae (cm)	Minimum vertical height from the hard palate (floor of the nasal cavity) to the most inferior portion of the right inferior concha – estimated based on the position of the inferior conchae in anterior or posterior slices if not yet attached at slice 3
3Hicl	Height of left inferior conchae (cm)	Minimum vertical height from the hard palate (floor of the nasal cavity) to the most inferior portion of the lefts inferior concha - estimated based on the position of the inferior conchae in anterior or posterior slices if not yet attached at slice 3
3Wmm	Width of middle meatus (cm)	Maximum width above the inferior conchae
3R	(Height at nasal crest/Width at nasal crest)	Ratio of height to width
	Slice 4	
4Him	Height at inferior margin (cm)	Vertical measurement from the centre of the artificial inferior margin of the region of interest (in line with the attachment of the inferior conchae to the nasal walls anteriorly) to the roof of the nasal cavity
4Wim	Width of inferior margin (cm)	Width of the artificial inferior margin of the region of interest

Table 1 (continued)

	Measurement	Definition
4Wav	Width at alae of vomer (cm)	Width tangential to the superior aspect of the alae of the vomer (if present)
4Himav	Height at inferior margin to alae of vomer (cm)	Vertical measurement from the artificial inferior margin of the region of interest to the line tangential to the superior aspect of the alae of the vomer (if present)
4Wlr	Width of lateral recess (cm)	Maximum width within the middle meatus
4R	(Height at inferior margin/Width of inferior margin)	Ratio of height to width
	Slice 5	
5Him	Height at inferior margin (cm)	Vertical measurement from the centre of the artificial inferior margin of the region of interest (in line with the attachment of the inferior conchae to the nasal walls anteriorly) to the roof of the nasal cavity
5Wim	Width of inferior margin (cm)	Width of the artificial inferior margin of the region of interest
5Wav	Width at alae of vomer (cm)	Width tangential to the superior aspect of the alae of the vomer (if present)
5Himav	Height at inferior margin to alae of vomer (cm)	Vertical measurement from the artificial inferior margin of the region of interest to the line tangential to the superior aspect of the alae of the vomer (if present)
5Wlr	Width of lateral recess (cm)	Maximum width within the middle meatus
5R	(Height at inferior margin/Width of inferior margin)	Ratio of height to width

Table 2 Levene's test for homogeneity of variance, $\alpha=0.05$, for the 45 features of the nasal cavity. Significant p-values are bolded, indicating that those features do not have homogeneity of variance.

Variable	Levene's F	p ($d.f._{1,2}=5,132$)
Volume $(cm^3)^{-3}$	2.271	0.051
Area slice 1 $(cm^2)^{-2}$	9.055	**0**
Area slice 2 $(cm^2)^{-2}$	3.137	**0.01**
Area slice 3 $(cm^2)^{-2}$	1.766	0.124
Area slice 4 $(cm^2)^{-2}$	2.218	0.056
Area slice 5 $(cm^2)^{-2}$	2.087	0.071
Bony cavity length (cm)	2.229	0.055
Total nasal cavity length (cm)	1.68	0.144
Nasopharynx length (cm)	3.642	**0.004**
Slice 1		
Height at nasal crest (cm)	2.574	**0.029**
Height of right inferior meatus (cm)	2.36	**0.044**
Height of left inferior meatus (cm)	7.18	**0**
Height of right inferior conchae (cm)	2.296	**0.049**
Height of left inferior conchae (cm)	8.158	**0**
Width at nasal crest (cm)	0.68	0.639
Width of inferior meatus (cm)	1.85	0.107
Width between inferior conchae (cm)	7.052	**0**
Width of middle meatus (cm)	5.184	**0**
(Height at nasal crest/Width of inferior meatus)	2.328	**0.046**
Slice 2		
Height at nasal crest (cm)	1.715	0.135
Height of right inferior conchae (cm)	1.444	0.213
Height of left inferior conchae (cm)	0.525	0.757
Width at nasal crest (cm)	3.964	**0.002**
Width of middle meatus (cm)	2.034	0.078

Table 2 (continued)

Variable	Levene's F	p (d.f.$_{1,2}$=5,132)
Width between inferior conchae (cm)	6.512	**0**
(Height at nasal crest/Width at nasal crest)	2.956	**0.015**
Slice 3		
Height at nasal crest (cm)	1.572	0.172
Width at nasal crest (cm)	2.422	**0.039**
Width between inferior conchae (cm)	1.778	0.122
Height of right inferior conchae (cm)	0.809	0.545
Height of left inferior conchae (cm)	0.674	0.644
Width of middle meatus (cm)	1.422	0.22
(Height at nasal crest/Width at nasal crest)	2.545	**0.031**
Slice 4		
Height at inferior margin (cm)	1.171	0.327
Width of inferior margin (cm)	2.97	**0.014**
Width at alae of vomer (cm)	0.875	0.5
Height at inferior margin to alae of vomer (cm)	3.058	**0.012**
Width of lateral recess (cm)	0.653	0.66
(Height at inferior margin/Width of inferior margin)	1.641	0.153
Slice 5		
Height at inferior margin (cm)	2.392	**0.041**
Width of inferior margin (cm)	1.172	0.326
Width at alae of vomer (cm)	2.052	0.075
Height at inferior margin to alae of vomer (cm)	1.944	0.091
Width of lateral recess (cm)	4.171	**0.001**
(Height at inferior margin/Width of inferior margin)	1.347	0.248

Table 3 Shapiro-Wilk normality tests, $\alpha = 0.05$, for the 45 features of the nasal cavity for male and female combined taxa after the correction for sexual dimorphism. Significant *p*-values are bolded, indicating that those features are not normally distributed.

		Shapiro-Wilk	
Variable	Group	*W*	*p*
Volume $(cm^3)^{-3}$	Olive (*d.f.* = 79)	.981	.286
	Hybrid (*d.f.* = 54)	.978	.427
	Yellow (*d.f.* = 5)	.932	.607
Area slice 1 $(cm^2)^{-2}$	Olive (*d.f.* = 79)	.974	.110
	Hybrid (*d.f.* = 54)	.954	.037
	Yellow (*d.f.* = 5)	.949	.732
Area slice 2 $(cm^2)^{-2}$	Olive (*d.f.* = 79)	.983	.386
	Hybrid (*d.f.* = 54)	.950	**.025**
	Yellow (*d.f.* = 5)	.823	.123
Area slice 3 $(cm^2)^{-2}$	Olive (*d.f.* = 79)	.970	.063
	Hybrid (*d.f.* = 54)	.982	.584
	Yellow (*d.f.* = 5)	.952	.752
Area slice 4 $(cm^2)^{-2}$	Olive (*d.f.* = 79)	.988	.701
	Hybrid (*d.f.* = 54)	.992	.974
	Yellow (*d.f.* = 5)	.986	.962
Area slice 5 $(cm^2)^{-2}$	Olive (*d.f.* = 79)	.985	.464
	Hybrid (*d.f.* = 54)	.946	**.017**
	Yellow (*d.f.* = 5)	.913	.488
Bony cavity length (cm)	Olive (*d.f.* = 79)	.866	**.000**
	Hybrid (*d.f.* = 54)	.980	.514
	Yellow (*d.f.* = 5)	.940	.664
Total nasal cavity length (cm)	Olive (*d.f.* = 79)	.830	**.000**
	Hybrid (*d.f.* = 54)	.985	.717
	Yellow (*d.f.* = 5)	.996	.997
Nasopharynx length (cm)	Olive (*d.f.* = 79)	.975	.132
	Hybrid (*d.f.* = 54)	.983	.627
	Yellow (*d.f.* = 5)	.940	.663
Slice 1			
Height at nasal crest (cm)	Olive (*d.f.* = 79)	.836	**.000**
	Hybrid (*d.f.* = 54)	.930	**.004**
	Yellow (*d.f.* = 5)	.930	.599

Table 3 (continued)		Shapiro-Wilk	
Variable	Group	*W*	*p*
Height of right inferior meatus (cm)	Olive (*d.f.*= 79)	.944	**.002**
	Hybrid (*d.f.* = 54)	.796	**.000**
	Yellow (*d.f.* = 5)	.977	.919
Height of left inferior meatus (cm)	Olive (*d.f.*= 79)	.975	.116
	Hybrid (*d.f.* = 54)	.826	**.000**
	Yellow (*d.f.* = 5)	.989	.977
Height of right inferior conchae (cm)	Olive (*d.f.*= 79)	.977	.171
	Hybrid (*d.f.* = 54)	.969	.169
	Yellow (*d.f.* = 5)	.979	.931
Height of left inferior conchae (cm)	Olive (*d.f.*= 79)	.987	.630
	Hybrid (*d.f.* = 54)	.847	**.000**
	Yellow (*d.f.* = 5)	.977	.919
Width at nasal crest (cm)	Olive (*d.f.*= 79)	.845	**.000**
	Hybrid (*d.f.* = 54)	.906	**.000**
	Yellow (*d.f.* = 5)	.890	.357
Width of inferior meatus (cm)	Olive (*d.f.*= 79)	.915	**.000**
	Hybrid (*d.f.* = 54)	.978	.401
	Yellow (*d.f.* = 5)	.894	.379
Width between inferior conchae (cm)	Olive (*d.f.*= 79)	.984	.442
	Hybrid (*d.f.* = 54)	.985	.730
	Yellow (*d.f.* = 5)	.942	.677
Width of middle meatus (cm)	Olive (*d.f.*= 79)	.983	.356
	Hybrid (*d.f.* = 54)	.977	.389
	Yellow (*d.f.* = 5)	.909	.463
(Height at nasal crest/Width of inferior meatus)	Olive (*d.f.*= 79)	.866	**.000**
	Hybrid (*d.f.* = 54)	.936	**.006**
	Yellow (*d.f.* = 5)	.882	.320
Slice 2			
Height at nasal crest (cm)	Olive (*d.f.*= 79)	.948	**.003**
	Hybrid (*d.f.* = 54)	.982	.575
	Yellow (*d.f.* = 5)	.934	.625
Height of right inferior conchae (cm)	Olive (*d.f.*= 79)	.967	**.039**
	Hybrid (*d.f.* = 54)	.992	.967
	Yellow (*d.f.* = 5)	.920	.527
Height of left inferior conchae (cm)	Olive (*d.f.*= 79)	.948	**.003**
	Hybrid (*d.f.* = 54)	.987	.831
	Yellow (*d.f.* = 5)	.840	.165

Table 3 (continued)		Shapiro-Wilk	
Variable	Group	*W*	*p*
Width at nasal crest (cm)	Olive (*d.f.*= 79)	.830	**.000**
	Hybrid (*d.f.* = 54)	.939	**.009**
	Yellow (*d.f.* = 5)	.957	.786
Width of middle meatus (cm)	Olive (*d.f.*= 79)	.920	**.000**
	Hybrid (*d.f.* = 54)	.931	**.004**
	Yellow (*d.f.* = 5)	.949	.728
Width between inferior conchae (cm)	Olive (*d.f.*= 79)	.989	.754
	Hybrid (*d.f.* = 54)	.956	**.047**
	Yellow (*d.f.* = 5)	.778	.053
(Height at nasal crest/Width at nasal crest)	Olive (*d.f.*= 79)	.339	**.000**
	Hybrid (*d.f.* = 54)	.962	.085
	Yellow (*d.f.* = 5)	.910	.467
Slice 3			
Height at nasal crest (cm)	Olive (*d.f.*= 79)	.972	.076
	Hybrid (*d.f.* = 54)	.955	.043
	Yellow (*d.f.* = 5)	.939	.662
Width at nasal crest (cm)	Olive (*d.f.*= 79)	.966	**.032**
	Hybrid (*d.f.* = 54)	.949	**.023**
	Yellow (*d.f.* = 5)	.907	.450
Width between inferior conchae (cm)	Olive (*d.f.*= 79)	.979	.234
	Hybrid (*d.f.* = 54)	.994	.994
	Yellow (*d.f.* = 5)	.897	.391
Height of right inferior conchae (cm)	Olive (*d.f.*= 79)	.983	.399
	Hybrid (*d.f.* = 54)	.819	**.000**
	Yellow (*d.f.* = 5)	.924	.553
Height of left inferior conchae (cm)	Olive (*d.f.*= 79)	.986	.565
	Hybrid (*d.f.* = 54)	.990	.940
	Yellow (*d.f.* = 5)	.930	.596
Width of middle meatus (cm)	Olive (*d.f.*= 79)	.939	**.001**
	Hybrid (*d.f.* = 54)	.986	.781
	Yellow (*d.f.* = 5)	.873	.279
(Height at nasal crest/Width at nasal crest)	Olive (*d.f.*= 79)	.988	.663
	Hybrid (*d.f.* = 54)	.940	**.009**
	Yellow (*d.f.* = 5)	.874	.281
Slice 4			
Height at inferior margin (cm)	Olive (*d.f.*= 79)	.976	.139
	Hybrid (*d.f.* = 54)	.942	**.011**
	Yellow (*d.f.* = 5)	.908	.454

Table 3 (continued)		Shapiro-Wilk	
Variable	Group	*W*	*p*
Width of inferior margin (cm)	Olive (*d.f.* = 79)	.991	.834
	Hybrid (*d.f.* = 54)	.975	.319
	Yellow (*d.f.* = 5)	.929	.587
Width at alae of vomer (cm)	Olive (*d.f.* = 79)	.984	.443
	Hybrid (*d.f.* = 54)	.977	.370
	Yellow (*d.f.* = 5)	.911	.471
Height at inferior margin to alae of vomer (cm)	Olive (*d.f.* = 79)	.976	.146
	Hybrid (*d.f.* = 54)	.978	.406
	Yellow (*d.f.* = 5)	.884	.327
Width of lateral recess (cm)	Olive (*d.f.* = 79)	.932	**.000**
	Hybrid (*d.f.* = 54)	.966	.126
	Yellow (*d.f.* = 5)	.851	.196
(Height at inferior margin/Width of inferior margin)	Olive (*d.f.* = 79)	.917	**.000**
	Hybrid (*d.f.* = 54)	.968	.155
	Yellow (*d.f.* = 5)	.976	.912
Slice 5			
Height at inferior margin (cm)	Olive (*d.f.* = 79)	.984	.442
	Hybrid (*d.f.* = 54)	.984	.704
	Yellow (*d.f.* = 5)	.915	.497
Width of inferior margin (cm)	Olive (*d.f.* = 79)	.979	.206
	Hybrid (*d.f.* = 54)	.979	.443
	Yellow (*d.f.* = 5)	.905	.440
Width at alae of vomer (cm)	Olive (*d.f.* = 79)	.985	.476
	Hybrid (*d.f.* = 54)	.978	.422
	Yellow (*d.f.* = 5)	.991	.985
Height at inferior margin to alae of vomer (cm)	Olive (*d.f.* = 79)	.977	.156
	Hybrid (*d.f.* = 54)	.980	.513
	Yellow (*d.f.* = 5)	.941	.673
Width of lateral recess (cm)	Olive (*d.f.* = 79)	.968	**.047**
	Hybrid (*d.f.* = 54)	.969	.180
	Yellow (*d.f.* = 5)	.907	.452
(Height at inferior margin/Width of inferior margin)	Olive (*d.f.* = 79)	.904	**.000**
	Hybrid (*d.f.* = 54)	.966	.126
	Yellow (*d.f.* = 5)	.861	.232

Table 4 Shapiro-Wilk normality tests, $\alpha = 0.05$, for the 45 features of the nasal cavity with all specimen combined after the correction for sexual dimorphism. Significant *p*-values are bolded, indicating that those features are not normally distributed.

	Shapiro-Wilk	
Variable	*W*	*p* (*d.f.*=138)
Volume (cm3)-3	.980	**.044**
Area slice 1 (cm2)-2	.952	**.000**
Area slice 2 (cm2)-2	.979	.032
Area slice 3 (cm2)-2	.985	.136
Area slice 4 (cm2)-2	.996	.961
Area slice 5 (cm2)-2	.984	.100
Bony cavity length (cm)	.929	**.000**
Total nasal cavity length (cm)	.888	**.000**
Nasopharynx length (cm)	.984	.120
Slice 1		
Height at nasal crest (cm)	.886	**.000**
Height of right inferior meatus (cm)	.837	**.000**
Height of left inferior meatus (cm)	.866	**.000**
Height of right inferior conchae (cm)	.987	.239
Height of left inferior conchae (cm)	.902	**.000**
Width at nasal crest (cm)	.897	**.000**
Width of inferior meatus (cm)	.952	**.000**
Width between inferior conchae (cm)	.996	.948
Width of middle meatus (cm)	.987	.215
(Height at nasal crest/Width of inferior meatus)	.865	**.000**
Slice 2		
Height at nasal crest (cm)	.981	.055

Table 4 (continued)

Variable	Shapiro-Wilk	
	W	*p* (*d.f.*=138)
Height of right inferior conchae (cm)	.983	.087
Height of left inferior conchae (cm)	.981	.054
Width at nasal crest (cm)	.866	**.000**
Width of middle meatus (cm)	.952	**.000**
Width between inferior conchae (cm)	.981	**.049**
(Height at nasal crest/Width at nasal crest)	.337	**.000**
Slice 3		
Height at nasal crest (cm)	.959	**.000**
Width at nasal crest (cm)	.974	**.009**
Width between inferior conchae (cm)	.991	.500
Height of right inferior conchae (cm)	.901	**.000**
Height of left inferior conchae (cm)	.989	.357
Width of middle meatus (cm)	.958	**.000**
(Height at nasal crest/Width at nasal crest)	.967	**.002**
Slice 4		
Height at inferior margin (cm)	.968	**.003**
Width of inferior margin (cm)	.993	.708
Width at alae of vomer (cm)	.991	.498
Height at inferior margin to alae of vomer (cm)	.989	.320
Width of lateral recess (cm)	.970	**.003**
(Height at inferior margin/Width of inferior margin)	.943	**.000**
Slice 5		
Height at inferior margin (cm)	.994	.796
Width of inferior margin (cm)	.986	.181

Table 4 (continued)

| | Shapiro-Wilk | |
Variable	*W*	*p (d.f.=138)*
Width at alae of vomer (cm)	.993	.739
Height at inferior margin to alae of vomer (cm)	.990	.399
Width of lateral recess (cm)	.974	**.010**
(Height at inferior margin/Width of inferior margin)	.956	**.000**

Table 5 Independent samples student t-tests, $\alpha=0.0011$, between olive males and females, independent samples student t-tests, $\alpha=0.0011$, between hybrid males and females for the 45 features of the nasal cavity. Significant *p*-values are bolded, indicating that the feature demonstrates sexual dimorphism in that trait. Welch's t-test, $\alpha=0.0011$, between the difference between olive males and females compared to the difference between hybrid males and females for the 45 nasal features of the nasal cavity. Significant *p*-values are bolded. The taxon with a greater degree of sexual dimorphism is listed in the final column. Results are illustrated in Figure 7a.

