Abstract

Dental topography has successfully predicted the diets of species in several extant and extinct mammalian clades. However, dental topographic dietary reconstructions have high success rates only when closely related taxa are compared. Given the dietary breadth that exists among extant apes and likely existed among fossil hominins, dental topographic values from many species and subspecies of great apes are necessary for making dietary inferences about the hominin fossil record. Here, we present the results of one metric of dental topography, Dirichlet normal energy (DNE), for seven groups of great apes (Pongo pygmaeus pygmaeus, Pan paniscus, Pan troglodytes troglodytes and schweinfurthii, Gorilla gorilla gorilla, Gorilla beringei graueri and beringei). DNE was inadequate at differentiating folivores from frugivores, but was adequate at predicting which groups had more fibrous diets among sympatric African apes. Character displacement analyses confirmed there is substantial dental topographic and relative molar size (M1:M2 ratio; length, width, and area) divergence in sympatric apes when compared to their allopatric counterparts, but character displacement is only present in relative molar size when DNE is also considered. Presence of character displacement is likely due to indirect competition over similar food resources. Assuming similar ecological conditions in the Plio-Pleistocene, the derived masticatory apparatuses of the robust australopithecines and early Homo may be due to indirect competition over dietary resources between the taxa, causing dietary niche partitioning. Our results imply that dental topography cannot be used to predict dietary categories in fossil hominins without consideration of ecological factors such as dietary and geographic overlap. In addition, our results may open new avenues for understanding the community compositions of early hominins and the formation of specific ecological niches among hominin taxa.
Introduction

Plio-Pleistocene hominin dietary ecology has been the focus of many studies over the past century (e.g. Dart, 1934; Jolly, 1970; Teaford and Ungar, 2000; Smith et al., 2005, 2015; Ungar et al., 2006a; Ungar, 2007; Strait et al., 2009, 2013; Berthaume et al., 2010; Grine et al., 2010, 2012; Ungar and Sponheimer, 2011; Daegling et al., 2013). Dietary ecology is inferred by determining the properties of the foods hominins consumed (e.g. isotropic (Sponheimer et al., 2013), microwear/microwear textural analyses (Ungar et al., 2008; Ungar, 2011; Ungar and Sponheimer, 2011), and dental calculus analysis (Henry et al., 2012)) or from aspects of morphology that suggest what the hominins may have been adapted to consume (e.g. morphological studies of the cranium, mandible, and/or the teeth (Spencer, 2003; Ungar, 2004; Smith et al., 2005; Lucas et al., 2008; Berthaume et al., 2010; Constantino et al., 2010; Skinner et al., 2015)). As with many studies dealing with extinct taxa, having an appropriate comparative dataset of extant taxa helps interpret how mechanical properties and morphology might relate to dietary ecology (Wood and Schroer, 2012), but see (Michael A. Berthaume, 2016). In the case of the hominins, a common extant reference is the great apes.

One recently developed method that has been successful in correlating dietary ecology to postcanine tooth shape is dental topography. Dental topography is the quantification of occlusal tooth shape using geographic information system (GIS) software (Zuccotti et al., 1998). Since its development, dental topography has broadened to include several other non-GIS specific metrics, such as Dirichlet normal energy (DNE; Bunn et al., 2011; Winchester et al., 2014) and ambient occlusion (portion de ciel visible or “portion of visible sky,” PCV; Berthaume, 2016b; Berthaume and Winchester, unpublished). Several studies have been conducted using dental topography to reconstruct the diets of extinct primates (see Table 1), all of which have compared the extinct taxa to closely related extant taxa. This is important as the same dental topographic score can be correlated to different dietary categories...
in different extant samples (Winchester et al., 2014), meaning a distantly related extant sample can lead to erroneous results. In the case of the hominins, this means using a sample that does not consist solely or partially of the great apes. What remains consistent across clades, however, is that a higher dental topographic score indicates a more insectivorous/folivorous/fibrous diet, while a lower dental topographic score indicates a more omnivorous/frugivorous/harder diet (Boyer, 2008; Bunn et al., 2011; Godfrey et al., 2012; Winchester et al., 2014; Allen et al., 2015). Two studies have used dental topography to better understand the dietary ecology of the hominins (Ungar, 2004, 2007), relying on the same extant sample (*Gorilla gorilla gorilla* and *Pan troglodytes troglodytes*). These apes are highly frugivorous, and do not capture the dietary or morphological variability that exists across populations of extant apes. Including a sample of apes that cover a larger dietary diversity may alter how we interpret the hominin record.

*Dietary Variability in the Great Apes*

Great apes are primarily frugivorous, with the exception of two primarily folivorous subspecies of *Gorilla beringei*. *Gorilla beringei beringei* is found in two populations: one in the Bwindi Impenetrable National Park (Uganda) and the other in the Virunga volcanoes (Uganda, Rwanda, and the Democratic Republic of Congo). These high-altitude environments, particularly in the Virunga volcanos, provide little to no fruit (Tutin and Fernandez, 1985; Hladik, 1988; Watts, 1990; Yamagiwa et al., 1992; Rogers et al., 2004), and as a consequence, *G. b. beringei* is highly folivorous (Robbins and McNeilage, 2003; Elgart-Berry, 2004; Ganas et al., 2004; Rothman et al., 2007). *Gorilla beringei graueri* lives in eastern portions of the Democratic of Congo in an environment that provides *G. b. graueri* more fruit than *G. b. beringei*. However, *G. b. graueri* still consumes more folivorous than frugivorous matter, and we classify *G. b. graueri* as a folivore (Yamagiwa et al., 1992, 1994, 1996, 2005).
The remaining species of great apes (i.e. *Gorilla gorilla*, *Pan troglodytes*, *Pan paniscus*, *Pongo abelii* and *Pongo pygmaeus*) are frugivores, though the pattern and degree of frugivory differs among these species. *Gorilla gorilla* is broken into two subspecies (*G. g. gorilla* and *G. gorilla diehli*) which are both primarily frugivorous, but also consume a significant amount of terrestrial and aquatic herbaceous vegetation. *Gorilla gorilla* predictably consumes more herbaceous vegetation during times when fruit is less available (Rogers et al., 2004) and *G. g. diehli* is somewhat less frugivorous than *G. g. gorilla*, potentially because of reduced fruit availability in its habitat (McFarland, 2007).

There are four subspecies of chimpanzees (*P. t. troglodytes*, *P. troglodytes schweinfurthii*, *P. troglodytes ellioti*, and *P. t. verus*) and one species of bonobos (*P. paniscus*). Eastern chimpanzees (*P. t. ellioti*, *P. t. troglodytes* and *P. t. schweinfurthii*) are found across central Africa and are broadly sympatric with species of *Gorilla*. *Pan troglodytes troglodytes* is frugivorous, but differs from sympatric *G. g. gorilla* in that *P. t. troglodytes* is a fruit pursuer, consumes fruit year-round and prefers compliant, ripe fruit, only consuming mechanically challenging fruits like figs during fallback episodes (Kuroda et al., 1996). Meanwhile *G. g. gorilla* is an opportunistic frugivore and falls back on more fibrous, folivorous matter (Tutin and Fernandez, 1985, 1993; Tutin et al., 1991; Wrangham et al., 2003; Head et al., 2011). The range of *P. t. schweinfurthii* includes the range of *G. b. graueri* (Yamagiwa and Basabose, 2006; Yamagiwa et al., 2012) and one population of *G. b. beringei* in Bwindi Impenetrable Forest, Rwanda (Stanford and Nkurunungi, 2003). Unlike the gorillas it is sympatric with, *P. t. schweinfurthii* consumes the same amount of fruit year-round, regardless of fruit availability (Nishida and Uehara, 1983; Yamagiwa et al., 1996; Reynolds et al., 1998). *Pan troglodytes schweinfurthii* differs from *P. t. troglodytes* in that it is more folivorous and consumes mechanically challenging figs year-round (Yamagiwa and Basabose, 2006). *Pan troglodytes ellioti* occupies a range north of *P. t. troglodytes*, where it is sympatric with both subspecies of *G. gorilla*. Although dietary data on *P. t. ellioti* is not as common as with the other subspecies of chimpanzees, it appears to have a diet similar to *P. t.*
*schweinfurthii*, seasonally consuming non-fruit matter including insects, animal matter, and honey, and consuming large quantities of figs year-round (Dutton and Chapman, 2015).

The western savanna chimpanzee, *P. t. verus*, can be found in Senegal, Mali, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Côte D’Ivoire, and Ghana, while the bonobo (also called the pygmy chimpanzee), *P. paniscus*, is endemic to the Democratic Republic of Congo. These are the only two (sub)species of *Pan* that are completely allopatric to *Gorilla, P. t. verus and P. paniscus*. *Pan troglodytes verus* appears to have a more restricted diet compared to *P. t. troglodytes* and *P. t. schweinfurthii*, consuming fewer types of foods, with animal matter making up a larger percentage of its diet (Mcgrew et al., 1988; Pruetz, 2006). Like other chimpanzees, it is primarily frugivorous. *Pan paniscus* is also primarily frugivorous, but consumes a large amount of terrestrial herbaceous vegetation and has been described as having a diet intermediate between gorillas and chimpanzees (Kano and Mulavwa, 1984; Malenky and Stiles, 1991). Although bonobos have been described to consume less vertebrate matter than chimpanzees, they can be vicious hunters, searching out and consuming larger mammals such as duiker, often beginning to consume the animals before they are killed (Fruth and Hohmann, 2002).

There are three subspecies of Bornean and one species of Sumatran orangutan which are found in Indonesia and Malaysia. All orangutans are primarily frugivorous, with diets sometimes consisting entirely of ripe fruit, particularly during times of extreme fruit abundance (i.e., masting events, Taylor, 2006; Kanamori et al., 2010). However, Sumatran orangutans (*Pongo abelii*) consume more ripe fruit and less mechanically challenging foods than Bornean orangutans (Vogel et al., 2014). There is also dietary variation among the three subspecies of Bornean orangutans (*P. pygmaeus morio, P. pygmaeus pygmaeus*, and *P. pygmaeus wurmbii*), with *P. p. morio* consuming more leaves and bark than *P. p. wurmbii* (Kanamori et al., 2010). Little is known about how the diet of *P. p. pygmaeus* compared to the other subspecies of *P. pygmaeus* (Vogel, personal communication).
Great apes are valuable referents for studies of fossil hominins due to their genetic similarities, similar body size, and similar life histories. The propensity for populations of *Gorilla* and *Pan* to overlap and negotiate broadly overlapping diets also lends itself to the study of dietary ecologies among fossil hominins. Recent fossil discoveries suggest that overlap among hominin taxa is an increasingly likely ecological scenario (Swisher et al., 1996; Spoor et al., 2007; Pickering et al., 2011; Leakey et al., 2012) and that dietary divergence between hominin groups may have occurred near the origin of *Homo* (William M. Schaffer, 1968; Wood and Strait, 2004; Ungar et al., 2008; Cerling et al., 2011, 2013; Ungar, 2011; Ungar and Sponheimer, 2011; Schroer and Wood, 2015; Spoor et al., 2015). Dietary overlap is a selective force on many animal populations (Mayr, 1966; Schoener, 1971, 1982; Roughgarden, 1976; Goldberg and Barton, 1992; Webb et al., 2002; Johnson and Stinchcombe, 2007; Emerson and Gillespie, 2008; Cavender-Bares et al., 2009), and determining eras of overlap is fundamental for reconstructing the emergence and maintenance of hominin dietary niches. Quantifying dental topography in subspecies of extant apes presents a unique opportunity to test for signals of dietary overlap and competition, and to determine whether similar signals may be recovered in the fossil record.

Character displacement is an evolutionary phenomenon by which sympatric taxa (i.e. taxa that overlap geographically and temporally) indirectly or directly compete with each other, causing selective pressures and consequently inducing population-level evolutionary changes. These changes can be detected through comparison with allopatric (i.e. isolated and non-overlapping) populations of the same taxa, which do not experience competition with one another and subsequently have different selection pressures. Character displacement can be assessed at taxonomic levels higher than the species or subspecies level (73, 111, 113, 114), so long as the allopatric taxa share the same phylogenetic distance as the sympatric taxa. Character displacement encompasses a number of different ecological
mechanisms, including both direct and indirect competition for dietary resources (Abrams and Cortez, 2015). Such a diversity of potential mechanisms can be seen in the living great apes, particularly among populations of *Gorilla* and *Pan* who have similar ecological needs and can have broadly overlapping ranges and diets (Figure 1; Tutin and Fernandez, 1993; Yamagiwa et al., 1996; Stanford and Nkurunungi, 2003; Yamagiwa and Basabose, 2006, 2009; Head et al., 2011).