	Olive M (*n*=27)		Olive F (*n*=52)		Sex Dim	Hybrid M (*n*=13)		Hybrid F (*n*=41)		Sex Dim	Olive M - F	Hybrid M - F	Olive-Hybrid		Degree of Sexual Dimorphism
	mean	*S*	mean	*s*	*p*	mean	*s*	mean	*s*	*p*	mean	mean	*s*	*p*	Greater
Vol	4.17	0.17	3.22	1.78	**0.0001**	4.33	0.27	3.27	0.15	**9.8E-42**	0.95	1.07	0.03	**2.9E-05**	hybrid
1A	2.60	0.17	1.93	1.41	**0.0004**	2.89	0.38	2.01	0.15	**7.9E-16**	0.66	0.88	0.03	**6.8E-16**	hybrid
2A	3.34	0.23	2.57	1.62	**0.0004**	3.47	0.33	2.65	0.15	**1.1E-17**	0.77	0.82	0.03	0.037	not sig
3A	3.49	0.21	2.72	1.62	**0.0003**	3.71	0.20	2.82	0.15	**1.3E-48**	0.78	0.89	0.03	**2.2E-05**	hybrid
4A	2.80	0.17	2.21	1.46	0.002	2.96	0.18	2.31	0.13	**3.4E-33**	0.59	0.64	0.02	0.013	not sig
5A	2.68	0.13	2.09	1.45	0.002	2.77	0.18	2.14	0.12	**4.6E-32**	0.59	0.63	0.02	0.022	not sig
BCL	5.57	0.63	4.46	2.13	**0.0003**	5.62	0.55	4.31	0.29	**5.5E-16**	1.11	1.31	0.04	**9.9E-07**	hybrid
NCL	6.76	0.66	5.34	2.26	**2.0E-5**	6.90	0.40	5.27	0.27	**9.0E-40**	1.42	1.63	0.04	**1.6E-07**	hybrid
NpL	1.19	0.24	0.88	0.76	0.004	1.28	0.41	0.96	0.23	0.004	0.31	0.32	0.02	0.27	not sig
Slice 1															
1Hnc	2.37	0.17	1.82	1.36	0.002	2.58	0.32	1.83	0.14	**8.8E-17**	0.55	0.75	0.02	**1.6E-17**	hybrid
1Himr	0.99	0.21	0.70	0.79	0.007	1.31	0.58	0.84	0.29	0.003	0.29	0.47	0.03	0	not sig
1Himl	1.00	0.24	0.75	0.84	0.02	1.38	0.71	0.83	0.21	0.003	0.25	0.55	0.03	0	not sig

Table 5 (continued)

	Olive M (*n*=27)		Olive F (*n*=52)		Sex Dim	Hybrid M (*n*=13)		Hybrid F (*n*=41)		Sex Dim	Olive M - F	Hybrid M - F	Olive-Hybrid	Degree of Sexual Dimorphism	
	mean	*S*	mean	*s*	*p*	mean	*s*	mean	*s*	*p*	mean	mean	*s*	*P*	Greater
1Hicr	0.98	0.20	0.66	0.75	0.002	1.18	0.25	0.76	0.13	**3.5E-09**	0.32	0.42	0.02	**2.0E-11**	Hybrid
1Hicl	0.99	0.20	0.71	0.86	0.01	1.26	0.48	0.79	0.16	**0.0002**	0.28	0.48	0.02	**1.9E-17**	Hybrid
1Wnc	3.11	0.45	2.11	1.54	**1.0E-5**	3.50	0.61	2.56	0.60	**8.9E-07**	1.00	0.94	0.04	0.037	not sig
1Wim	3.30	0.50	2.51	1.59	**0.001**	3.70	0.55	2.82	0.32	**2.7E-08**	0.78	0.88	0.03	0.002	not sig
1Wic	2.09	0.35	1.51	1.26	**0.001**	2.37	0.45	1.55	0.20	**1.3E-10**	0.58	0.82	0.03	**1.4E-18**	hybrid
1Wmm	2.54	0.28	1.88	1.42	**0.001**	2.76	0.34	1.87	0.16	**2.5E-19**	0.66	0.89	0.03	**6.4E-18**	hybrid
1R	0.74	0.14	0.75	0.85	0.46	0.71	0.13	0.65	0.08	0.07	-0.01	0.06	0.01	0	not sig
Slice 2															
2Hnc	2.83	0.32	2.15	1.56	**0.001**	2.95	0.21	2.23	0.24	**1.8E-24**	0.68	0.71	0.03	0.10	not sig
2Hicr	2.83	0.28	2.01	1.42	**3.0E-5**	2.87	0.34	2.06	0.26	**3.7E-15**	0.82	0.80	0.03	0.29	not sig
2Hicl	2.83	0.25	2.02	1.36	**2.0E-5**	2.92	0.26	2.08	0.26	**1.0E-23**	0.81	0.84	0.02	0.074	not sig
2Wnc	3.36	0.78	3.00	1.74	0.107	3.52	0.64	3.15	0.30	0.02	0.35	0.37	0.04	0.34	not sig
2Wmm	4.02	0.36	3.16	1.76	**0.0004**	4.26	0.45	3.30	0.23	**1.7E-13**	0.86	0.96	0.03	0.0013	not sig
2Wic	2.31	0.40	1.98	1.51	0.07	2.41	0.64	2.03	0.25	0.02	0.33	0.39	0.04	0.06	not sig
2R	1.02	0.97	0.73	0.90	0.09	0.86	0.16	0.72	0.13	**0.001**	0.30	0.14	0.03	**1.3E-09**	olive
Slice 3															
3Hnc	3.62	0.28	3.02	1.85	**0.01**	3.97	0.49	3.16	0.29	**8.9E-09**	0.60	0.81	0.04	**7.6E-10**	hybrid

Table 5 (continued)

	Olive M (*n*=27)		Olive F (*n*=52)		Sex Dim	Hybrid M (*n*=13)		Hybrid F (*n*=41)		Sex Dim	Olive M - F	Hybrid M - F	Olive-Hybrid	Degree of Sexual Dimorphism	
	mean	*S*	mean	*s*	*p*	mean	*s*	mean	*s*	*p*	mean	mean	*s*	*P*	Greater
3Wnc	2.38	0.33	2.07	1.38	0.06	2.43	0.33	2.06	0.17	**0.0001**	0.31	0.37	0.03	0.015	not sig
3Wic	1.97	0.31	1.78	1.28	0.15	2.12	0.21	1.76	0.23	**5.2E-08**	0.19	0.37	0.02	**2.6E-14**	hybrid
3Hicr	1.37	0.20	1.05	0.88	**0.006**	1.46	0.16	1.11	0.27	**8.3E-09**	0.32	0.35	0.02	0.060	not sig
3Hicl	1.38	0.21	1.06	0.90	**0.006**	1.45	0.19	1.08	0.17	**3.3E-10**	0.33	0.36	0.02	0.022	not sig
3Wmm	4.10	0.41	2.98	1.59	**1.0E-6**	4.24	0.34	3.16	0.38	**2.2E-22**	1.13	1.08	0.03	0.080	not sig
3R	1.55	0.26	1.47	1.34	0.34	1.67	0.33	1.55	0.23	0.11	0.08	0.12	0.03	0.04	hybrid
Slice 4															
4Him	2.91	0.30	2.60	1.70	0.10	3.18	0.49	2.75	0.39	0.002	0.31	0.42	0.03	0	not sig
4Wim	2.13	0.22	1.82	1.40	0.06	2.23	0.22	1.77	0.12	**5.1E-13**	0.31	0.46	0.02	**2.3E-11**	hybrid
4Wav	2.86	0.62	1.81	1.26	**4.0E-7**	3.24	0.45	2.06	0.59	**4.0E-14**	1.05	1.18	0.03	**2.4E-05**	hybrid
4 Himav	1.70	0.48	1.64	1.22	0.37	1.48	0.64	1.58	0.39	0.29	0.06	-0.11	0.03	**3.0E-07**	
4Wlr	3.42	0.42	2.70	1.59	**0.001**	3.53	0.33	2.81	0.33	**7.3E-12**	0.72	0.72	0.03	0.45	not sig
4R	1.39	0.23	1.45	1.21	0.36	1.45	0.31	1.57	0.26	0.10	-0.06	-0.12	0.02	0.01	not sig
Slice 5															
5Him	3.21	0.42	2.69	1.70	0.02	3.38	0.65	2.84	0.45	0.003	0.52	0.54	0.04	0.26	not sig
5Wim	2.18	0.26	1.85	1.37	0.046	2.21	0.31	1.83	0.20	**0.00001**	0.33	0.38	0.03	0.025	not sig

Table 5 (continued)

	Olive M (*n*=27)		Olive F (*n*=52)		Sex Dim	Hybrid M (*n*=13)		Hybrid F (*n*=41)		Sex Dim	Olive M - F	Hybrid M - F	Olive- Hybrid	Degree of Sexual Dimorphism	
	mean	*S*	mean	*s*	*p*	mean	*s*	mean	*s*	*p*	mean	mean	*s*	*P*	Greater
5Wav	2.75	0.31	1.75	1.32	**1.0E-7**	2.72	0.50	1.79	0.41	**9.3E-10**	1.00	0.93	0.03	0.012	not sig
5 Himav	1.77	0.31	1.54	1.22	0.10	1.85	0.50	1.60	0.29	0.042	0.23	0.25	0.03	0.23	not sig
5Wlr	3.01	0.11	2.39	1.58	0.003	3.15	0.32	2.40	0.21	**2.3E-15**	0.62	0.75	0.03	**3.4E-06**	hybrid
5R	1.50	0.32	1.48	1.24	0.46	1.58	0.45	1.57	0.31	0.49	0.02	0.00	0.03	0.27	not sig

Table 6 Independent samples student t-tests, *α*=0.05, between olive males and hybrid males of the 45 features of the nasal cavity. Significant *p*-values are bolded. The last column lists the larger taxon for significant features. Results are illustrated in Figure 7b.

	Male Olive (*n*=27)		Male Hybrid (*n*=13)		Independent student t-test with unequal sample sizes (*d.f.*= 38) (*α*=0.05)		
	mean	*s*	mean	*s*	*t*	*p*	Larger group
Vol	4.17	0.17	4.33	0.27	2.39	**0.02**	hybrid
1A	2.60	0.17	2.89	0.38	3.36	**0.00**	hybrid
2A	3.34	0.23	3.47	0.33	1.51	0.14	
3A	3.49	0.21	3.71	0.20	3.08	**0.00**	hybrid
4A	2.80	0.17	2.96	0.18	2.66	**0.01**	hybrid
5A	2.68	0.13	2.77	0.18	1.80	0.08	
BCL	5.57	0.63	5.62	0.55	0.25	0.81	
NCL	6.76	0.66	6.90	0.40	0.70	0.49	
NpL	1.19	0.24	1.28	0.41	0.89	0.38	
Slice 1							
1Hnc	2.37	0.17	2.58	0.32	2.75	**0.01**	hybrid
1Himr	0.99	0.21	1.31	0.58	2.57	**0.01**	hybrid
1Himl	1.00	0.24	1.38	0.71	2.54	**0.02**	hybrid
1Hicr	0.98	0.20	1.18	0.25	2.72	**0.01**	hybrid
1Hicl	0.99	0.20	1.26	0.48	2.55	**0.01**	hybrid
1Wnc	3.11	0.45	3.50	0.61	2.28	**0.03**	hybrid
1Wim	3.30	0.50	3.70	0.55	2.34	**0.02**	hybrid
1Wic	2.09	0.35	2.37	0.45	2.18	**0.04**	hybrid
1Wmm	2.54	0.28	2.76	0.34	2.19	**0.03**	hybrid
1R	0.74	0.14	0.71	0.13	0.58	0.57	
Slice 2							
2Hnc	2.83	0.32	2.95	0.21	1.21	0.23	
2Hicr	2.83	0.28	2.87	0.34	0.35	0.73	
2Hicl	2.83	0.25	2.92	0.26	1.03	0.31	
2Wnc	3.36	0.78	3.52	0.64	0.66	0.51	
2Wmm	4.02	0.36	4.26	0.45	1.82	0.08	
2Wic	2.31	0.40	2.41	0.64	0.63	0.53	
2R	1.02	0.97	0.86	0.16	0.60	0.55	
Slice 3							
3Hnc	3.62	0.28	3.97	0.49	2.90	**0.01**	hybrid
3Wnc	2.38	0.33	2.43	0.33	0.46	0.65	
3Wic	1.97	0.31	2.12	0.21	1.56	0.13	
3Hicr	1.37	0.20	1.46	0.16	1.29	0.20	
3Hicl	1.38	0.21	1.45	0.19	0.92	0.36	
3Wmm	4.10	0.41	4.24	0.34	1.03	0.31	
3R	1.55	0.26	1.67	0.33	1.23	0.23	

Table 6 (continued)

	Male Olive (*n*=27)		Male Hybrid (*n*=13)		Independent student t-test with unequal sample sizes (*d.f.*= 38) (*α*=0.05)		
	mean	*s*	mean	*s*	*t*	*p*	Larger group
Slice 4							
4Him	2.91	0.30	3.18	0.49	2.14	**0.04**	hybrid
4Wim	2.13	0.22	2.23	0.22	1.43	0.16	
4Wav	2.86	0.62	3.24	0.45	1.95	0.06	
4Himav	1.70	0.48	1.48	0.64	1.25	0.22	
4Wlr	3.42	0.42	3.53	0.33	0.84	0.41	
4R	1.39	0.23	1.45	0.31	0.68	0.50	
Slice 5							
5Him	3.21	0.42	3.38	0.65	0.97	0.34	
5Wim	2.18	0.26	2.21	0.31	0.30	0.77	
5Wav	2.75	0.31	2.72	0.50	0.25	0.81	
5Himav	1.77	0.31	1.85	0.50	0.59	0.56	
5Wlr	3.01	0.11	3.15	0.32	2.09	**0.04**	hybrid
5R	1.50	0.32	1.58	0.45	0.59	0.56	

Table 7 ANOVA tests, *α*=0.05, between olive females, hybrid females, and yellow females of each of the 45 features of the nasal cavity. Significant *p*-values are bolded. Significant pairwise comparisons identified by Dunnett's C are listed and of these, the larger taxon for that feature is given. In the column "Dunnett's C," "none" means that the trait was significant at ANOVA, but has no psignificant pairwise comparison. Results are illustrated in Figure 7c.

	Female Olive (*n*=52)		Female Hybrid (*n*=41)		Female Yellow (*n*=4)		ANOVA	Dunnett's C	Larger group
	mean	*s*	mean	*s*	mean	*s*	*p*	Significant Taxa	
Vol	3.22	0.15	3.27	0.15	3.10	0.19	0.082	Olive and Hybrid	Hybrid
1A	1.93	0.12	2.01	0.15	1.90	0.18	**0.018**	Olive and Hybrid	Hybrid
2A	2.57	0.17	2.65	0.15	2.63	0.19	0.051		
3A	2.72	0.19	2.82	0.15	2.71	0.32	**0.024**	Olive and Hybrid	Hybrid
4A	2.21	0.19	2.31	0.13	2.25	0.21	**0.017**	Olive and Hybrid	Hybrid
5A	2.09	0.17	2.14	0.12	2.03	0.09	0.224		
BCL	4.46	0.39	4.31	0.29	3.91	0.13	**0.003**	none	
NCL	5.34	0.35	5.27	0.27	4.73	0.20	**0.002**	none	
NpL	0.88	0.20	0.96	0.23	0.83	0.31	0.171		
Slice 1									
1Hnc	1.82	0.27	1.83	0.14	1.78	0.05	0.915		
1Himr	0.70	0.24	0.84	0.29	0.66	0.18	**0.031**	none	
1Himl	0.75	0.21	0.83	0.21	0.61	0.22	**0.045**	Olive and Hybrid	Hybrid
1Hicr	0.66	0.16	0.76	0.13	0.70	0.12	**0.011**	Olive and Hybrid	Hybrid
1Hicl	0.71	0.16	0.79	0.16	0.70	0.11	0.074		
1Wnc	2.11	0.75	2.56	0.60	2.38	0.49	**0.007**	none	
1Wim	2.51	0.39	2.82	0.32	2.49	0.51	**<0.005**	Olive and Yellow	Olive
1Wic	1.51	0.22	1.55	0.20	1.49	0.29	0.614		
1Wmm	1.88	0.16	1.87	0.16	1.80	0.21	0.696		
1R	0.75	0.20	0.65	0.08	0.74	0.19	**0.017**	Olive and Yellow	Olive
Slice 2									
2Hnc	2.15	0.24	2.23	0.24	2.29	0.16	0.166		
2Hicr	2.01	0.23	2.06	0.26	2.08	0.32	0.58		
2Hicl	2.02	0.22	2.08	0.26	2.00	0.29	0.541		

Table 7 (continued)

	Female Olive (*n*=52)		Female Hybrid (*n*=41)		Female Yellow (*n*=4)		ANOVA	Dunnett's C	Larger group
	mean	*s*	mean	*s*	mean	*s*	*p*		
2Wnc	3.00	0.36	3.15	0.30	3.00	0.03	0.092		
2Wmm	3.16	0.29	3.30	0.23	3.24	0.29	0.053		
2Wic	1.98	0.26	2.03	0.25	1.99	0.26	0.646		
2R	0.73	0.13	0.72	0.13	0.76	0.05	0.782		
Slice 3									
3Hnc	3.02	0.26	3.16	0.29	3.27	0.42	**0.027**	none	
3Wnc	3Wnc	3Wnc	3Wnc	3Wnc	3Wnc	3Wnc	3Wnc	3Wnc	3Wnc
3Wnc	2.07	0.20	2.06	0.17	1.79	0.20	**0.016**	Olive and Hybrid	Olive
3Wic	1.78	0.22	1.76	0.23	1.64	0.30	0.456		
3Hicr	1.05	0.17	1.11	0.27	0.91	0.14	0.132		
3Hicl	1.06	0.18	1.08	0.17	0.94	0.12	0.274		
3Wmm	2.98	0.52	3.16	0.38	2.96	0.72	0.192		
3R	1.47	0.19	1.55	0.23	1.87	0.47	**0.002**	Olive and Hybrid	Hybrid
Slice 4									
4Him	2.60	0.40	2.75	0.39	2.94	0.40	0.094		
4Wim	1.82	0.17	1.77	0.12	1.53	0.22	**0.001**	Olive and Hybrid	Olive
4Wav	1.81	0.58	2.06	0.59	2.07	0.43	0.115		
4Himav	1.64	0.45	1.58	0.39	1.48	0.13	0.653		
4Wlr	2.70	0.36	2.81	0.33	2.65	0.50	0.27		
4R	1.45	0.31	1.57	0.26	1.97	0.52	**0.002**	none	
Slice 5									
5Him	2.69	0.39	2.84	0.45	3.03	0.40	0.12		
5Wim	1.85	0.23	1.83	0.20	1.51	0.21	**0.015**	Olive and Hybrid	Olive
5Wav	1.75	0.46	1.79	0.41	1.50	0.28	0.443		
5Himav	1.54	0.35	1.60	0.29	1.66	0.24	0.62		
5Wlr	2.39	0.20	2.40	0.21	2.13	0.21	**0.035**	Olive and Hybrid	Hybrid
5R	1.48	0.33	1.57	0.31	2.03	0.38	**0.006**	none	

Table 8 ANOVA tests, *α*=0.0011, between olive, hybrid, and yellow baboons (males +females) of each of the 45 features of the nasal cavity. The significant pairwise comparisons identified by Dunnett's C are listed and of these, the larger taxon for that feature is given. Results are illustrated in Figure 7d. This test was performed after the correction for sexual dimorphism.