Although gorillas and chimpanzees tend to avoid each other (Yamagiwa and Basabose, 2006), particularly during feeding, this is not always possible and can lead to both peaceful interactions such as co-feeding (Suzuki et al., 1995; Tutin, 1996; Stanford and Nkurunungi, 2003; Yamagiwa and Basabose, 2006) and aggressive displays by chimpanzees toward gorillas (Kuroda et al., 1996; Yamagiwa et al., 1996; Stanford and Nkurunungi, 2003). Physical altercations have never been reported due to feeding competition between the species. Encounters are also more likely to occur during times of fruit scarcity (i.e. during fallback episodes) (Stanford and Nkurunungi, 2003; Yamagiwa and Basabose, 2006). Though direct competition over resources is relatively sparse between gorillas and chimpanzees, indirect competition is relatively high. Sympatric gorillas and chimpanzees broadly consume the same food resources, each diminishing the availability of food for the other species (Tutin et al., 1991; Tutin and Fernandez, 1993; Kuroda et al., 1996; Tutin, 1996; Yamagiwa et al., 1996; Stanford and Nkurunungi, 2003; Yamagiwa and Basabose, 2006). Such indirect resource competition has been hypothesized to act as a selective pressure that leads to adaptations in the masticatory apparatus and digestive system in gorillas (to allow them to have a higher fiber diet) and in the locomotor and social system in chimpanzees (that permits fission-fusion societies and increased home ranges) (Yamagiwa and Basabose, 2009). Behavioral differences do not preclude the possibility that character displacement has occurred in the masticatory apparatuses of both species (Schoener, 1971; Yamagiwa and Basabose, 2006). It is possible that sustained dietary overlap has left a morphological signature in the jaws and teeth of both sympatric gorillas and chimpanzees that could manifest itself as character displacement.
Character displacement analysis can detect these potential signatures by quantifying the differences in morphology between pairs of sympatric and allopatric taxa. When the difference observed in sympatric taxa is greater than the difference observed in allopatric taxa, competition (direct or indirect) is implicated. Character displacement analysis can use behavioral characters (L. and O., 1956; Husar, 1976; Gerhardt, 1994; Allen et al., 2014) or morphological characters (William M. Schaffer, 1968; Malmquist, 1985; Schluter and McPhail, 1992; Dayan and Simberloff, 1994, 2005; Losos, 2000; Schluter, 2000; Simberloff et al., 2000; Collyer and Adams, 2007; Davies et al., 2007; Schroer and Wood, 2015), provided these characters are ecologically-informed (Yom-Tov, 1991; Schluter and McPhail, 1992; Jones, 1997; Dayan and Simberloff, 2005; Grant and Grant, 2006; Albert et al., 2007). Gnathic and dental structures correlate with diet (Kay, 1975; Lucas and Luke, 1984; Maier, 1984; Lucas et al., 1986b; Lucas, 2004; Berthaume, 2014; Schroer and Wood, 2015) and jaws and teeth are often the source of morphological data for character displacement analyses (Malmquist, 1985; Dayan et al., 1989, 1990; Schluter and McPhail, 1992; Jones, 1997; Adams and Rohlf, 2000; Schroer and Wood, 2015). Character displacement analysis can accommodate any taxonomic level, including different genera (Dayan et al., 1990; Monroe, 2012; Schroer and Wood, 2015) and guild structures (Schluter, 1986), although the degree of evolutionary distance between the sympatric taxa and between the allopatric taxa must be the same. Character displacement has not been widely integrated with dental topography metrics (but see Boyer et al., 2012), and our study provides a test-case of its utility for understanding dental morphological variation among extant apes.

In this study, we conduct two related analyses: a comparison of one metric of dental topography (DNE) among seven species and subspecies of great apes with varying diets, and a character displacement analysis of the resulting DNE scores. In our dental topographic comparison, we test two hypotheses. First, that more folivorous apes with more fibrous diets (G. b. beringei and G. b. graueri) will have higher DNE scores than the more frugivorous apes with less fibrous diets (P. t. schweinfurthii,
Second, the apes that consume the “hardest” foods (P. t. schweinfurthii and P. pygmaeus) will have the lowest DNE scores. In the character displacement analysis, we test whether the overlapping subspecies of Gorilla and Pan have greater divergence in dental topographic scores. If competition over food resources, indirect or otherwise, is occurring in populations of apes and affecting dental morphology, then character displacement analysis should uncover greater divergence in DNE scores among sympatric, but not allopatric, taxa.

As previous character displacement analyses on the masticatory apparatus have frequently relied on linear and size measurements, data on M₁ and M₂ tooth size (width, length, and size) was gathered on the same specimens and submitted to a character displacement analysis. Tooth size is roughly correlated with diet in primates, with more folivorous primates having larger teeth (e.g. (Lucas, 2004; Boyer, 2008; Winchester et al., 2014)). Given the high level of sexual dimorphism in great ape tooth size (Swindler, 2002), either sex must be kept constant or relative tooth size must be used. There is some evidence suggesting a distally expanding tooth row may be correlated to the degree of folivory in some primates (e.g. (Lucas et al., 1986a; Teaford and Ungar, 2000)), but this is largely confined to M₁:M₃ ratio. Given the difficulties in obtaining a single sex or a balanced mixed sex sample with minimal wear and well preserved, erupted M₃’s, we used an unbalanced mixed sample and excluded the confounding effects of body by investigating relative molar size, which was quantified using M₁:M₂ ratio.

Should the relative molar size analyses yield the same results, it would suggest that relative molar size can be reliably used in lieu of DNE in future studies. This would be useful to researchers, as relative molar size is preserved in the fossil record and in museum specimens more frequently than tooth shape, quantified by DNE.

Materials and Methods
A mixed sex sample of 44 frugivorous and 17 folivorous ape M2’s were chosen for analysis. Teeth with minimal wear were chosen (i.e. no or low levels of dentin exposure), as dental topographic measurements are known to be highly sensitive to tooth wear (Ungar and Williamson, 2000; M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Ungar, 2004; Klukkert et al., 2012; Venkataraman et al., 2014). This resulted in a mixed sample of left and right molars, but no antimeres from the same individual were used in the study. As the potential effects of sex or bilateral asymmetry on dental topographic measurements have yet not been investigated, we cannot say whether or not these assumptions will have an effect on our results. In Pan troglodytes verus, small sex based differences have been observed hypocone sharpness (Stuhltraeger et al., 2016), but this could be due to allometry, as males tend to have larger teeth (Swindler, 2002) and cusp size is positively correlated with cusp sharpness (Berthaume, 2014). While some studies have found small sexual differences in ape diet (e.g. differences in nut and meat consumption in Pan (Boesch and Boesch-Achermann, 2000)), other studies have found no systematic differences between male and female diet (e.g. (Doran et al., 2002)). There is also the possibility that, even if there are sex-based differences in diet, they will not manifest in dental morphology due to genetic similarities between males and females of the same species. Here, our sample is too small to meaningfully analyze male and female data separately, and we thus pool sexes.

Second molars were chosen because their structure is usually representative of the postcanine mandibular tooth row (Kay, 1975; Sheine and Kay, 1977), and they have been shown to contain a dietary signature in dental topographic studies on platyrrhines and prosimians(Godfrey et al., 2012; Ledogar et al., 2013; Winchester et al., 2014; Boyer et al., 2015). This does not preclude other postcanine teeth from also carrying dietary signatures (Kay, 1975, 1981, Sheine and Kay, 1977, 1982; Berthaume, 2014; Allen et al., 2015; Boyer et al., 2015).
Character displacement analysis is improved by an understanding of how long populations have been sympatric. Hypothetically, populations sympatric for a longer time will have a higher level of specialization than populations sympatric for a shorter time. However, length of sympathy is often unknown or poorly understood, and character displacement can be detected even in species phylogenetically close enough to hybridize (90). The effects of the so-called “ghost of competition past” imply that while the timing and duration of character displacement cannot easily be pinpointed, the contribution (or not) of sympatric pressures on morphological evolution can (Pritchard and Schluter, 2001). It is therefore possible to detect character displacement (in morphological characters) in taxa that have both sympatric and allopatric populations if gene flow has occurred from the sympatric to the allopatric populations. This would make the exact location of the individuals used in the character displacement analysis irrelevant. Exact location of individuals from the allopatric taxa is always irrelevant in the character displacement analysis. Due to the difficulties in obtaining an ideal sample (due to variation in tooth wear, and year and site at which specimens were collected), we are assuming that, due to gene flow, tooth shape and size is relatively homogeneous within each subspecies.

The frugivorous apes included in this study were *G. g. gorilla*, *P. t. troglodytes*, *P. p. pygmaeus*, and the folivorous apes were *G. b. beringei* and *G. b. graueri* (Table 2). Two pairs of sympatric apes (*G. g. gorilla* and *P. t. troglodytes*, and *G. b. graueri* and *P. t. schweinfurthii*), and one pair of allopatric apes (*P. paniscus* and *G. b. beringei*) were chosen for the character displacement analysis. While *P. p. pgymaeus* was included in the dental topographic analysis, it was excluded from the character displacement analysis because the genetic distance between *Pongo* and the African apes exceeds the genetic distance between *Gorilla* and *Pan*. Exact locations and sexes for each specimen can be found in the supplementary material.

Digital representations of the teeth were produced by taking laser scans of casts of the teeth, which are housed at the Paleoanthropology Laboratory at the University of Arkansas and were supplied
courtesy of Peter Ungar (Figure 2). Casts were produced by pouring translucent epoxy mixed with a pale pink pigment into high resolution negative molds of tooth rows of museum specimens (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Klukkert et al., 2012). Casts were coated with a thin layer of Magnaflux Spotcheck SKD-S2 Developer to aid the XSM multisensory scanner (Xystrum Corp., Turin, Italy) in picking up the surface of the tooth (Ungar, 2004; Berthaume, 2014). 2.5D scans of the teeth were taken, with teeth in anatomically correct position such that the y-axis ran in the mesiodistal direction, the x-axis ran in the buccolingual direction, and the z-axis ran in the superior-inferior direction, with the most distal molar closest to the origin of the scan. (2.5D scans are scans where a surface is a projection of a plane into the 3rd dimension. In this case, this means there is one height coordinate for each pair of length and width coordinates.) Scans were taken at a resolution of 50 µm, resulting in point cloud representations of the teeth that had a resolution of 400 data points per square millimeter.

Dental topographic analyses can be performed with the entire enamel crown (Boyer, 2008) or the superior portion of the occlusal surface (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003). DNE is relatively insensitive to the cropping method (Bunn et al., 2011). As it is not possible to capture the entire tooth crown with this laser scanner, we chose the latter cropping method, using just the superior portion of the occlusal surface.

DNE is a summative metric that measures the curviness of a 2.5D or 3D surface constructed by triangles, meaning it is sensitive to the number of triangles in a mesh. Teeth meshed with more triangles have higher DNE scores than the same teeth meshed with fewer triangles, making it important to keep the number of triangles constant across all teeth. Triangular surface meshes of the tooth rows were constructed from the point clouds using the Delaunay Triangulation command in AVIZO 6.1 and saved as *.ply files. The 2.5D surfaces were imported into CloudCompare, where M2s were isolated and
all triangles inferior to the lowest point on the occlusal surface were deleted. Surfaces were again exported as *.ply files and reimported into AVIZO 6.1, where M₂s were simplified down to 19,990-20,000 triangles and smoothed using the Smooth Surface command (lambda=3, 100 iterations). This protocol is similar to that set forth in Bunn et al. (2011) with one distinct change: the molars in Bunn et al. (2011) were simplified down to 9,990-10,000 instead of 19,990-20,000 triangles. We chose to simplify our teeth to a larger number of triangles because we felt too much of the occlusal topography was lost at the lower resolution (i.e. crenulated teeth began to look like flat surfaces). While a significant amount of detail was still lost at the resolution used in this study, we felt it was a high enough to capture the general shape of the tooth (see Figure 3). This loss in resolution was not observed in crenulated platyrhine teeth (i.e. the *Pithecia* teeth used in Winchester et al., 2014) and implies there may be a size effect that needs to be taken into account when performing DNE (Winchester, personal communication). Furthermore, as two of the most commonly used dental topographic measurements (DNE and orientation patch count, OPC) are summative, measurements taken at different resolutions cannot be directly compared. The numerical results from this study are therefore not comparable to previous DNE studies; the patterns of results, however, are. To foster additional comparisons between studies, we have reported our results from lower resolution M₂s in the electronic supplementary material (ESM 1).

DNE was calculated in a beta version of MorphoTester, which is now available for download at http://morphotester.apotropa.com/ (Winchester, 2016), with 1% energy*area outlier removal. It is also possible to calculate DNE using a recently released R package named molaR (Pampush et al., 2016). Some teeth encountered the *CHOL error*, which prevents DNE from being calculated. For surfaces encountering this problem, it is recommended a 1 or 2-iteration Laplacian smooth be applied in Meshlab (Cignoni et al., 2008). As this can decrease DNE scores by around 20-30%, all teeth were imported into Meshlab and had 2 iterations of Laplacian smooth applied to them.
Determining the Presence of a Dietary Signature

The importance of controlling for phylogeny when deriving dietary signatures from tooth shape is well documented (Kay and Ungar, 1997; Ungar, 2004; Winchester et al., 2014; Allen et al., 2015). In order to control for phylogeny in our study, we used phylogenetically-corrected ANOVA with a Bonferroni correction to determine if DNE was correlated to diet. This was done using the Geiger package (Harmon et al., 2008) in R (R Development Core Team and Team, 2015), and a published primate phylogeny created using a supermatrix (Springer et al., 2012).

As there is no published phylogeny that differentiates apes at the subspecies level, we ran our phylogenetically corrected ANOVAs using the same protocol as in Berthaume (2014). Briefly, we created four trees, with each of the pair of subspecies splitting either 10,000 years after speciation (i.e. G. b. beringei and G. b. graueri split only 10,000 years ago (Figure 4)). This encompasses the full range of times in which subspecies may have divided. We then ran four phylogenetically-corrected ANOVAs, one with each tree. If the P-values were significant (p < 0.05) for all trees, this implied that our results were significant and robust. If the P-values were not significant (p > 0.05) for all trees, this implied that our results were robust but not significant. If the P-values were a mix of significant and not significant, we considered our results not robust. All P-values were adjusted using a Bonferroni correction for multiple comparisons.