	Olive (*n*=79)		Yellow (*n*=5)		Hybrid (*n*=54)		ANOVA	Dunnett's C	
Variable	mean	*s*	mean	*s*	mean	*s*	*p*	Sig taxa	Largest
Vol	3.22	0.16	3.10	0.20	3.27	0.18	0.068		
1A	1.93	0.14	1.90	0.15	2.01	0.23	0.036		
2A	2.57	0.19	2.63	0.15	2.65	0.21	0.054		
3A	2.72	0.20	2.71	0.32	2.82	0.16	0.007		
4A	2.21	0.18	2.25	0.18	2.31	0.14	0.003		
5A	2.09	0.16	2.03	0.08	2.14	0.14	0.129		
BCL	4.46	0.48	3.91	0.19	4.31	0.37	0.007		
NCL	5.34	0.48	4.73	0.39	5.27	0.31	0.007		
NpL	0.88	0.21	0.83	0.28	0.96	0.28	0.141		
Slice 1									
1Hnc	1.82	0.24	1.78	0.04	1.83	0.20	0.895		
1Himr	0.70	0.23	0.66	0.16	0.84	0.38	0.022		
1Himl	0.75	0.22	0.61	0.20	0.83	0.39	0.117		
1Hicr	0.66	0.18	0.70	0.12	0.76	0.16	0.008		
1Hicl	0.71	0.17	0.70	0.11	0.79	0.27	0.128		
1Wnc	2.11	0.65	2.38	0.30	2.56	0.60	**<0.001**	olive and hybrid	hybrid
1Wim	2.51	0.43	2.49	0.45	2.82	0.38	**<0.001**	olive and hybrid	hybrid
1Wic	1.51	0.27	1.49	0.20	1.55	0.28	0.654		
1Wmm	1.88	0.21	1.80	0.10	1.87	0.22	0.755		
1R	0.75	0.18	0.74	0.16	0.65	0.09	0.002		
Slice 2									
2Hnc	2.15	0.27	2.29	0.08	2.23	0.23	0.109		
2Hicr	2.01	0.24	2.08	0.23	2.06	0.28	0.508		
2Hicl	2.02	0.23	2.00	0.22	2.08	0.26	0.432		
2Wnc	3.00	0.53	3.00	0.03	3.15	0.41	0.209		
2Wmm	3.16	0.31	3.24	0.24	3.30	0.29	0.041		

Table 8 (continued)

Variable	Olive (*n*=79)		Yellow (*n*=5)		Hybrid (*n*=54)		ANOVA	Dunnett's C	
	mean	*s*	mean	*s*	mean	*s*	*p*	Sig taxa	Largest
2Wic	1.98	0.31	1.99	0.08	2.03	0.37	0.705		
2R	0.73	0.57	0.76	0.03	0.72	0.13	0.975		
Slice 3									
3Hnc	3.02	0.27	3.27	0.29	3.16	0.34	0.013		
3Wnc	2.07	0.25	1.79	0.24	2.06	0.22	0.035		
Variable	mean	*s*	mean	*s*	mean	*s*	*p*	Sig taxa	Largest
3Wic	1.78	0.25	1.64	0.31	1.76	0.22	0.413		
3Hicr	1.05	0.18	0.91	0.29	1.11	0.24	0.057		
3Hicl	1.06	0.19	0.94	0.24	1.08	0.17	0.214		
3Wmm	2.98	0.49	2.96	0.73	3.16	0.36	0.076		
3R	1.47	0.21	1.87	0.41	1.55	0.26	**0.001**	none	
Slice 4									
4Him	2.60	0.38	2.94	0.38	2.75	0.41	0.031		
4Wim	1.82	0.19	1.53	0.19	1.77	0.15	**0.001**	none	
4Wav	1.81	0.59	2.07	0.48	2.06	0.56	0.044		
4Himav	1.64	0.46	1.48	0.29	1.58	0.45	0.607		
4Wlr	2.70	0.38	2.65	0.50	2.81	0.33	0.177		
4R	1.45	0.28	1.97	0.48	1.57	0.27	**<0.001**	olive and hybrid	hybrid
Slice 5									
5Him	2.69	0.39	3.03	0.38	2.84	0.50	0.074		
5Wim	1.85	0.24	1.51	0.19	1.83	0.23	0.01		
5Wav	1.75	0.41	1.50	0.45	1.79	0.42	0.326		
5Himav	1.54	0.34	1.66	0.40	1.60	0.33	0.545		
5Wlr	2.39	0.17	2.13	0.21	2.40	0.24	0.013		
5R	1.48	0.32	2.03	0.38	1.57	0.35	0.002		

Table 9 The intra-observer standard deviation and range of +/- 1 standard deviation for each variable. The level of measurement accuracy is also noted.

Variable	SD	Range of +/-1 standard deviation	Measurement accuracy
Volume $(cm^3)^{-3}$	0	8.930E-16	<0.005 $(cm^3)^{-3}$
Area slice 1 $(cm^2)^{-2}$	0	2.783E-09	<0.005 $(cm^2)^{-2}$
Area slice 2 $(cm^2)^{-2}$	0	5.757E-10	<0.005 $(cm^2)^{-2}$
Area slice 3 $(cm^2)^{-2}$	0	4.178E-10	<0.005 $(cm^2)^{-2}$
Area slice 4 $(cm^2)^{-2}$	0	1.154E-08	<0.005 $(cm^2)^{-2}$
Area slice 5 $(cm^2)^{-2}$	0	5.212E-08	<0.005 $(cm^2)^{-2}$
Bony cavity length (cm)	0	0	<0.005 (cm)
Total nasal cavity length (cm)	0	0	<0.005 (cm)
Nasopharynx length (cm)	0	0	<0.005 (cm)
Slice 1			
Slice 1 Height at nasal crest (cm)	0.021	0.041	<0.05 (cm)
Slice 1 Height of right inferior meatus (cm)	0.035	0.069	<0.1 (cm)
Slice 1 Height of left inferior meatus (cm)	0.021	0.041	<0.05 (cm)
Slice 1 Height of right inferior conchae (cm)	0.017	0.033	<0.05 (cm)
Slice 1 Height of left inferior conchae (cm)	0.019	0.038	<0.05 (cm)
Slice 1 Width at nasal crest (cm)	0.029	0.058	<0.1 (cm)
Slice 1 Width of inferior meatus (cm)	0.022	0.045	<0.05 (cm)
Slice 1 Width between inferior conchae (cm)	0.022	0.045	<0.05 (cm)
Slice 1 Width of middle meatus (cm)	0.008	0.017	<0.025 (cm)
Slice 2			
Slice 2 Height at nasal crest (cm)	0.136	0.272	<0.5 (cm)
Slice 2 Height of right inferior conchae (cm)	0.014	0.028	<0.05 (cm)
Slice 2 Height of left inferior conchae (cm)	0.015	0.030	<0.05 (cm)
Slice 2 Width at nasal crest (cm)	0.074	0.148	<0.25 (cm)
Slice 2 Width of middle meatus (cm)	0.037	0.073	<0.1 (cm)
Slice 2 Width between inferior conchae (cm)	0.024	0.047	<0.05 (cm)
Slice 3			
Slice 3 Height at nasal crest (cm)	0.132	0.264	<0.5 (cm)
Slice 3 Width at nasal crest (cm)	0.026	0.051	<0.1 (cm)

Table 9 (continued)

Variable	SD	Range of +/-1 standard deviation	Measurement accuracy
Slice 3 Width between inferior conchae (cm)	0.022	0.044	<0.05 (cm)
Slice 3 Height of right inferior conchae (cm)	0.042	0.083	<0.1 (cm)
Slice 3 Height of left inferior conchae (cm)	0.045	0.089	<0.1 (cm)
Slice 3 Width of middle meatus (cm)	0.052	0.103	<0.25 (cm)
Slice 4			
Slice 4 Height at inferior margin (cm)	0.089	0.177	<0.25 (cm)
Slice 4 Width of inferior margin (cm)	0.009	0.019	<0.025 (cm)
Slice 4 Width at alae of vomer (cm)	0.332	0.665	<1 (cm)
Slice 4 Height at inferior margin to alae of vomer (cm)	0.036	0.072	<0.1 (cm)
Slice 4 Width of lateral recess (cm)	0.009	0.018	<0.025 (cm)
Slice 5			
Slice 5 Height at inferior margin (cm)	0.082	0.163	<0.25 (cm)
Slice 5 Width of inferior margin (cm)	0.013	0.026	<0.05 (cm)
Slice 5 Width at alae of vomer (cm)	0.378	0.755	<1 (cm)
Slice 5 Height at inferior margin to alae of vomer (cm)	0.075	0.150	<0.25 (cm)
Slice 5 Width of lateral recess (cm)	0.027	0.053	<0.1 (cm)

Table 10 The definition of the scores for each nonmetric trait. Figure 18 illustrates each trait.

Nonmetric Trait	Score	Definition
Dentition: Roots	0	No roots penetrate nasal cavity
	1	1 or 2 roots penetrate nasal cavity
	2	3+ roots penetrate nasal cavity
Dentition: Ectopic Teeth	0	none
	1	1 tooth with no interference with nasal cavity
	2	1 tooth with severe impact on nasal cavity
	3	2+ teeth with no interference with nasal cavity
	4	2+ teeth with severe impact on nasal cavity
Deviated Septum	0	No deviated septum
scores derived from Sinha and Maheshwari	1	Minor deviated septum
(1963)	2	Moderate deviated septum
	3	Severe deviated septum
Divided Greater Palatine Canal	0	No division
	1	One side divided
	2	Both sides divided
Lateral Recess in Orbit	0	Flat orbits
	1	Moderate curvature at lateral recess in orbits
	2	Large curvature at lateral recess in orbits
Attachment of Inferior Nasal Conchae in slice 3	0	Attached
	1	Not attached
Presence of alae of vomer in slice 4	0	Present
	1	Not Present

Table 11 Observed and expected values, in parentheses, for each score and baboon group are listed in the contingency table. Results of Fisher's Exact test, α=0.05, on each nonmetric trait for different combinations of taxa are also given. Significant p-values are bolded. a) Roots, b) Ectopic Teeth, c) Deviated Septum d) Division of Greater Palatine Canals e) Lateral Recess in Orbits f) Attached Inferior Nasal Conchae in Slice 3 g) Presence of alae of vomer in Slice 4 * were not included in the Fisher's Exact test calculation

a) Roots

Score	Olive	Yellow	Total	χ^2	p
0	76 (75.3)	3 (3.7)	79	4.304	0.145
1	23 (22.9)	1(1.1)	24		
2	2(2.9)	1(0.1)	3		
Total	101	5	106		
	Parental	Hybrid	Total		
0	79(79.3)	49(48.7)	128	4.031	0.123
1	24(21.1)	10(12.9)	34		
2	3(5.6)	6(3.4)	9		
Total	106	65	171		
	Male Parental	Male Hybrid	Total		
0	27(27.1)	12(11.9)	39	0.793	0.78
1	13(12.5)	5(5.5)	18		
2	1	1	2		
Total	41	18	59		
	Female Parental	Female Hybrid	Total		
0	52(51.7)	37(37.3)	89	3.096	0.212
1	11(9.3)	5(6.7)	16		
2	2(4.1)	5(2.9)	7		
Total	65	47	112		
	All Female	All Male	Total		
0	89(83.8)	39(44.2)	128	6.289	**0.04**
1	16(22.3)	18(11.7)	34		
2	7(5.9)	2(3.1)	9		
Total	112	59	171		

Table 11 (continued)
b) Ectopic Teeth

Score	Olive	Yellow	Total	χ^2	*P*
0	91(90.5)	4(4.5)	95	3.892	0.428
1	7(7.6)	1(0.4)	8		
2	1(1)	0(0)	1		
3	0*	0*	0		
4	2(1.9)	0(0.1)	2		
Total	101	5	106		
	Parental	Hybrid	Total		
0	95(95.5)	59(58.5)	154	2.901	0.635
1	8(74.)	4(4.6)	12		
2	1(1.2)	1(0.8)	2		
3	0(0.6)	1(0.4)	1		
4	2(1.2)	0(0.8)	2		
Total	106	65	171		
	Male Parental	Male Hybrid	Total		
0	31(32.0)	15(14.0)	46	3.066	0.411
1	8(6.9)	2(3.1)	10		
2	0*	0*	0		
3	0(0.7)	1(0.3)	1		
4	2(1.4)	0(0.6)	2		
Total	41	18	59		
	Female Parental	Female Hybrid	Total		
0	64(62.7)	44(45.3)	108	2.733	0.319
1	0(1.2)	2(0.8)	2		
2	1(1.2)	1(0.8)	2		
3	0*	0*	0		
4	0*	0*	0		
Total	65	47	112		
	All Female	All Male	Total		
0	108 (100.9)	46(53.2)	154	18.822	**6.3E-5**
1	2(7.9)	10(4.2)	12		
2	2(1.3)	0(0.7)	2		
3	0(0.7)	1(0.3)	1		
4	0(1.3)	2(0.7)	2		
Total	112	59	171		

Table 11 (continued)
c) Deviated Septum

Score	Olive	Yellow	Total	χ^2	P
0	59(59.1)	3(2.9)	62	1.698	0.7
1	25(25.7)	2(1.3)	27		
2	15(14.2)	0(0.7)	15		
3	2(1.9)	0(0.1)	2		
Total	101	5	106		
	Parental	Hybrid	Total		
0	62(59.5)	34(36.5)	96	1.787	0.644
1	27(29.1)	20(17.9)	47		
2	15(16.1)	11(9.9)	26		
3	2(1.2)	0(0.8)	2		
Total	106	65	171		
	Male Parental	Male Hybrid	Total		
0	21(17.4)	4(7.6)	25	4.491	0.10
1	12(14.6)	9(6.4)	21		
2	8(9.0)	5(4.0)	13		
3	0*	*0	0		
Total	41	18	59		
	Female Parental	Female Hybrid	Total		
0	41(41.2)	30(29.8)	71	1.240	0.829
1	15(15.1)	11(10.9)	26		
2	7(7.5)	6(5.5)	13		
3	2(1.2)	0(0.8)	2		
Total	41	30	112		
	All Female	All Male	Total		
0	71(62.9)	25(33.1)	96	8.6	**0.023**
1	26(30.8)	21(16.2)	47		
2	13(17.0)	13(9.0)	26		
3	2(1.3)	0(0.7)	2		
Total	112	59	171		

Table 11 (continued)
d) Divided Greater Palatine Canals

Score	Olive	Yellow	Total	χ^2	P
0	67(67.7)	4(3.3)	71	2.374	0.307
1	26(24.8)	0(1.2)	26		
2	8(8.6)	1(0.4)	9		
Total	101	5	106		
	Parental	Hybrid	Total		
0	71(70.7)	43(43.3)	114	2.366	0.315
1	26(23.6)	12(14.4)	38		
2	9(11.8)	10(7.2)	19		
Total	106	65	171		
	Male Parental	Male Hybrid	Total		
0	28(28.5)	13(12.5)	41	0.199	1.00
1	10(9.7)	4(4.3)	14		
2	3(2.8)	1(1.2)	4		
Total	41	18	59		
	Female Parental	Female Hybrid	Total		
0	43 (42.4)	30(30.6)	73	2.694	0.259
1	16(13.9)	8(10.1)	24		
2	6(8.7)	9(6.3)	15		
Total	41	30	112		
	All Female	All Male	Total		
0	73(74.7)	41(39.3)	114	1.650	0.456
1	24(24.9)	14(13.1)	38		
2	15(12.4)	4(6.6)	19		
Total	112	59	171		

Table 11 (continued)

e) Lateral Recess in Orbits					
Score	Olive	Yellow	Total	χ^2	P
0	60(61.0)	4(3.0)	64	0.635	0.741
1	35(34.3)	1(1.7)	36		
2	6(5.7)	0(0.3)	6		
Total	101	5	106		
	Parental	Hybrid	Total		
0	64(58.9)	31(36.1)	95	5.195	0.075
1	36(37.1)	24(22.8)	60		
2	6(9.9)	10(6.1)	16		
Total	106	65	171		
	Male Parental	Male Hybrid	Total		
0	16(13.9)	4(6.1)	20	2.304	0.342
1	22(22.9)	11(10.1)	33		
2	3(4.2)	3(1.8)	6		
Total	41	18	59		
	Female Parental	Female Hybrid	Total		
0	48(43.5)	27(31.5)	75	4.642	0.103
1	14(15.7)	13(11.3)	27		
2	3(5.8)	7(4.2)	10		
Total	41	30	112		
	All Female	All Male	Total		
0	75(62.2)	20(32.8)	95	18.693	**6.3E-5**
1	27(39.3)	33(20.7)	60		
2	10(10.5)	6(5.5)	16		
Total	112	59	171		

Table 11 (continued)
f) Attachment of Inferior Conchae in Slice 3

Score	Olive	Yellow	Total	χ^2	p
0	63(64.8)	5(3.2)	68	2.932	0.157
1	38(36.2)	0(1.8)	38		
Total	101	5	106		
	Parental	Hybrid	Total		
0	68(71.3)	47(43.7)	115	1.217	0.315
1	38(34.7)	18(21.3)	56		
Total	106	65	171		
	Male Parental	Male Hybrid	Total		
0	23(20.8)	7(9.2)	30	1.482	0.267
1	18(20.2)	11(8.8)	29		
Total	41	18	59		
	Female Parental	Female Hybrid	Total		
0	45(49.3)	40(35.)	85	3.758	0.073
1	20(15.7)	7(11.3)	27		
Total	41	30	112		
	All Female	All Male	Total		
0	85(75.3)	30(39.7)	115	11.006	**0.001**
1	27(36.7)	29(19.3)	56		
Total	112	59	171		

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Table 11 (continued)
g) Presence of Alae of Vomer in Slice 4

Score	Olive	Yellow	Total	χ^2	p
0	91(91.5)	5(4.5)	96	0.547	1.00
1	10(9.5)	0(0.5)	10		
Total	101	5	106		
	Parental	Hybrid	Total		
0	96(96.1)	59(58.9)	155	0.002	1.00
1	10(9.9)	6(6.1)	16		
Total	106	65	171		
	Male Parental	Male Hybrid	Total		
0	34(33.4)	14(14.6)	48	0.219	0.721
1	7(7.6)	4(3.4)	11		
Total	41	18	59		
	Female Parental	Female Hybrid	Total		
0	62(62.1)	45(44.9)	107	0.008	1.00
1	3(2.9)	2(2.1)	5		
Total	41	30	112		
	All Female	All Male	Total		
0	107(101.5)	48(53.5)	155	9.161	**0.004**
1	5(10.5)	11(5.5)	16		
Total	112	59	171		

Appendix B: Figures

Figure 1 Neanderthal depictions; a) 'The Neanderthal Man' pubished in Harper's Weekly, 1873, p. 617, gave the public the first view of an ape-like Neanderthal (Moser 1998: 138). b) Maximim Lohest's drawing of Neanderthal Spy 1 in 1886, based on anatomical analysis of the Spy 1 skeleton, presents an ape-like Neanderthal that must walk with bent legs (Natuurinformatie N.d.). c) The Neanderthal from La Chapelle-aux-Saints, drawn by Frantisek Kupka and directed by Marcellin Boule, depicts a hairy, ape-like, frightening Neanderthal. This image was published in Illustrated London News in February 1909, pp. 302-303 (Moser 1998: xxiii). d) In response to Boule's 1909 image of a Neanderthal, Sir Arthur Kieth directed artist Amadée Forestier in the reconstruction of 'Not in the "Gorilla" stage,' portraying the Neanderthal from La Chapelle-aux-Saints as intelligent and cultured. The image was published in Illustrated London News in May 1911, pp. 778-779 (Sommer 2007: 230; Moser 1998: xxiii).

a)

Nasal
Crest

Middle
Meatus

Inferior
Concha

Inferior
Meatus

Palate

1st Molar

b)

Vomer
Alae

Lateral
recess

Nasal
Crest

Middle
Concha

Middle
Meatus

Inferior
Concha

Inferior
Meatus

Palate

3rd Molar

c)

Nasal cavity

Nasopharynx

Bony cavity

Lateral
Recess

Middle
Concha

Middle
Meatus

Inferior
Concha

Inferior
Meatus

Choana

Rhinion

Conchal
Crest

Palate
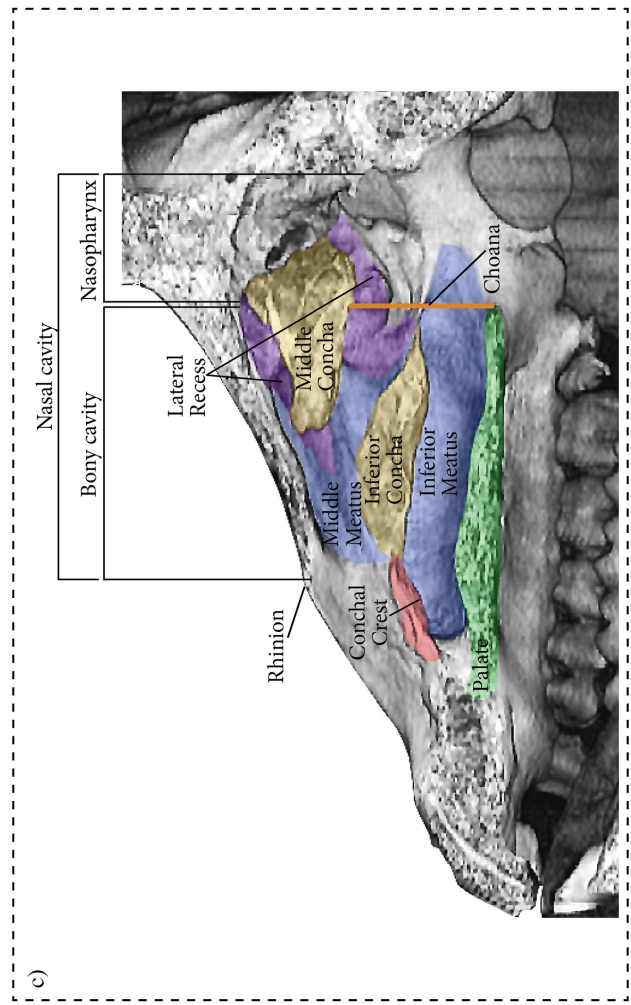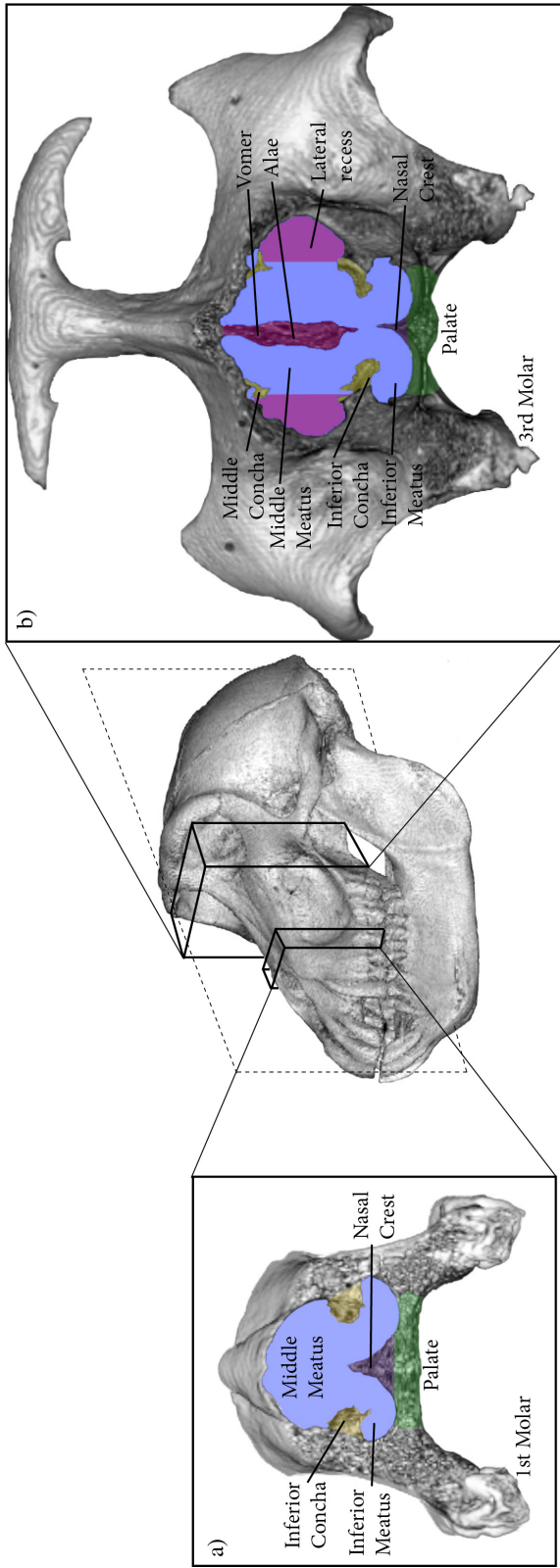
Previous page (pg 164)
Figure 2 Major features of the nasal cavity are labeled within a 3D reconstruction from CT scans of a male olive specimen. a) coronal section of the anterior bony cavity, b) coronal section of the nasopharynx, c) sagittal section of nasal cavity.

Following page (pg 166)
Figure 3 i) The location of the five analyzed and segmented CT slices, ii) an example of five slices from the CT scans of a male olive specimen with the measurements used in this study labeled; the labels correspond to Table 1, iii) a model of nasal cavity volume and the five slices based on the average values of male olive baboons; labels correspond to Table 1. Blue guidelines demonstrate the relative locations of the five scans to each other.
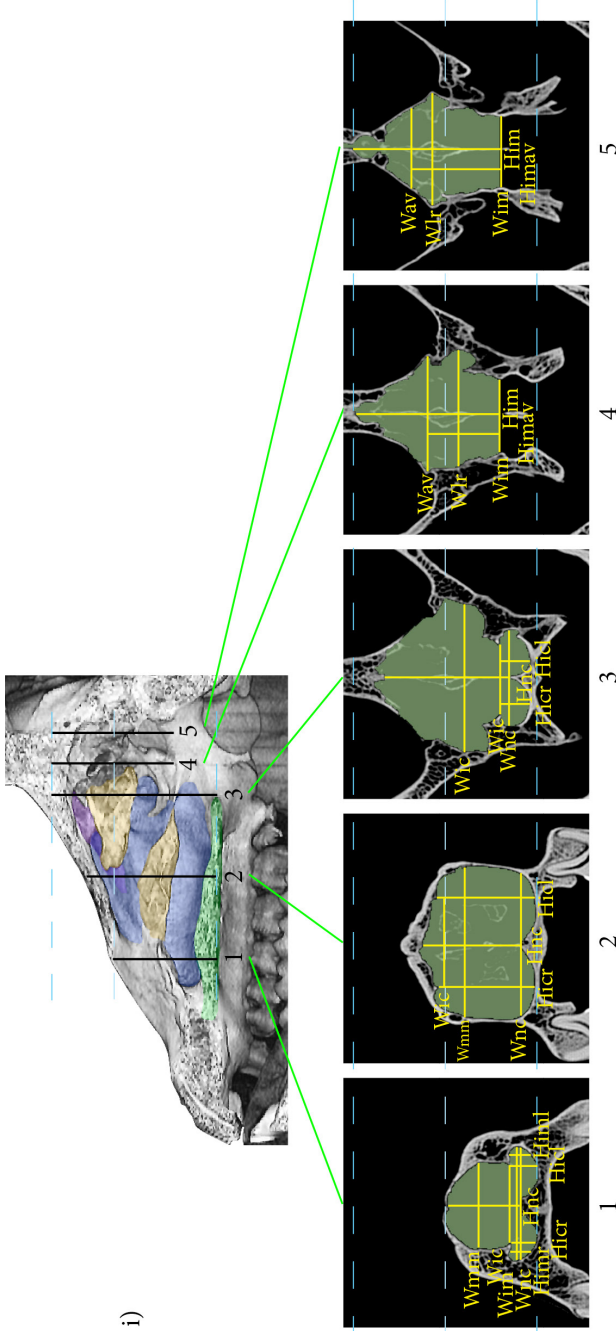
i)

ii) Olive Male Specimen
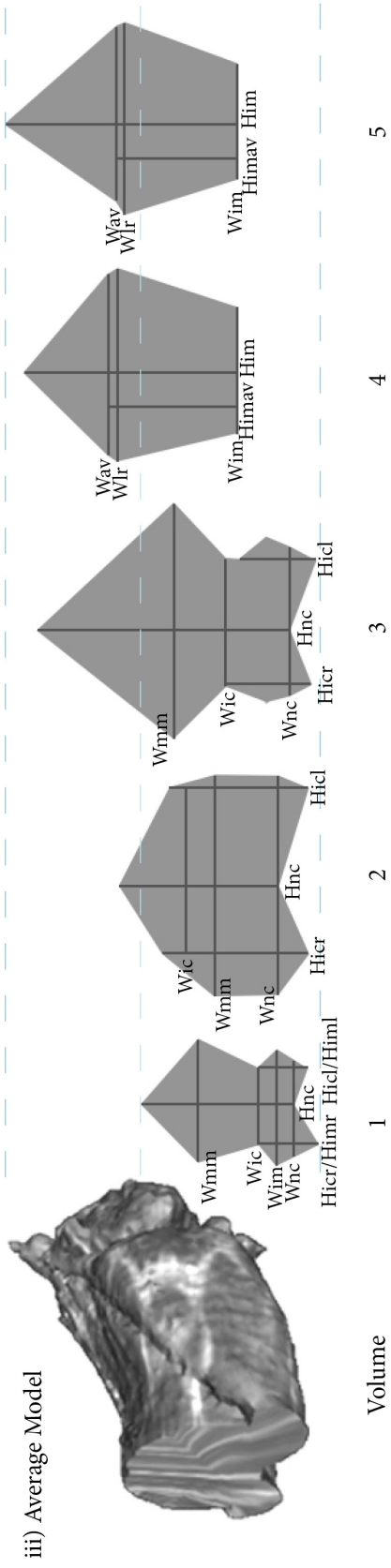
iii) Average Model

Volume
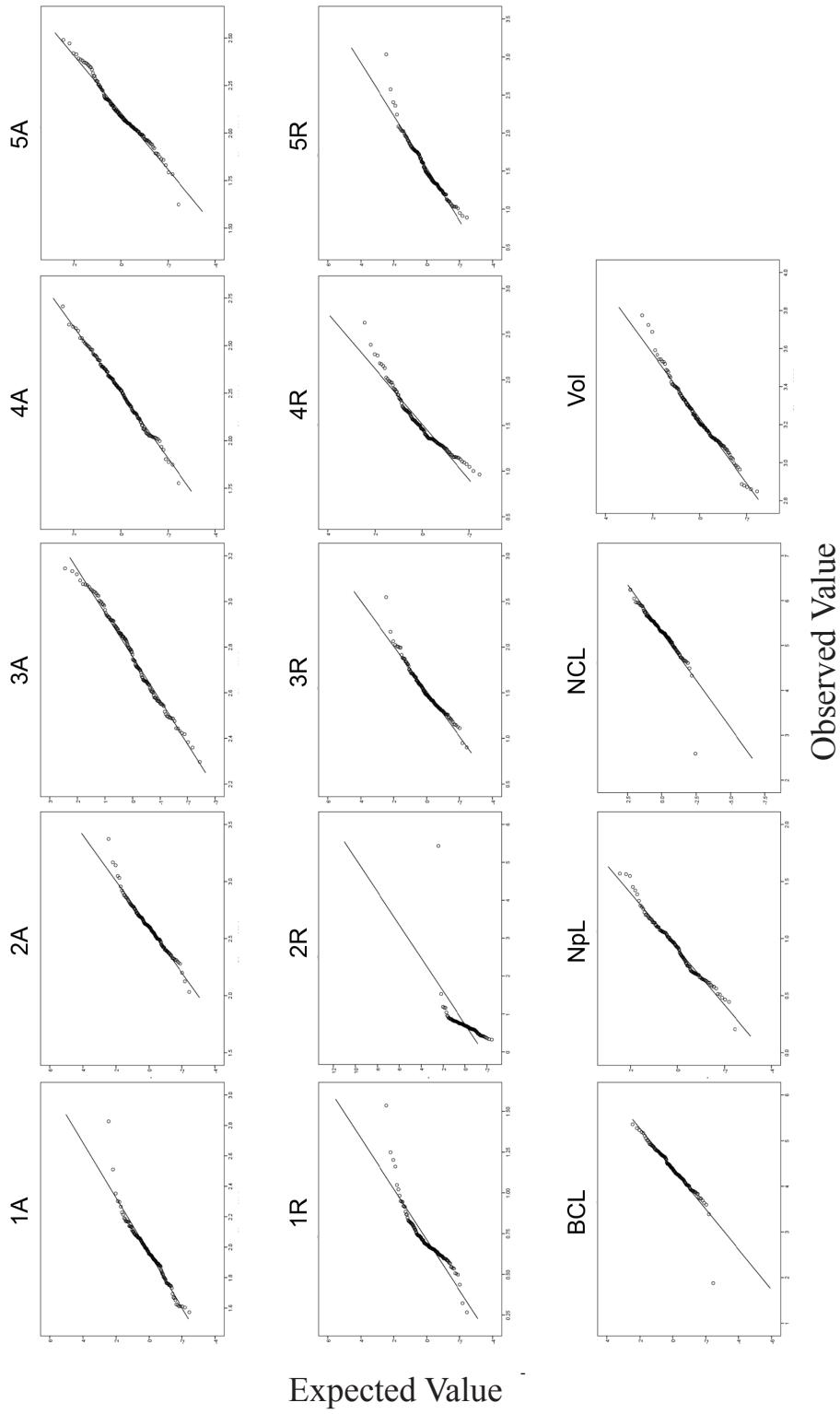
Figure 4 Q-Q plots of the 45 analyzed features show deviations from the expected normal values. Q-Q plots were made after the correction for sexual dimorphism with all groups combined. Labels correspond to Table 1. (Figure continues on page 168)