Character Displacement

Character displacement analysis was used to test for significant differences between the DNE scores of sympatric and allopatric apes. Previous character displacement analyses on gnathic and dental morphologies have relied on linear and relative molar size measurements. Our study is among the first to use topographic measurements as input variables for character displacement analysis. In order to test the validity of our model and compare the results of our DNE analysis with previous character
displacement analyses, we ran three versions of the analysis: one with only relative molar size variables, one with only DNE scores, and a combined analysis of relative molar size variables and DNE scores. We obtained three relative molar size variables from the $M_1$s and $M_2$s of our specimens: the mesiodistal (MD) diameter, the buccolingual (BL) diameter, and the occlusal area. To obtain these measurements, we rotated surface reconstructions of our $xyz$ coordinates to obtain maximum occlusal area and imported a screenshot of the scaled tooth into TPSdig (Rohlf, 2009). Tooth diameters were maximum linear measurements and occlusal area was calculated from 20 semilandmarks equidistantly fitted around the occlusal margin. All measurements were log-transformed and, in order to reduce the number of variables in our model, we indexed our measurements by dividing the $M_1$ measurement with the corresponding $M_2$ measurement.

Three pairs of sympatric populations were included in our character displacement analysis: $P. t. troglodytes$ and $G. g. gorilla$, $P. t. schweinfurthii$ and $G. b. graueri$, and a combined sample of all sympatric Pan and all sympatric Gorilla. Our allopatric comparison for all three comparisons was $P. paniscus$ and a sample of $G. b. beringei$ from the Virunga Mountains, where gorillas do not overlap with chimpanzees.

General linear model

Character displacement is quantified as the displacement statistic $D_S - D_A$, where $D_S$ indicates divergence between sympatric taxa that may compete for resources and $D_A$ indicates divergence between allopatric taxa (Schluter and McPhail, 1992; Figure 5). When $D_S - D_A > 0$, competition is implicated, and significance can be determined by resampling the populations. To quantify divergence and perform resampling, we apply a general linear model derived from Collyer and Adams (2007).

A general linear model follows the form $Y = BX + U$. In our model, $Y$ is the morphological matrix of relative molar size or dental topography variables, $X$ is a matrix of general ecological conditions, and $U$ is
the residual error, which is assumed at zero. By dividing each side by $X$, we can solve for $B$, a matrix that translates the two matrices. The model is described in more detail in Schroer and Wood (2015), which includes examples of the matrices and an R-based script for conducting the analysis. Here, we summarize the most important elements of the analysis. Our raw data is provided in the supplementary material accompanying this manuscript (ESM 2) and at [DOI @ PUBLICATION].

The $X$ matrix uses dummy variables (i.e. Boolean indicators) to encode the ecological situation of individual specimens and reduce them to binary conditions. Each specimen belongs to one of four categories: a sympatric population of the first taxon, an allopatric population of the first taxon, a sympatric population of the second taxon, or an allopatric population of the second taxon. We subsequently assign each specimen a series of dummy variables. For taxonomic designations, each specimen in the first taxon is encoded as 1 and each specimen in the second taxon is encoded as -1. For the presence or absence of overlap, sympatric taxa are encoded as 1 and allopatric taxa are encoded as -1. The two values now given for each specimen are multiplied to give a third variable—the interaction of taxon and overlap.

Using the $X$ and $Y$ matrices, $B$ is solved. $B$ is a matrix of partial regression coefficients and effectively translates between the ecological conditions and morphological outputs. We can apply this matrix to the least squares mean of each of our four ecological groups (i.e. the two taxa in sympatry and the two taxa in allopatry). This results in four phenotypic change vectors, one for each population. The difference between vectors of the sympatric taxa is $D_s$, and the difference between vectors of the allopatric taxa is $D_a$. Subtracting these vectors from one another yields $D_s - D_a$, the character displacement statistic.

Using a probability distribution, we can determine whether the observed $D_s - D_a$ value is significant. To generate this probability distribution, we remove the interaction variable from the design matrix so that individuals remain encoded by their taxon and the presence/absence of overlap, but the...
interaction between these variables no longer creates an effect in the model. We solve again for the B matrix and randomly assign the residual effects to the least squares means of our four populations. This results in four different phenotypic change vectors, and from these vectors we derive a new $D_S-D_A$ value. We encode this value as 1 (greater than or equal to the observed $D_S-D_A$) or 0 (less than the observed $D_S-D_A$). We iterate this procedure 999 times to obtain a distribution of possible $D_S-D_A$ values from our randomized study sample and assume significance for our original, observed $D_S-D_A$ if it appears less than 5% of the time.

**Results**

DNE scores broadly overlapped between frugivorous and folivorous apes, with *P. p. pygmaeus* having a range of DNE scores that encompassed nearly all other apes (Figure 6). Phylogenetically-corrected ANOVAs revealed that DNE scores could not group apes based on their dietary categories (Tree1 $P=0.304$, Tree2 $P=0.381$, Tree3 $P=0.418$, Tree4 $P=0.319$). Non-phylogenetically corrected Mann-Whitney U-tests indicated statistically significant differences existed between sympatric gorillas and chimpanzees, with sympatric gorillas having higher DNE scores than sympatric chimpanzees (Table 3, significance at $P<0.0083$). Among *Gorilla* and *Pan*, *G. b. graueri* and *P. t. troglodytes* were found to have the highest and lowest DNE scores, respectively, suggesting that *G. b. graueri* has the most fibrous diet and *P. t. troglodytes* had the least fibrous diet among African apes. *Pan troglodytes troglodytes* had significantly lower DNE scores than all other apes, and *G. b. graueri* had significantly higher DNE scores than all other apes save *P. p. pygmaeus*. No other significant differences existed among the apes (Table 3).

The results of character displacement analyses broadly indicate that sympatric populations of *Gorilla* and *Pan* diverge in their macromorphology and DNE scores compared to allopatric *Gorilla* and
Pan (Table 4). The two analyses that included DNE scores had significant results in all three sympatric populations of Gorilla and Pan (i.e. G. g. gorilla-P. t. troglodytes, G. b. graueri-P. t. schweinfurthii, and the combined Gorilla-Pan samples). When relative molar size variables are included in the analysis, results are more significant than when DNE scores are used alone (P<0.03 compared to P<0.05). In the analysis that included only relative molar size variables, results were not significant in the comparisons containing P. t. troglodytes (P>0.05), and were only significant in the comparison between G. b. graueri and P. t. schweinfurthii (P<0.05). Additional character displacement analyses, analyzing each relative molar size index independently, relative molar size variables, can be found in the ESM and generally upholds this result.

Discussion

Dental topography, measured by DNE, was unsuccessful at predicting dietary categories for apes, yielding similar scores for folivores and frugivores (Figure 6). G. b. beringei, an obligate folivore in the Virunga Mountains, had lower DNE scores than the more frugivorous G. b. graueri (p=0.0079), even though both are primarily folivorous. Statistically significant differences between folivores and frugivores existed only between G. b. beringei and P. t. troglodytes, and G. b. graueri and all frugivores save P. p. pygmaeus (Table 3). In previous DNE studies, primates with higher fiber diets tended to have higher DNE scores compared to primates with lower fiber diets (Bunn et al., 2011; Godfrey et al., 2012; Winchester et al., 2014). In the apes, this distinction was significant in comparisons of sympatric apes (G. b. graueri and P. t. schweinfurthii, P=0.0030, G. g. gorilla and P. t. troglodytes, P=0.0003) but not allopatric apes (Table 3).