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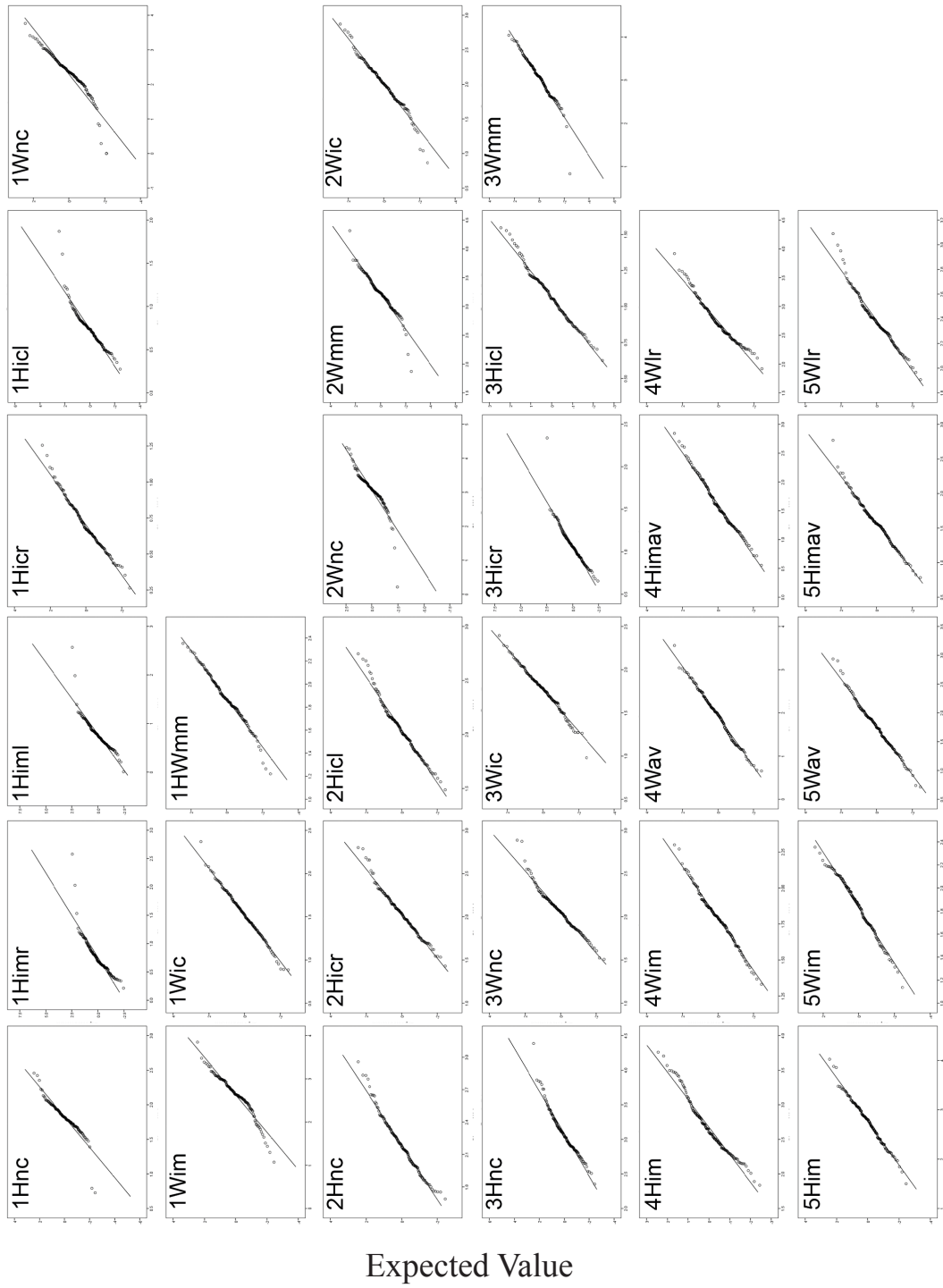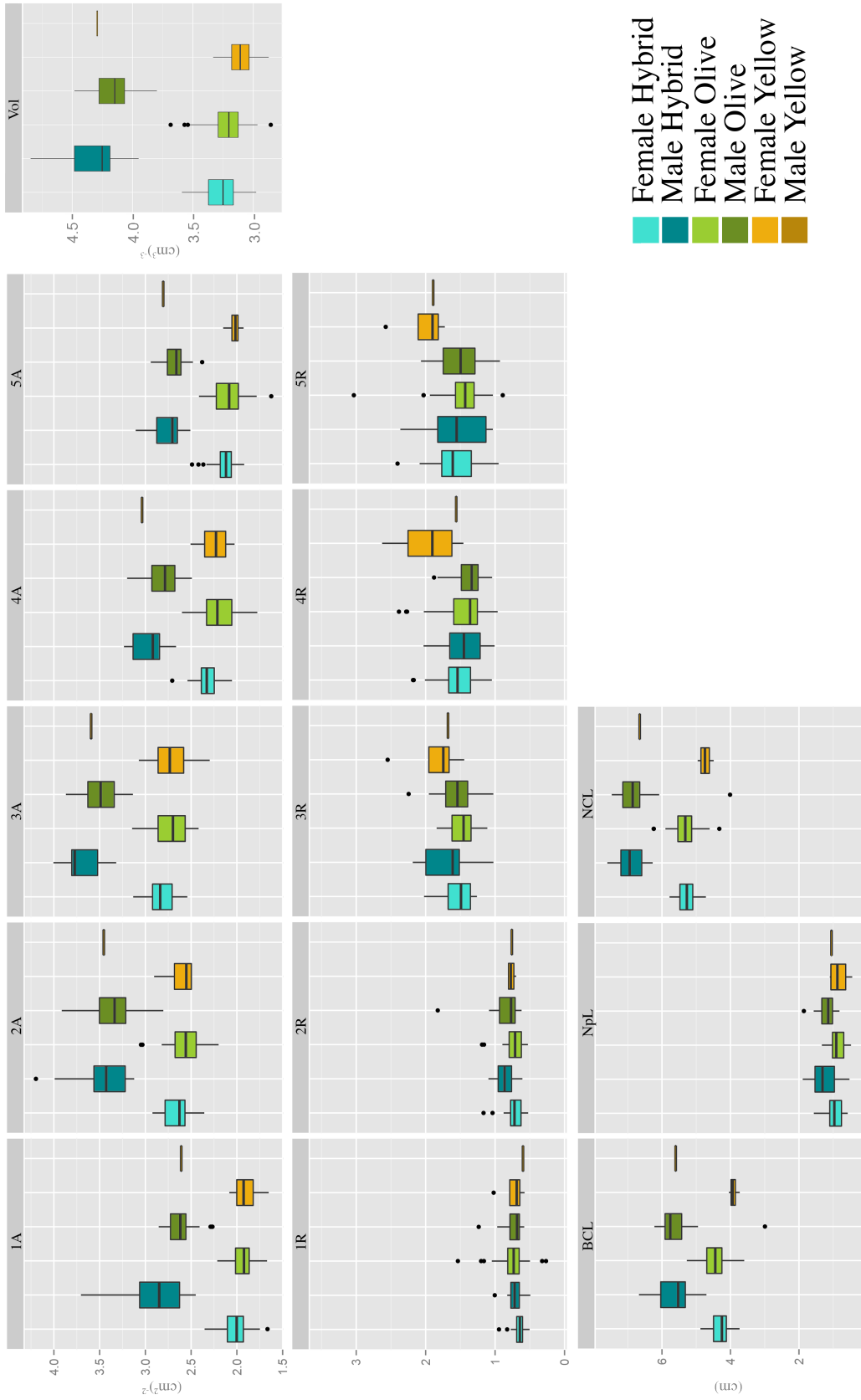
Figure 5 i) The box plots of the 45 analyzed features from all of the baboon specimens prior to sexual dimorphism correction show variation between taxa. Labels for each box plot correspond to Table 1. (Fogire continued on page 170)
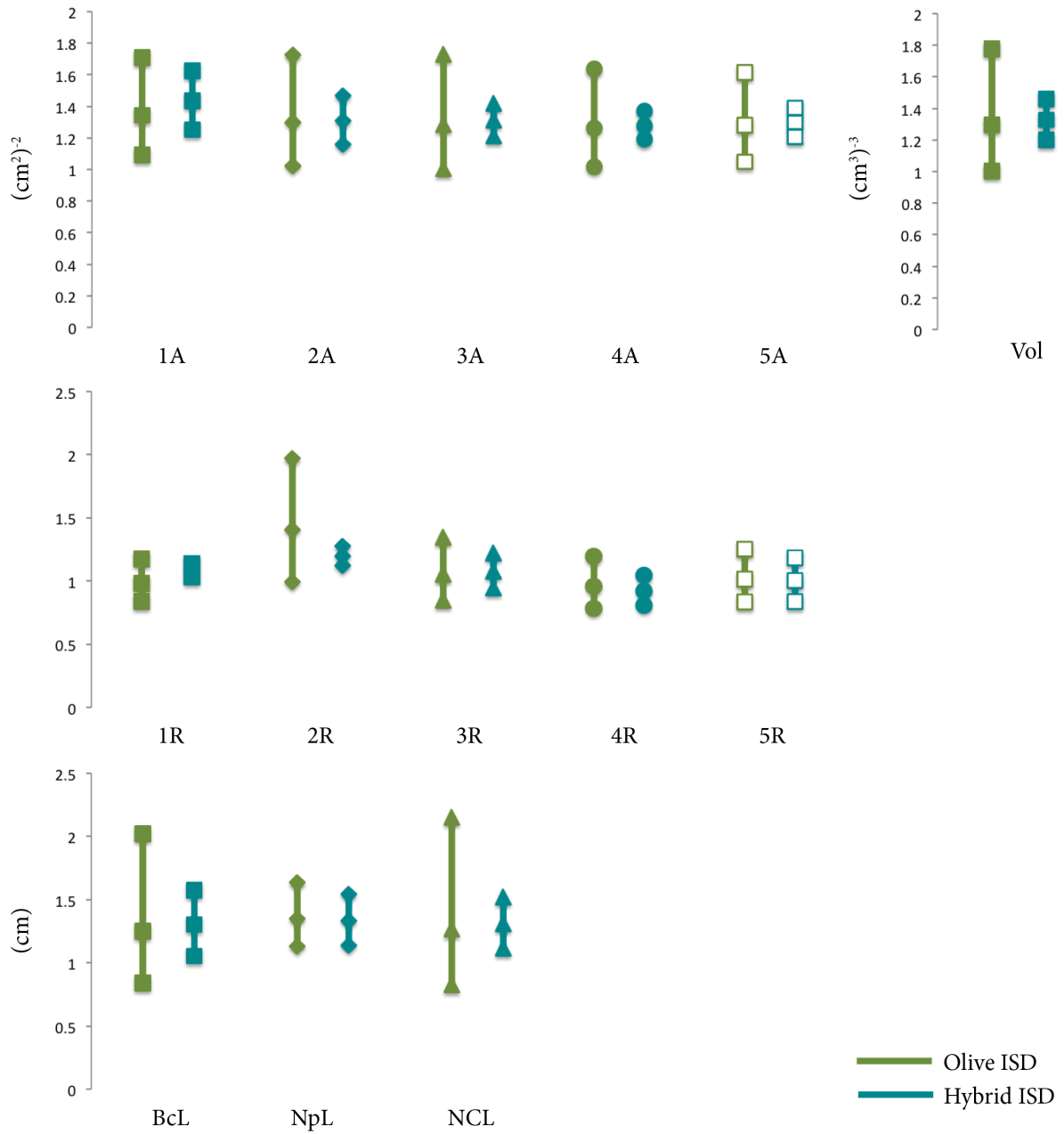
Figure 6 The plots of the index of sexual dimorphism (ISD) show overlapping 90% confidence intervals for each of the 45 traits for olive and hybrid baboons. Labels for each plot correspond to Table 1. (Figure continued on page 172)

a) Degree of sexual dimorphism between Olive and Hybrid

b) Average difference for each trait between Olive and Hybrid Males

c) Average difference for each trait between Olive, Yellow and Hybrid Females

d) Average difference for each trait between Olive, Yellow and Hybrid groups, after sexual dimorphism correction

Volume   Slice 1   Slice 2   Slice 3   Slice 4   Slice 5

Hybrid has significantly larger value for that trait

Olive has significantly larger value for that trait

Significant at ANOVA but no significant post-hoc pairwise comparisons

No significant differences

Yellow was not significantly larger for any trait

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Figure 7 Nasal cavity models representing significant features of interest in the nasal cavity. a) Significant features for the degree of sexual dimorphism between olive and hybrid baboons, statistical results are listed in Table 5. b) Significant features that differed between male olive and male hybrid baboons, statistical results are listed in Table 6. c) Significant features that differed between female olive, female hybrid, and female yellow baboons, statistical results are listed in Table 7. d) Significant features that differed between olive, hybrid, and yellow baboons, males and females combined in each taxon, after the data were corrected for sexual dimorphism. Statistical results are listed in Table 8. Background shapes of the nasal cavity of each of the five slices represent calculated areas. Traits are found to be significant if coloured blue (hybrid has significantly larger values), green (olive has significantly larger values), or magenta (found significant in the ANOVA, but not in post-hoc pairwise comparisons). Gray indicates that no significance was found for that trait. Additional traits that could not be illustrated, lengths and ratios, are listed with statistical results in Tables 5, 6, 7, and 8.
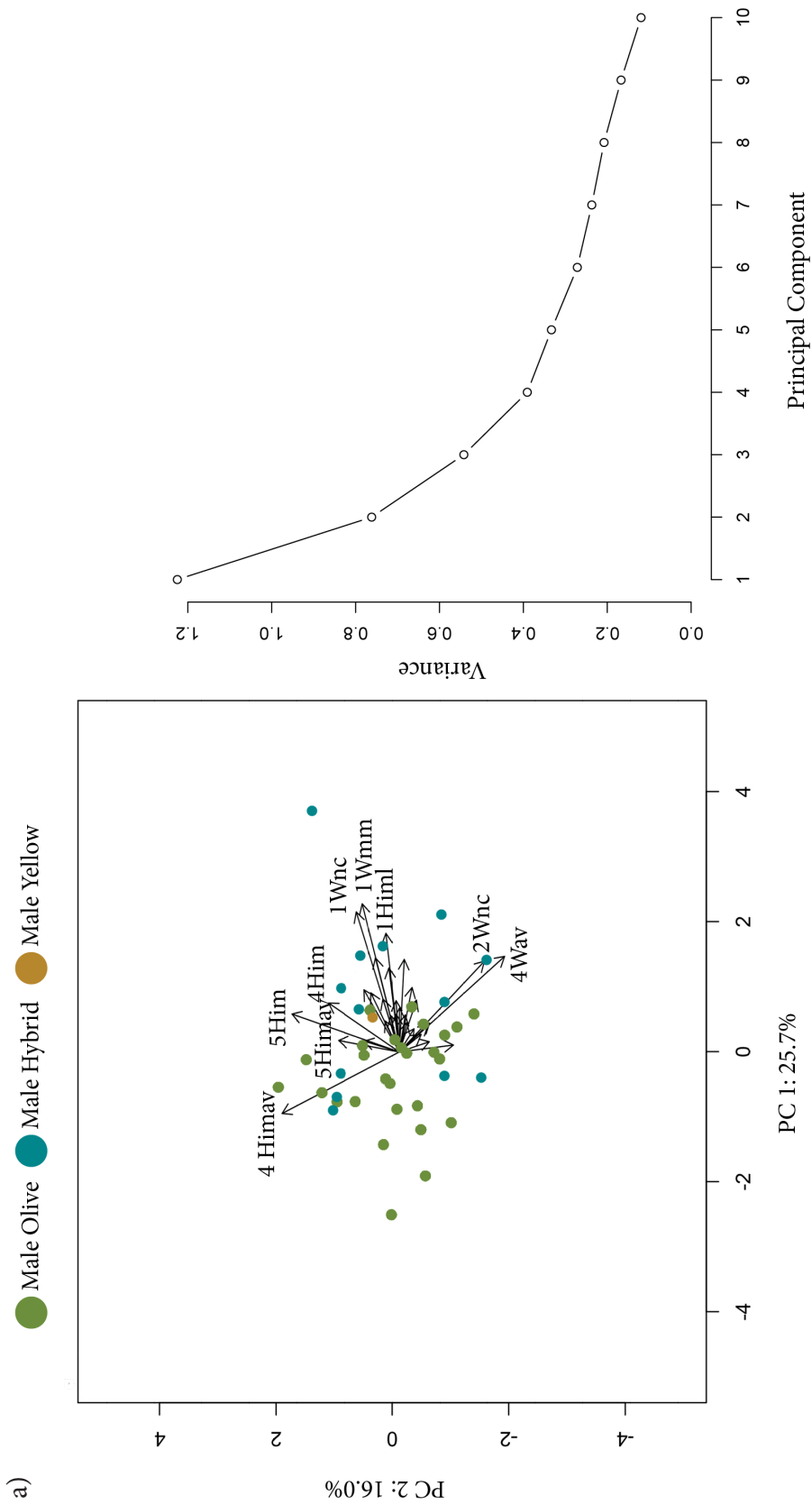
Figure 8 a) The biplot of PCA of male baboons shows minor separation between taxa along PC 1, with olive baboons grouped on the left and the hybrid baboons grouped on the right, though overlap is substantial. The single yellow baboon specimen is not differentiated by PC 1 or PC 2. Vectors with loadings in PC 1 or PC 2 that are greater than 0.25 or less than -0.25 are labeled on the graph; labels correspond to Table 1. No further separation of taxa were observed in b) the biplot of PC 2 and PC 3, and the biplot of PC 3 and PC 4.(Fogire continued on page 176)

Figure 9 a) The biplot of PCA of female baboons shows little separation of taxa along either PC 1 or PC 2. Vectors with loadings in PC1 or PC2 that are greater than 0.25 or less than -0.25 are labeled on the graph; labels correspond to Table 1. No further separation of taxa were observed in b) the biplot of PC 2 and PC 3...(Fogire continued on page 178)
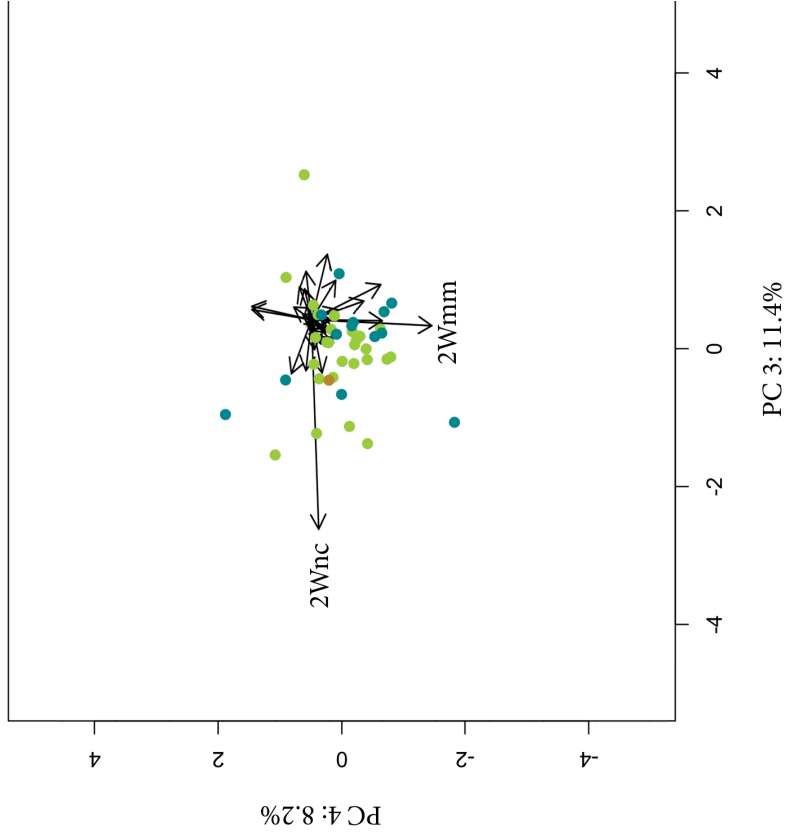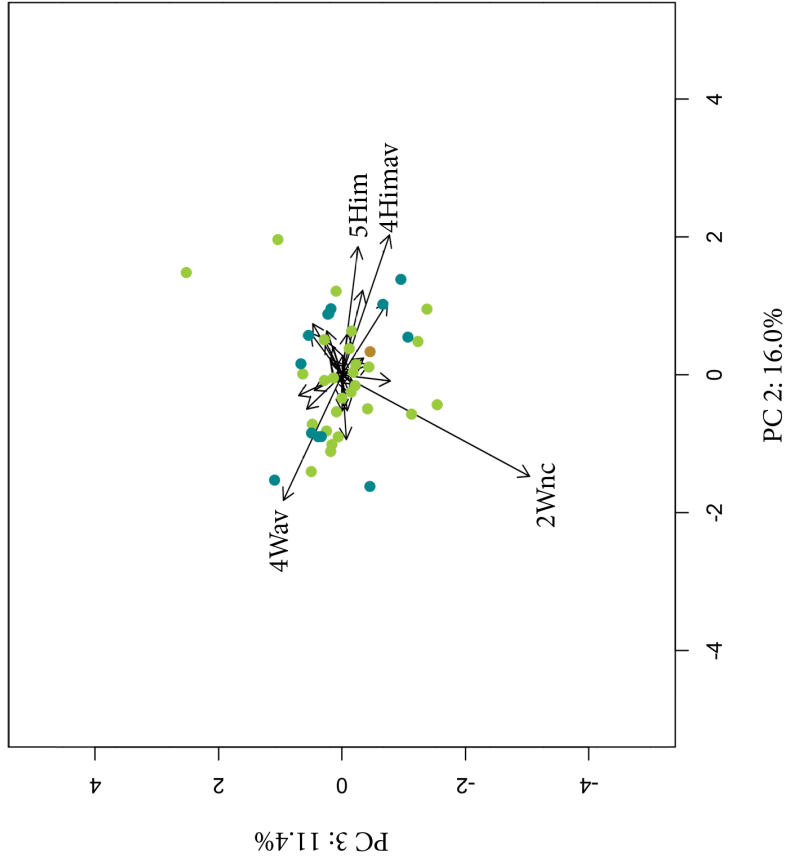
b)