Teeth with higher DNE scores have curvier surfaces, which are hypothesized to be more efficient at cutting and breaking down foods with low digestibility and high cell wall content, such as chitinous and fibrous foods (Sheine and Kay, 1977). Breaking down these foods increases digestibility by
increasing the surface area to volume ratio, which in turn increases the caloric intake for the animal (Kay and Sheine, 1979). Conversely, foods high in digestibility and low in cell wall content do not need to be broken down as thoroughly—breaking down these foods too efficiently is a waste of energy and can have adverse effects of bolus formation (Sheine and Kay, 1982; Lucas, 2004). Within sympatric apes, gorillas consistently have a higher DNE scores. As chitinous foods make up a small percentage of their diet, it is reasonable to assume the curvier teeth in gorillas is an adaptation to a higher fiber diet.

These conclusions are consistent with the literature gathered on diet, where G. b. graueri has been observed eating leaves when fruit was readily available (Yamagiwa and Basabose, 2006), and P. t. troglodytes has been described as being a ripe fruit specialist, avoiding fibrous foods whenever possible (Tutin et al., 1991; Tutin and Fernandez, 1993; Kuroda et al., 1996). The increase in fiber consumption in gorillas has been quantified in many studies. For example, Yamagiwa and Basabose (2006) provided results following an 8 year study of sympatric populations of G. b. graueri’s and P. t. schweinfurthii. Based the analysis of 14,367 gorilla and 8,070 chimpanzee fecal samples, sieved using a 1 mm mesh, they found that the range for mean proportion of fibrous food remains per fecal sample was 42-100% for G. b. graueri’s diet and 7-78% for P. t. schweinfurthii’s diet. This demonstrated that, while eastern chimpanzees can have seasonally high fiber diets, gorillas tend to, on average, have high fiber diets throughout the year. Similar results have been found in western gorillas and chimpanzees (Tutin and Fernandez, 1985, 1993; Kuroda et al., 1996). This supports the hypothesis that the curvier teeth in gorillas may be an adaptation in this genus to a higher fiber diet (Berthaume, 2014).

It was previously found that dental topography is sensitive to phylogeny (Winchester et al., 2014), but was concluded that, when comparing closely related taxa, dental topography can still be used to predict dietary categories within primates. The results from this study suggest that, while diet can be predicted with dental topographic measures in some groups of closely related primates, such as
platyrhines and strepsirrhines, it is not true for all primates, such as apes and possibly other catarrhines. Additional studies are needed to determine when dental topography is a reliable indicator of dietary categories in fossil hominins.

However, dental topography combined with character displacement analysis may provide useful interpretations for dietary distinctions between potentially overlapping populations. Results from the character displacement analysis indicate that the difference in DNE scores between the sympatric apes of two genera was significantly greater than the difference in scores between allopatric apes of the same genera (Table 4). This suggests that sympatry in closely related taxa such as *Gorilla* and *Pan* may relate to divergence in postcanine tooth morphology and occlusal complexity, probably through dietary partitioning. These results are likely generalizable to more aspects of the masticatory apparatus, not just tooth shape, although additional research is needed. While sympatric taxa form natural testing grounds for hypotheses dealing with interactions between morphological and ecological variables (see also Janson, 2000), caution should be taken when using allopatric taxa to test these hypotheses, as allopatric taxa exist in different locations and will likely face different selection pressures.

If character displacement has occurred between in the postcanine of gorillas and chimpanzees, it is more likely to relate to indirect competition between these two groups rather than direct competition. Gorillas and chimpanzees generally avoid each other during feeding, and any sustained direct competition between them over food resources is likely due to scramble competition. However, ecological competition often occurs indirectly, such as when one taxon affects another taxon by consuming its dietary resources and limiting the amount of available food in its range. Dietary partitioning through adaptations of the masticatory apparatus is one way in which mammalian taxa can reduce indirect competition. Differences in foraging strategies, social systems, and modes of locomotion may also lead to reduced competition. Evidence of such behavioral differences exists in
gorillas and chimpanzees. For example, when chimpanzees find a tree full of ripe fruit, they spend a
long time in the tree and consume large quantities of fruit (Kuroda et al., 1996). Conversely, gorillas will
only forage for a short period of time before moving on, leaving large quantities of ripe fruit behind
(Kuroda et al., 1996). Chimpanzees are more likely to deplete most of the resources in a small location,
while gorillas are more likely to deplete resources to a lesser extent, but over a larger range. In addition,
during fallback episodes, chimpanzees tend to forage further and in smaller groups, while gorillas tend
to consume more herbaceous vegetation and bark. This could lead to unequal pressures on the
masticatory apparatuses, locomotor systems, and social systems of gorillas and chimpanzees diet
(Yamagiwa and Basabose, 2006, 2009), which could result in changes in the general morphology and
behavior of a population overtime. While character displacement analysis cannot necessarily pinpoint
the time of the origin of competition between sympatric *Gorilla* and *Pan*, nor separate the effects of
direct and indirect competition between these taxa, it suggests that sustained and substantial resource
competition has affected the masticatory features of these taxa.

*Implications for the Hominin Record and the Evolution of Early Homo*

During the Plio-Pleistocene, hominin taxa existed sympatrically and allopatrically throughout
Africa (e.g. (Schroer and Wood, 2015)). When sympatric, competition between taxa would have led to
population extinction, reinforced and maintained allopatry, or sufficient niche separation to allow for
continued sympathy (Swedlund, 1974). The idea that character displacement was occurring in the
hominins was first introduced in Brown, 1958. Schaffer, 1968 built on this and tested for character
displacement in the hominins using postcanine tooth size measurements. They found evidence for
character displacement in postcanine tooth area when comparing the robust australopithecines to early
*Homo*; differences were exaggerated where the taxa were likely sympatric (Olduvai Gorge and
Swartkrans) compared to where they were likely allopatric (Kromdraai, Sterkfontein, and Makapansgat)
(Brown, 1958; William M. Schaffer, 1968). Differences in tooth size were hypothesized to have occurred due to different dietary specializations in taxa. Recent dietary reconstructions have confirmed large levels of overlap and specialization in sympatric Plio-Pleistocene hominins (e.g. (Grine et al., 2012; Sponheimer et al., 2013)), suggesting that character displacement may have occurred where taxa were sympatric. More recent work on character displacement by Schroer and Wood (2015) has supported this idea by showing that character displacement likely occurred in hominin premolar tooth size (Schroer and Wood, 2015).