Female Olive   Female Hybrid   Female Yellow

PC 3: 10.9%

PC 2: 15.7%

1Wnc

4Himav

5Himav

4Him

5Him

3Wmm

4Wav
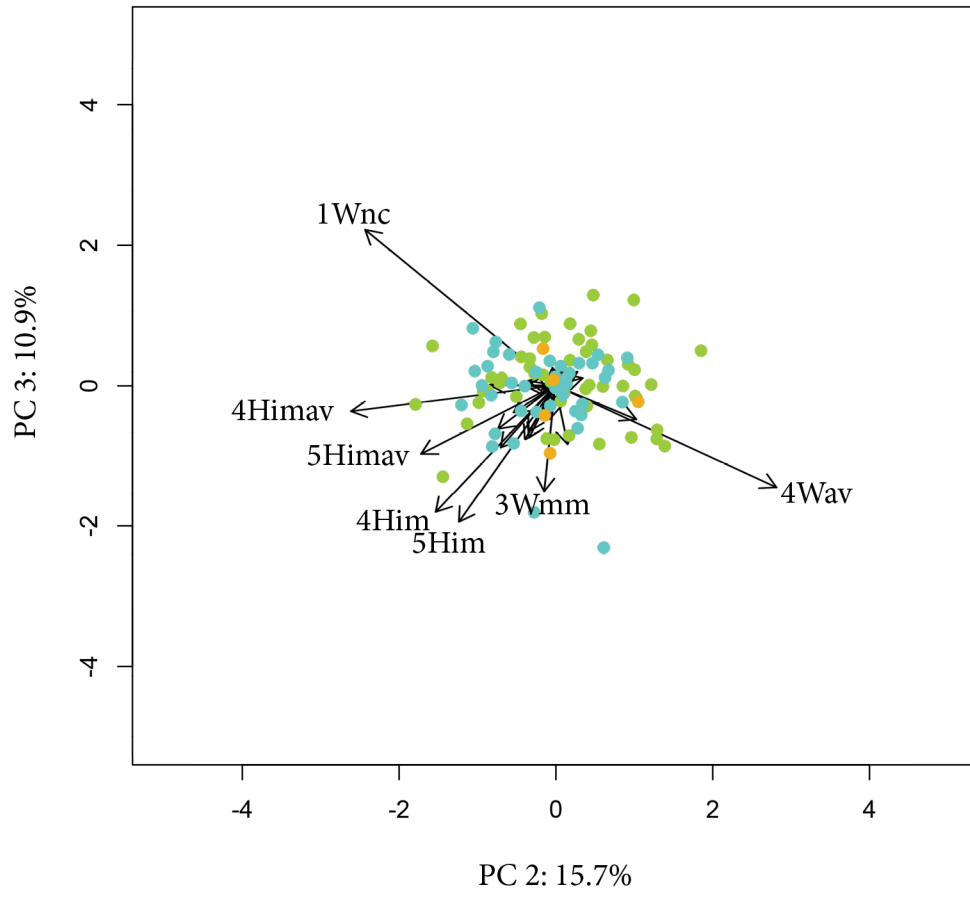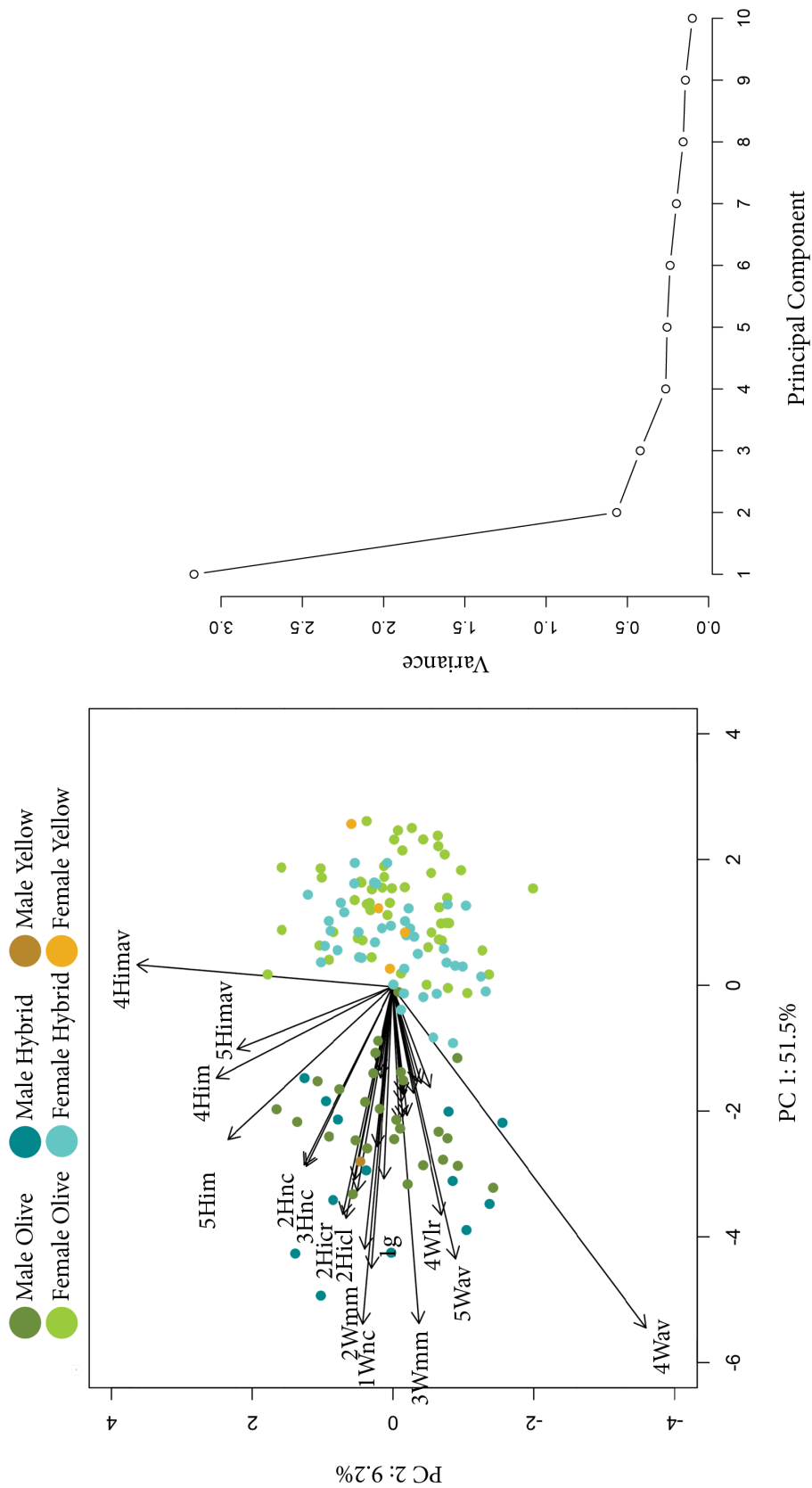
Figure 10 The biplot of PCA of all six groups of baboons prior to correction for sexual dimorphism shows separation between sex though not between taxa along PC 1, with male baboons grouped on the left and female baboons grouped on the right. Vectors with loadings in PC 1 or PC 2 that are greater than 0.25 or less than -0.25 are labeled on the graph; labels correspond to Table 1.
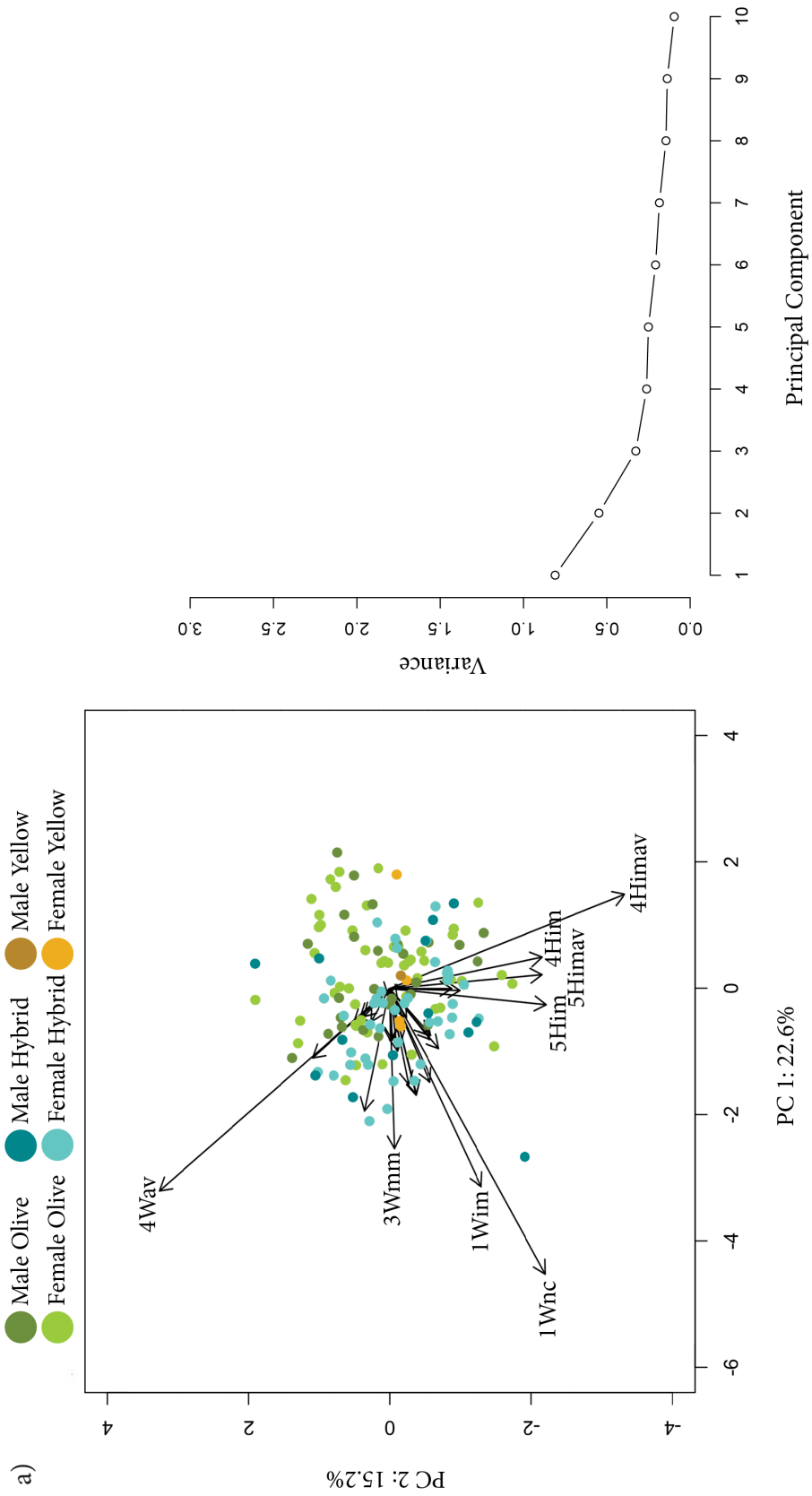
Figure 11 a) The biplot of PCA of all six groups of baboons after correction for sexual dimorphism fails to show separation between taxa. Vectors with loadings in PC 1 or PC 2 that are greater than 0.25 or less than -0.25 are labeled on the graph; labels correspond to Table 1. No further separation of taxa were observed in b) the biplot of PC 2 and PC 3. (Figure continues on page 181)
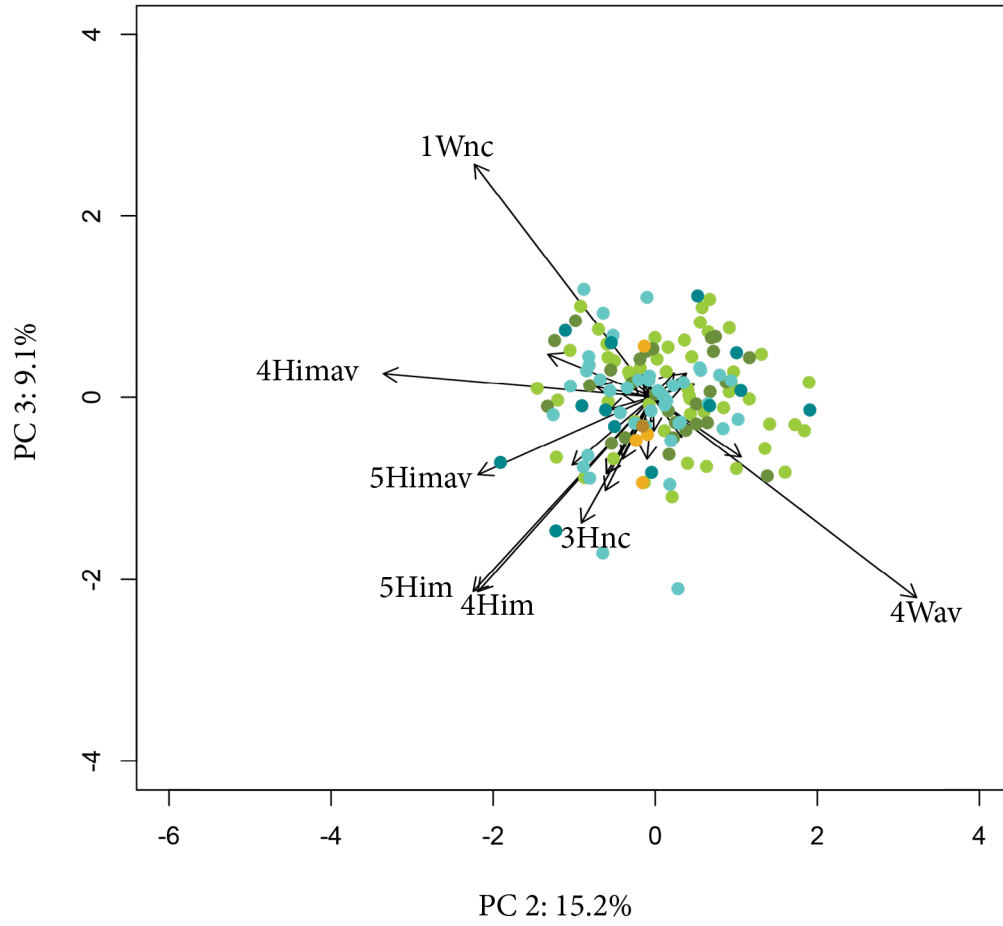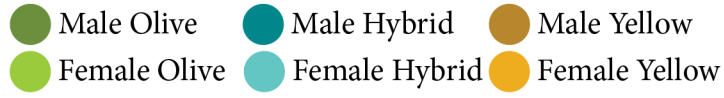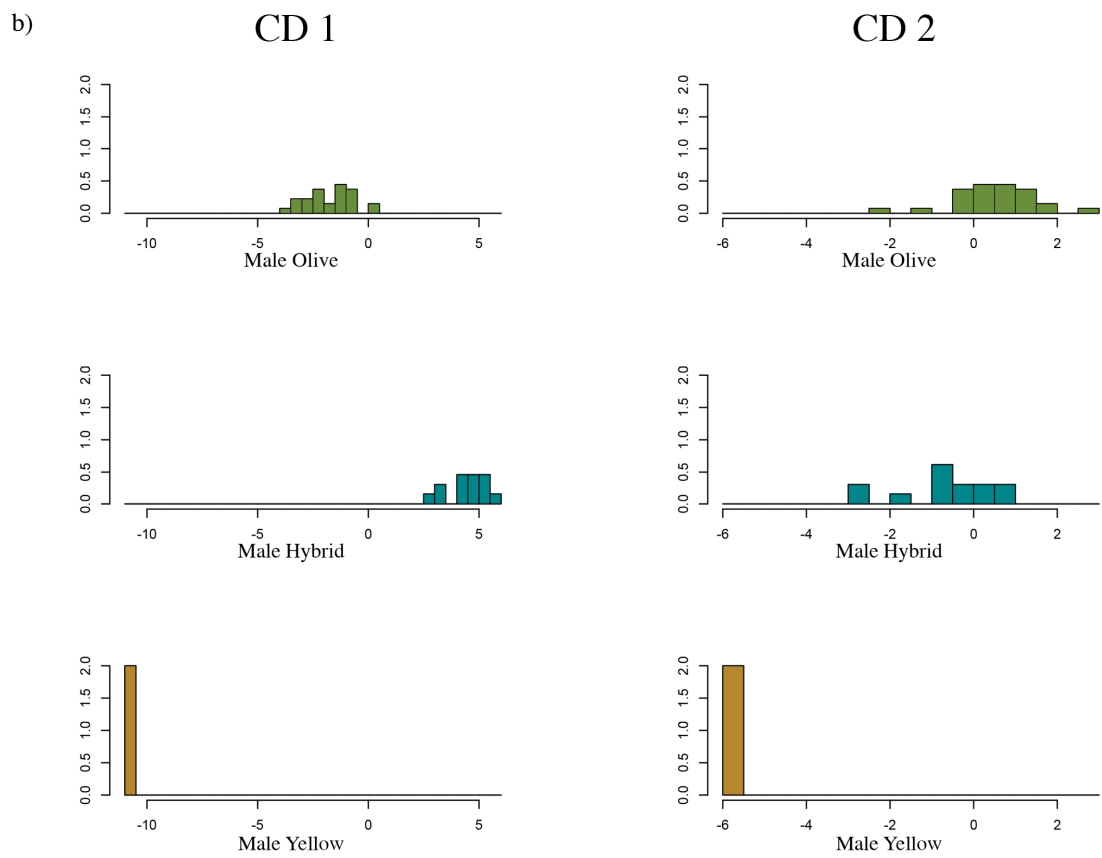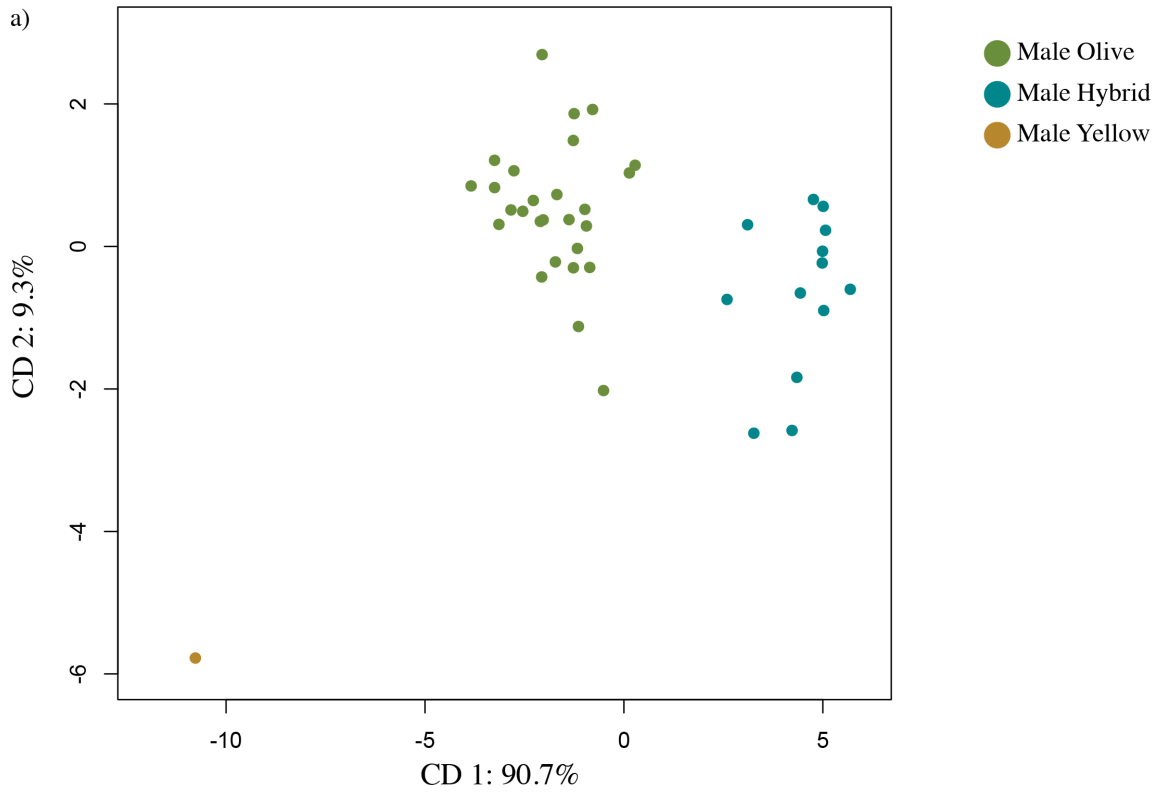
Previous page (pg 182)

Figure 12 a) The canonical score plot of CDA of male baboons successfully separated taxa along CD 1, with yellow to the left, then olive, then hybrid on the right, and along CD 2 with olive and hybrids near the top and yellow near the bottom. b) Histograms of each group for CD 1 and CD 2 similarly show separation between groups with some overlap.

Following page (pg 184)

Figure 13 a) The canonical score plot of CDA of male baboons, not including the single male yellow, successfully separated taxa along CD1, with olive to the left and hybrid to the right. There is no CD 2 because only two groups were analyzed and the number of canonical discriminant functions that can be calculated is equal to the number of groups minus 1. The CD 1 scores were distributed along the y-axis based on specimen ID number in order to see all of the scores. The y-axis should, therefore, not be used in the interpretation of this CDA. b) Histograms of each group for CD 1 similarly show separation between groups with some overlap.

a)

b)

CD 1

a)

b)

CD 1

C D2
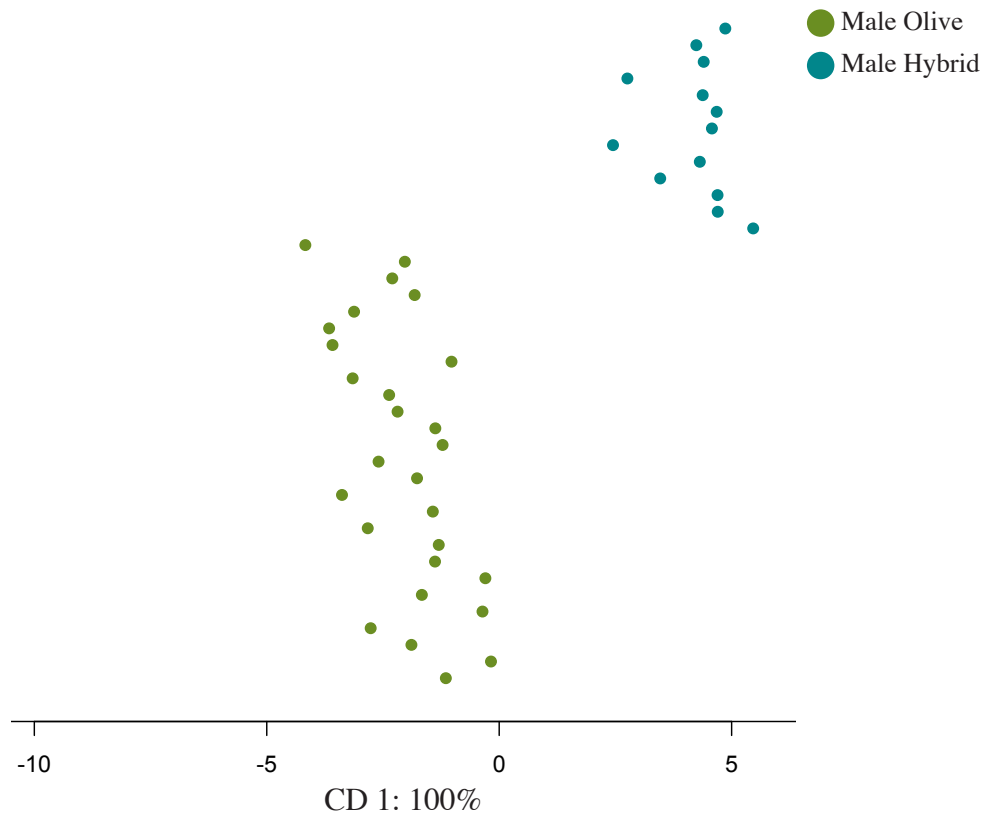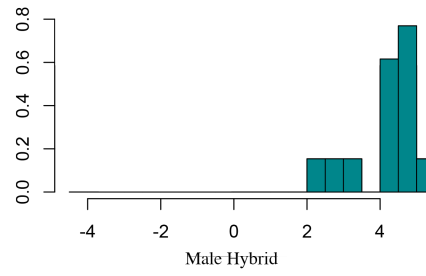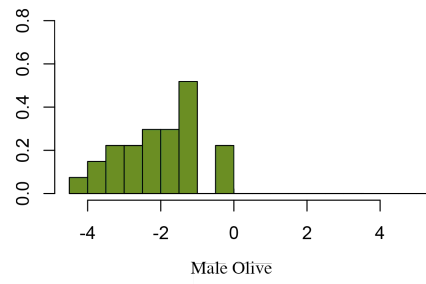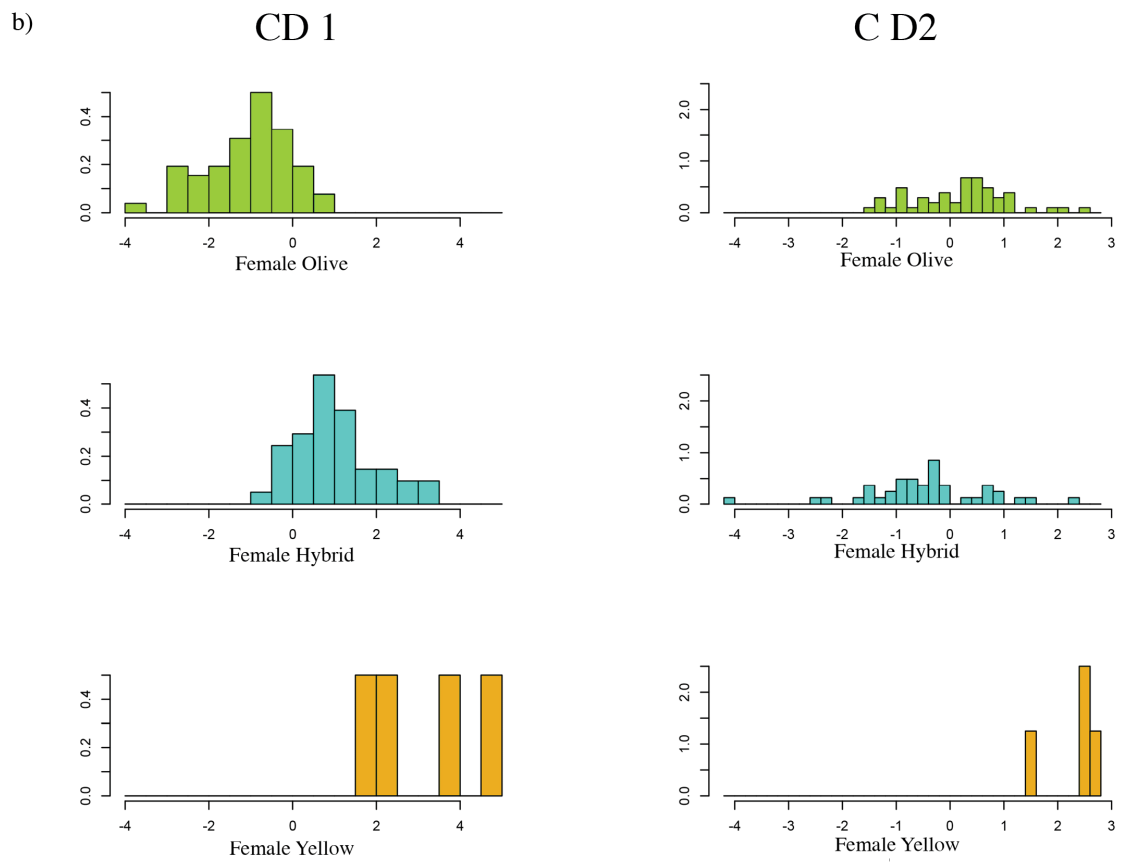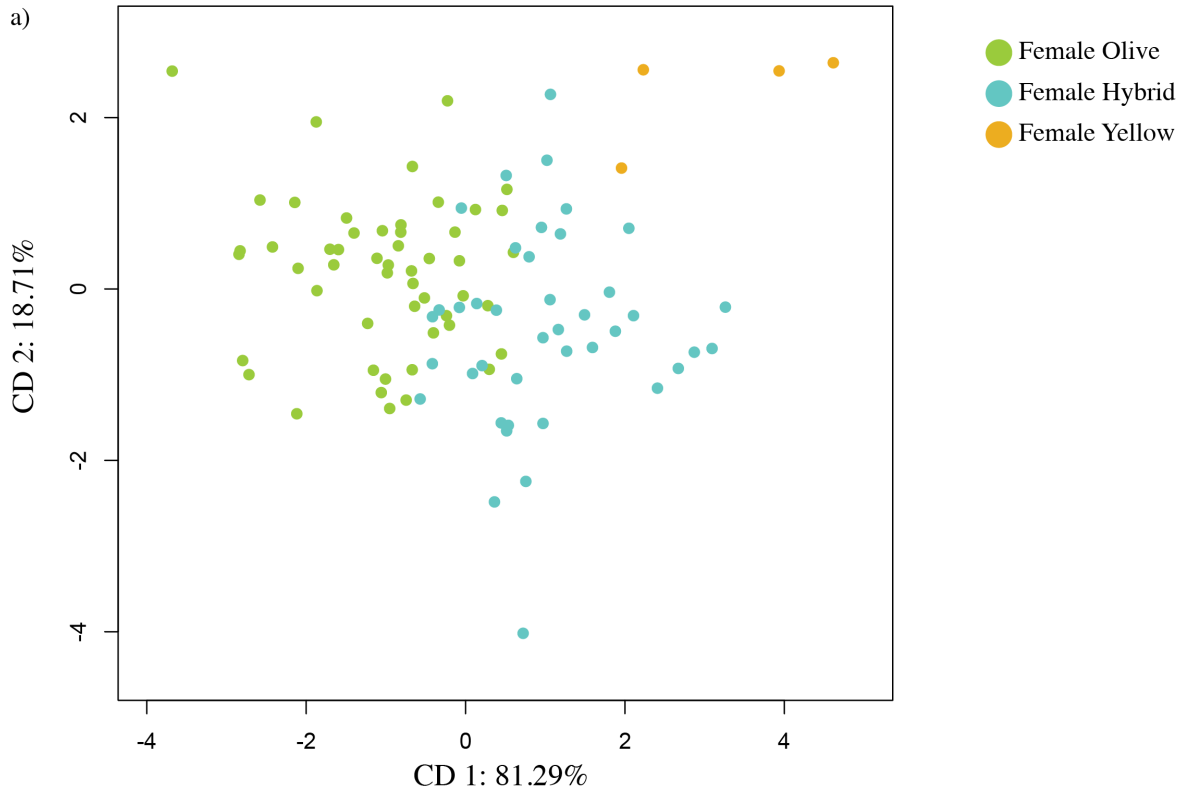
Figure 14 a) The canonical score plot of CDA of female baboons successfully separated taxa along CD1, with olive to the left and hybrid to the right, and along CD2 with yellow grouping greater than 0, while olive and hybrids remain centered around 0. b) Though the groups separate, the overlap between taxa is more obvious in the histograms of CD 1 and CD 2.

a)
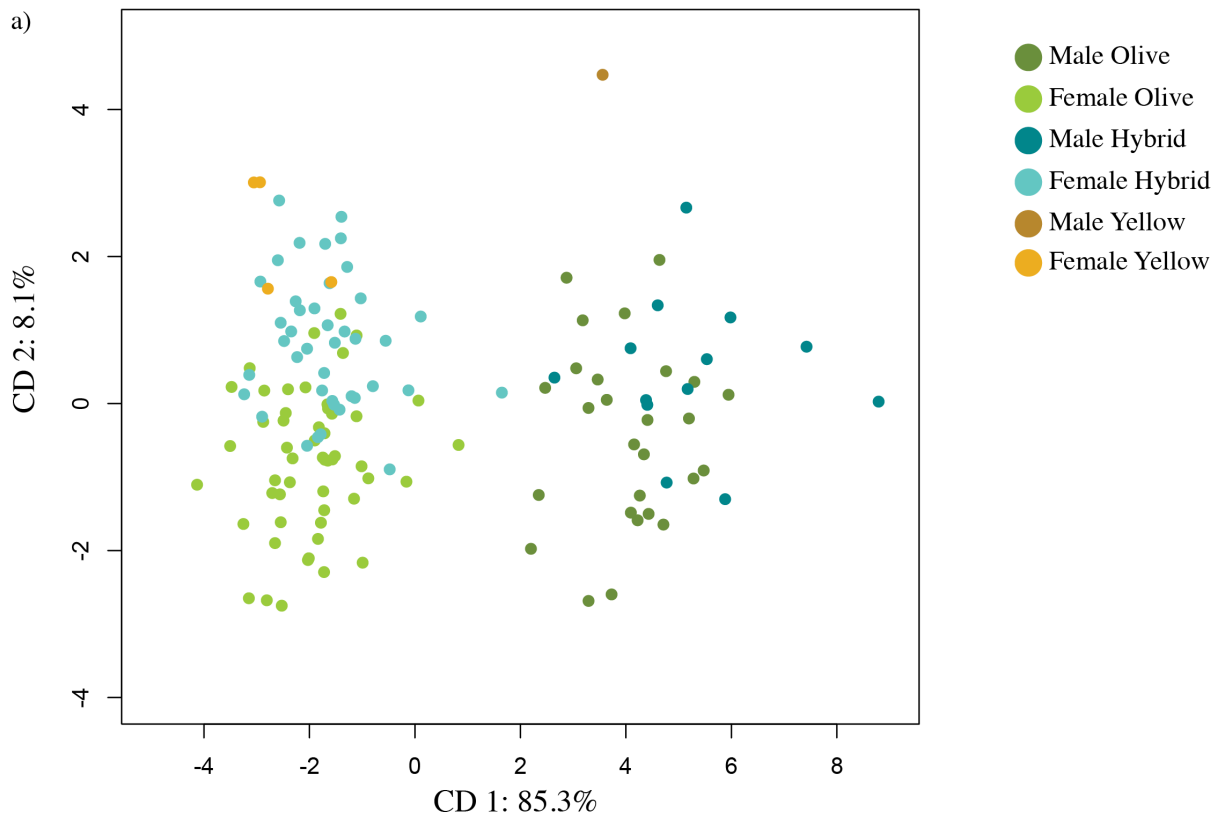
Figure 15 a) The canonical score plot of CDA of all baboons prior to the correction for sexual dimorphism successfully separated sex along CD 1, with males to the left and females on the right, and separated taxa along CD 2 with yellow and hybrids greater than 0 and olives less than 0. Most separation observed is due to sex along CD 1, where males and females are substantially separated as shown in the histograms. b) The histograms of CD 2 show only minimal separation between taxa. (Figure continued on page 187)

b)