As new sites are discovered and old sites are expanded, it has become increasingly apparent that there were several species of hominins living sympatrically or allopatrically around the time of emergence of early Homo. Table 5 shows a pairwise comparison between the Plio-Pleistocene African hominins depicting which hominin taxa may have been sympatric or allopatric. Species can be classified as likely sympatric (taxa likely have definite overlapping temporal and geographic ranges), probably sympatric (taxa have potentially overlapping temporal and geographic ranges), geographically separated (temporal, but not geographic, overlap), temporally separated (geographic, but not temporal, overlap) or none-of-the-above (neither temporal nor geographical overlap). Dates were taken from Wood and Boyle (2016) and are inclusive of dating error (Wood and K Boyle, 2016). Early Homo is inclusive of Homo erectus, H. ergaster, H. georgicus, H. habilis, H. rudolfensis, and the Ledi Geraru mandible. H. naledi was excluded from this grouping due to lack of confirmed dates and because the Rising Star cave system is within the geographic range of early Homo.

In East Africa, there were at least three species of hominins that were likely or probably sympatric with early Homo: Paranthropus boisei, Paranthropus aethiopicus, and Australopithecus garhi (Wood and Lonergan, 2008; Villmoare et al., 2015). Numerous fossils from both genera have been found in the same sites and date to similar periods, and the remains of these genera are more closely
associated with one another than to other primate taxa at these sites (e.g. Shungura Formation, Lake Malawi, Olduvai, and Koobi Fora all have *P. boisei* and/or *P. aethiopicus* in the same layers as early *Homo*; Bobe and Behrensmeyer, 2004). Additionally, there is mounting evidence that multiple taxa of early *Homo* occupied these sites, potentially at the same time (Spoor et al., 2007; Leakey et al., 2012). Dietary overlap and resource competition – which occurs commonly in living primates such as the great apes – must be considered as a potential selection pressure on these fossil taxa. Such selection pressures may have also led to niche specialization in the east African hominins, led to the derived morphologies observed in the masticatory features of *Paranthropus* (Wood and Strait, 2004; Constantino and Wood, 2007; Wood and Constantino, 2007; Berthaume et al., 2010; Dzialo et al., 2013; Schroer and Wood, 2013; Smith et al., 2015) and the dietary shifts observed in *P. boisei* (high C₄ consumption). Likewise, dietary overlap and resource competition may have caused a selective pressure that influenced the development of the gnathic and dental diversity observed in early *Homo* (Spoor et al., 2015).

In South Africa, there is growing evidence that several species of australopithecines were living sympatrically with each other and early *Homo* (e.g. (Berger et al., 2010; Pickering et al., 2011)) with varying levels of dietary partitioning. An immense number of Plio-Pleistocene hominin bearing sites can be found in South Africa, some yielding hominin specimens of a single species (e.g. Malapa, *A. sediba*; Gondolin, *P. robustus*), and some yielding several hominin species (e.g. Kromdraai, *P. robustus* and early *Homo*; Swartkrans, *P. robustus* and early *Homo*; Sterkfontein, *P. robustus*, *A. africanus*, and early *Homo*), making it likely and probable that early *Homo* was sympatric with *P. robustus* and *A. africanus*, respectively (e.g. (Brain, 1981; Braga and Thackeray, 2003; Moggi-Cecchi et al., 2006)). Although *A. sediba* and early *Homo* have not yet been found in the same member at the same site, it is possible that the two were living sympatrically due to their overlapping temporal and close geographic ranges (Berger et al., 2010; Pickering et al., 2011).
With diet, there is strong evidence that *A. africanus* and *P. robustus* had overlapping diets, likely in preferred foods, with some dietary partitioning in fallback foods (see Grine et al., 2012 and sources there within). Similar dietary overlap likely existed between these species and the early *Homo* living in South Africa. Competition over resources between early *Homo* and *A. africanus*, *P. robustus*, and early *Homo* could have provided a selective force that led to the niche specialization observed in the diets of *A. sediba* (high C\textsubscript{3} consumption) (Cerling et al., 2011; Henry et al., 2012), *P. robustus* (derived masticatory apparatus, consumption of hard, brittle food items) (Scott et al., 2005), and South African Early *Homo* (derived masticatory apparatus, consumption of compliant foods) (Ungar et al., 2006a, 2006b).

Although time-averaging can affect how we interpret occupation of a site, character displacement analysis using dental topographic variables may provide a framework for assessing the likelihood of overlap among fossil hominins based on the patterns observed in living apes. That is to say, the results of our study indicate that character displacement may be useful for quantifying the potential of ecological overlap in fossil taxa. In our study, DNE scores out performed relative molar size in detecting divergence between living populations and more closely reflected the observed overlap among populations of great apes. This suggests that, when available, DNE may be a useful metric for quantifying character displacement in fossil hominins and determining their likelihood of overlap, although we caution the use of this method when comparing allopatric populations that may have different regional ecologies (i.e. comparing southern African to East African hominins). Character displacement may also be generalizable to other skeletal proxies of diet (e.g. mandibular cross-sectional geometry, skull shape), although this has not been rigorously tested in extant apes or fossil hominins.

**Conclusion**
Contrary to findings among other primate groups, dental topography does not reliably predict broad dietary categories within apes. However, differences in dental topography can separate higher and lower fiber diets within sympatric groups of apes. This divergence was significant in a character displacement analysis, suggesting that some degree of ecological competition may influence dental topography in extant apes. A combined character displacement and dental topographic analysis may be informative for reconstructing the dietary niches of fossil apes, including fossil hominins. Although this conclusion presupposes that fossil taxa are subject to similar selection pressures as modern taxa, including the presence of ecological overlap, it may open new avenues for understanding the community compositions of early hominins and the formation of specific ecological niches among hominin taxa.

If natural selection via character displacement operated to produce contrasting tooth shapes in multiple groups of extant apes, as is suggested by our analyses, these results are likely applicable to extinct apes and the fossil hominins. If this proves to be true, it is possible that competition between early Australopithecine lineages resulted in character displacement and divergent evolution leading to the evolution of both robust Australopithecines and early Homo.

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Nishida, T., Uehara, S., 1983. Natural Diet of Chimpanzees (Pan troglodytes schweinfurthii): Long-Term Record from the Mahale Mountains, Tanzania.


Figure 1: Distribution of extant great apes in Africa. Note there are no overlapping ranges between species and subspecies of Gorilla, or species and subspecies of Pan. However, there are some overlapping ranges between Gorilla and Pan.

Figure 2: Diversity in ape mandibular M2's. Each tooth has a DNE value close to the mean of the taxon, indicating it is the most "average" shaped tooth. From top to bottom left for both views, moving clockwise: G. g. gorilla (CMNH B1845), G. b. graueri (MRAC RG881), G. b. beringei (NMNH 396935), P. p. pygmaeus (SAPM 1981-30), P. paniscus (MRAC RG29057), P. t. schweinfurthii (MRAC RG6043), and P. t. troglodytes (CMNH B1720). Figures were created using CloudCompare v2.6.1 (http://www.danielgm.net/cc/).