CD 1

CD 2

Female Olive

Male Olive

Female Hybrid

Male Hybrid

Female Yellow

Male Yellow

187
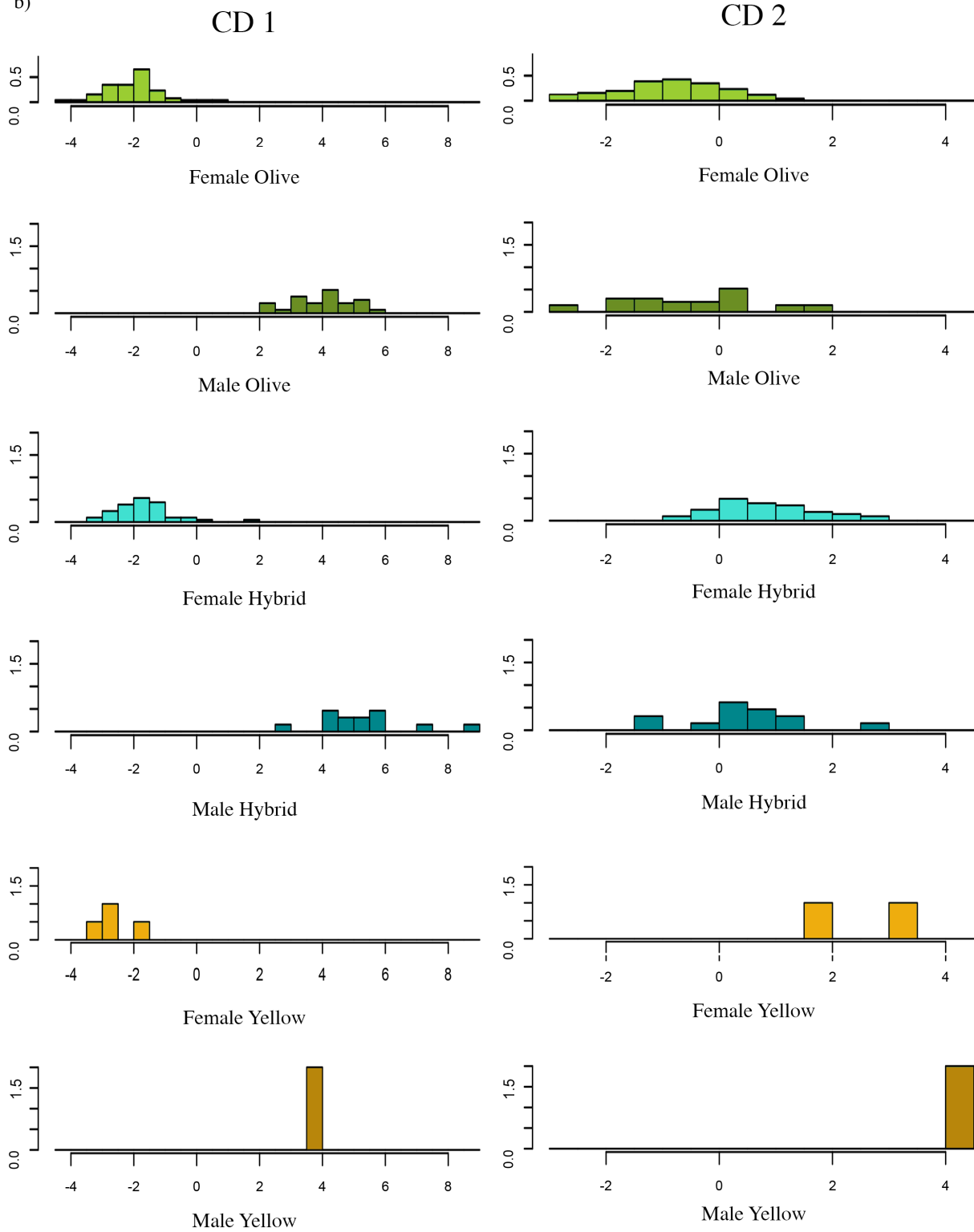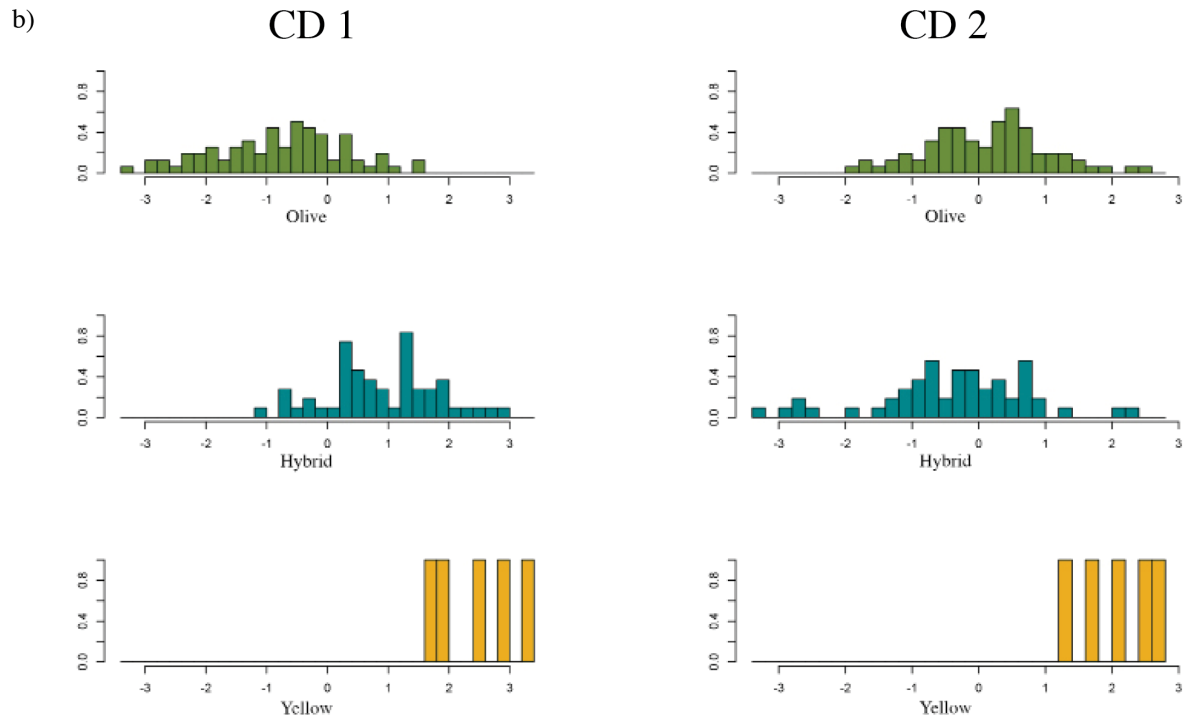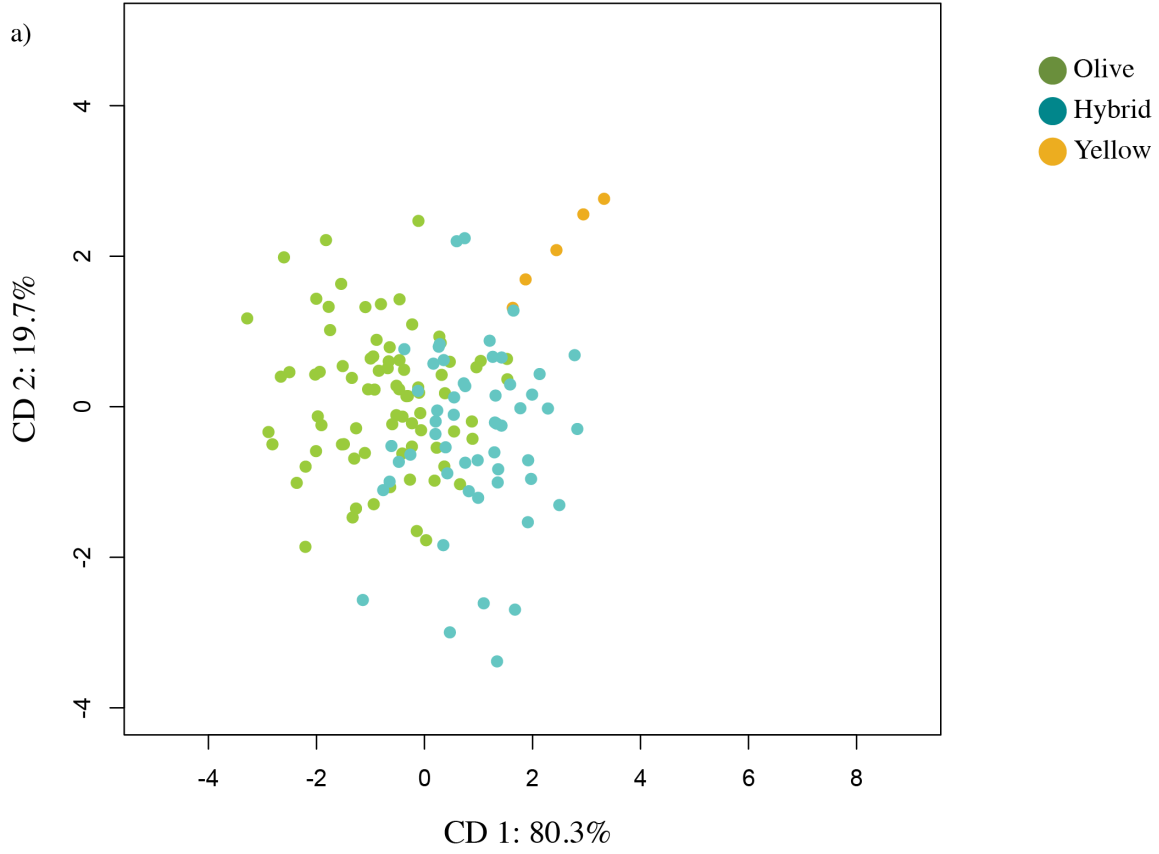
Previous page (pg 188)

Figure 16 a) The canonical score plot of CDA of all baboons after the correction for sexual dimorphism successfully separated taxa along CD 1, with olive to the left and hybrid and yellow to the right. CD 2 separated yellow, with scores greater than 0, from olive and hybrid with scores centered around 0. b) The histograms of CD 1 and CD 2 more clearly show overlap between groups.

Following page (pg 190)

Figure 17 Photos and CT scans of examples of the seven analyzed nonmetric traits; features and variability of the trait are circled in red. Corresponding scoring is found inTable 10. a) Root of molar entered the nasal cavity; b) ectopic teeth in the nasal cavity: left has a score of 1, example on the right shows greater nasal cavity obstruction by the ectopic tooth with a score of 2; c) deviated septum: left is moderate with a score of 2, right is severe with a score of 3; d) division of the greater palatine canals: left has no division with a score of 0, right has division in both canals with a score of 2. e) The size of the lateral recess in the orbit: left is flat with a score of 0, middle is moderate with a score of 1, right is large with a score of 2; f) left shows the attached inferior nasal conchae in slice 3 with a score of 0, right shows unattached inferior nasal conchae in slice 3 with a score of 1; g) left shows the presence of the alae of the vomer in slice 4 with a score of 0, right shows the absence of the alae of the vomer in slice 4 with a score of 1.
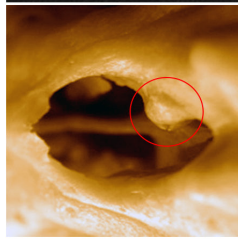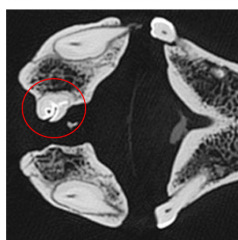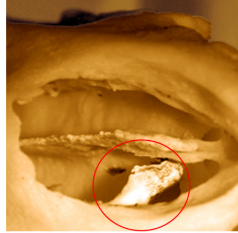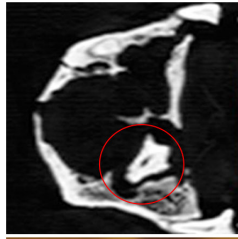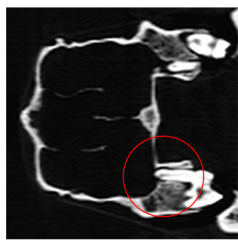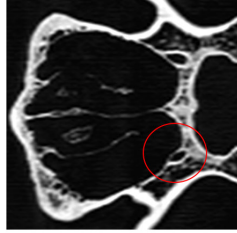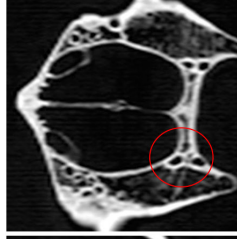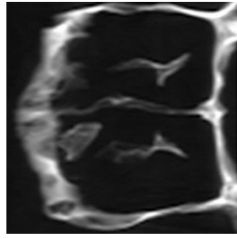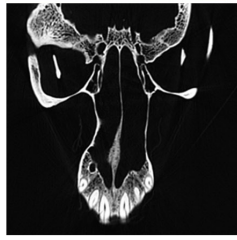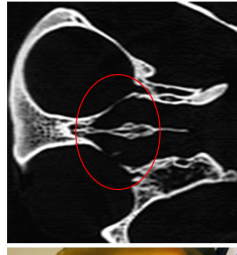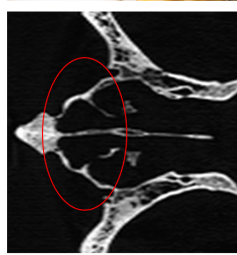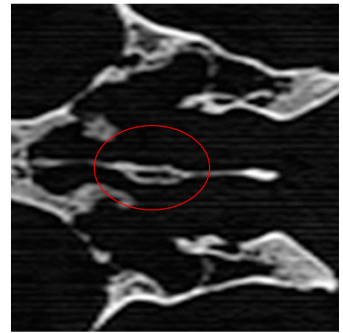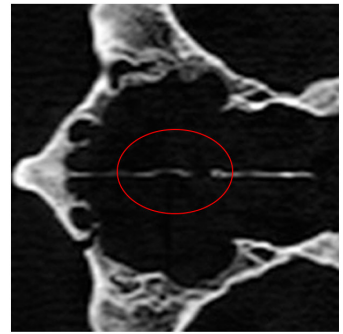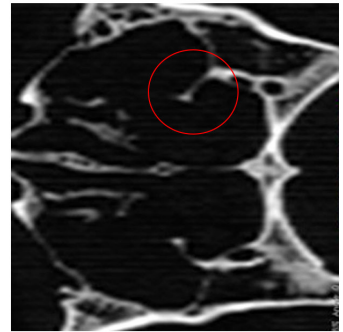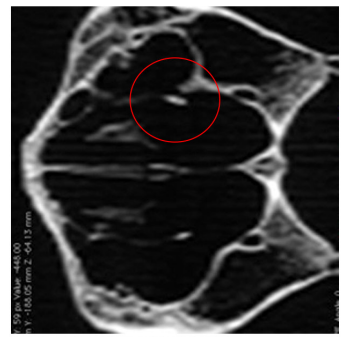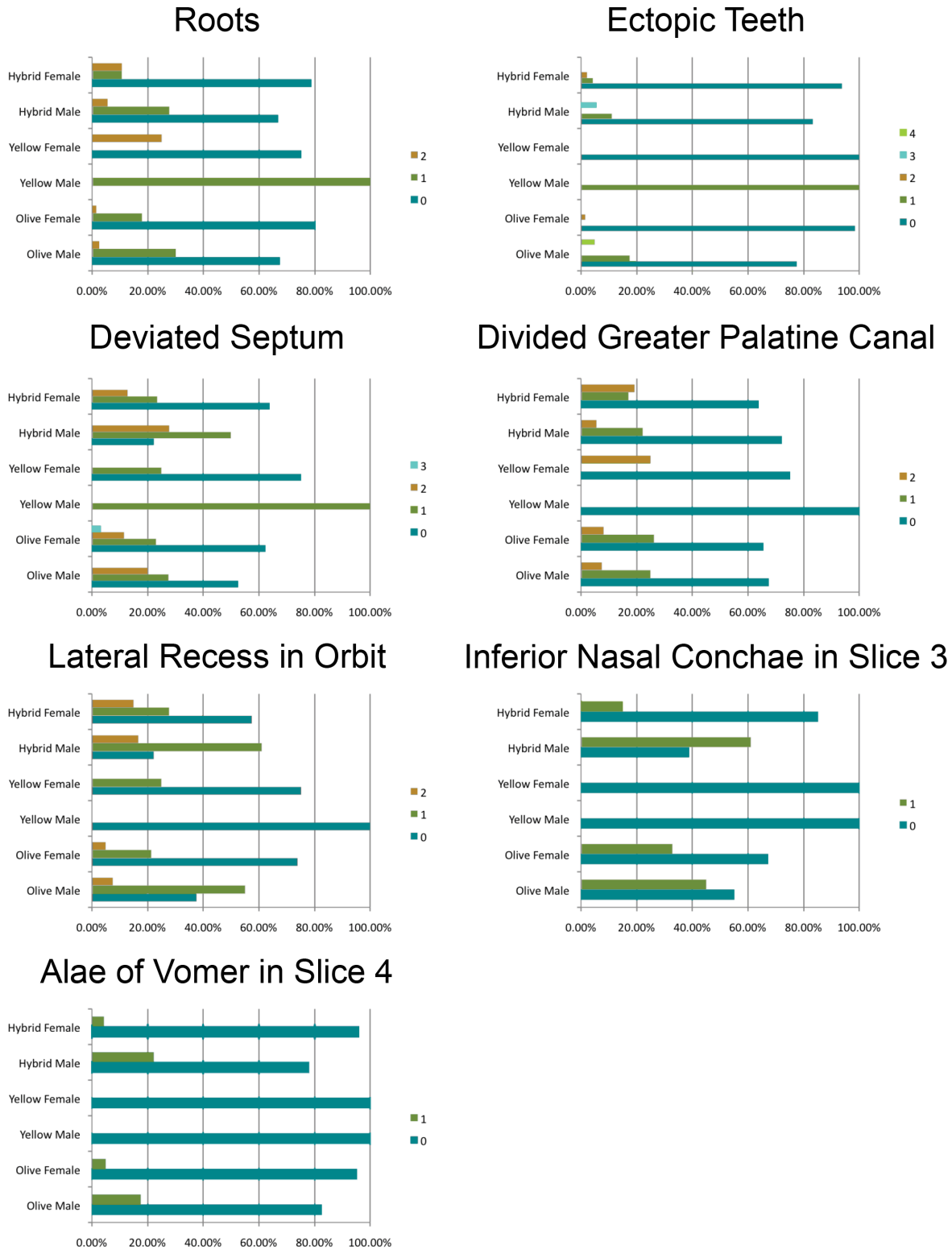
Figure 18 Bar graphs of the scores of each nonmetric trait for hybrid females, hybrid males, yellow females, yellow males, olive females, and olive males. Related statistical tests are presented in Table 11.

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