Figure 3: Effects of reducing the number of triangles that represent the surface of a G. b. graueri tooth (MRAC RG881).

Figure 4: Four possible ape phylogenies encompassing the extremes in subspecies divergence. Tree1 and Tree4 assume G. b. beringei and G. b. graueri diverged 10,000 years after the split with G. g. gorilla, while Tree2 and Tree3 assume the split occurred 10,000 years ago. A similar pattern is seen in the Pan troglodytes clade.

Figure 5: Schematic of character displacement. A behavioral or morphological character is measured in two sympatric (i.e. overlapping) taxa, and the difference between character expression in the two taxa is summarized as “D_s.” When the same character is measured in allopatric (i.e. isolated) populations of the same two taxa, the divergence is summarized as “D_A.” When D_s is greater than D_A, character displacement is indicated. A greater D_s than D_A is represented in this schematic by the thickness of the lines, rather than their length. Solid circles represent one taxon and patterned circles represent another taxon. Although described here for one character, character displacement analyses may include multiple characters.

Figure 6: DNE results. Sympatric species are framed in dotted boxes, while allopatric species are framed in a solid box. Our specimens
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<td>(Prufrock et al., 2016a; b)</td>
</tr>
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<td>jepi</td>
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<td>(Prufrock et al., 2016a; b)</td>
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<td>(López-Torres et al., 2017)</td>
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<td>fuscus</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
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<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
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<td>rougieri</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
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<td>herbekmoi</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
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<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Ignacius</td>
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<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Ignacius</td>
<td>frugivorus</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Genus</td>
<td>Species</td>
<td>Sites</td>
<td>Authors</td>
</tr>
<tr>
<td>------------------</td>
<td>------------------</td>
<td>-------------------</td>
<td>--------------------</td>
</tr>
<tr>
<td>Ignacius</td>
<td>graybullianus</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
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<td>farrandi</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
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<td>maturus</td>
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<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Phenacolemur</td>
<td>archus</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
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<td>Phenacolemur</td>
<td>citatus</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
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<td>fortiors</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
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<td>jepseni</td>
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<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Phenacolemur</td>
<td>pagei</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Phenacolemur</td>
<td>praecox</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
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<td>praecox-fortior</td>
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<td>(López-Torres et al., 2017)</td>
</tr>
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<td>(López-Torres et al., 2017)</td>
</tr>
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<td>Premnoides</td>
<td>douglassi</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Purgatorius</td>
<td>coracis</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Purgatorius</td>
<td>janisaeh</td>
<td>DNE, OPCR, RFI</td>
<td>(López-Torres et al., 2017)</td>
</tr>
<tr>
<td>Homo</td>
<td>rudolfensis</td>
<td>RFI*, slope</td>
<td>Ungar, 2004</td>
</tr>
<tr>
<td>Homo</td>
<td>erectus</td>
<td>RFI*, slope</td>
<td>Ungar, 2004</td>
</tr>
<tr>
<td>Homo</td>
<td>habilis</td>
<td>RFI*, slope</td>
<td>Ungar, 2004</td>
</tr>
<tr>
<td>Australopithecus</td>
<td>afarensis</td>
<td>RFI*, slope</td>
<td>Ungar, 2004</td>
</tr>
<tr>
<td>Australopithecus</td>
<td>africanus</td>
<td>Slope</td>
<td>Ungar, 2007</td>
</tr>
<tr>
<td>Paranthopus</td>
<td>robustus</td>
<td>Slope</td>
<td>Ungar, 2007</td>
</tr>
</tbody>
</table>
Table 1: Sample for this study. Museum abbreviations are as follows: CMNH=Cleveland Museum of Natural History, AMNH=American Museum of Natural History, MRAC=Musée royal de l’Afrique centrale (Royal Museum for Central Africa) in Tervuren, SAPM=Staatssammlung für Anthropologie und Paläoanatomie München (State Museum of Anthropology and Paleoanatomy in Munich), NMNH=National Museum of Natural History.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Sample size</th>
<th>Museums</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Frugivores</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pan troglodytes troglodytes</em></td>
<td>9</td>
<td>CMNH</td>
</tr>
<tr>
<td><em>Pan troglodytes schweinfurthii</em></td>
<td>8</td>
<td>AMNH, MRAC</td>
</tr>
<tr>
<td><em>Gorilla gorilla gorilla</em></td>
<td>8</td>
<td>AMNH, CMNH</td>
</tr>
<tr>
<td><em>Pongo pygmaeus pygmaeus</em></td>
<td>10</td>
<td>SAPM</td>
</tr>
<tr>
<td><em>Pan paniscus</em></td>
<td>9</td>
<td>MRAC</td>
</tr>
<tr>
<td><strong>Folivores</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gorilla beringei beringei</em></td>
<td>9</td>
<td>NMNH</td>
</tr>
<tr>
<td><em>Gorilla beringei graueri</em></td>
<td>8</td>
<td>MRAC</td>
</tr>
</tbody>
</table>
Table 1: Mann-Whitney U-test comparing DNE values between species (not phylogenetically corrected). Test statistics are presented followed by the P-value in brackets. Student t-tests had the same pattern of results.

<table>
<thead>
<tr>
<th>Mann-Whitney U-test</th>
<th>G. b. beringi</th>
<th>P. paniscus</th>
<th>G. b. graueri</th>
<th>P. t. schweinfurthii</th>
<th>G. g. gorilla</th>
<th>P. t. troglodytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>(W [P-value])</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. p. pygmaeus</td>
<td>54 [0.4967]</td>
<td>70 [0.0435]</td>
<td>26 [0.237]</td>
<td>57 [0.1457]</td>
<td>56 [0.1728]</td>
<td>88 [&lt;0.0001]*</td>
</tr>
<tr>
<td>G. b. beringi</td>
<td></td>
<td>63 [0.0503]</td>
<td>9 [0.0079]*</td>
<td>50 [0.1996]</td>
<td>44 [0.4807]</td>
<td>81 [&lt;0.0001]*</td>
</tr>
<tr>
<td>P. paniscus</td>
<td></td>
<td></td>
<td>3 [0.0006]*</td>
<td>30 [0.6058]</td>
<td>28 [0.4807]</td>
<td>78 [0.0003]*</td>
</tr>
<tr>
<td>G. b. graueri</td>
<td></td>
<td></td>
<td></td>
<td>59 [0.003]*</td>
<td>57 [0.007]*</td>
<td>72 [&lt;0.0001]*</td>
</tr>
<tr>
<td>P. t. schweinfurthii</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>22 [0.3282]</td>
<td>66 [0.0025]*</td>
</tr>
<tr>
<td>G. g. gorilla</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>70 [0.0003]*</td>
</tr>
</tbody>
</table>

*significant using a Bonferroni adjusted P-value of 0.0083
Table 4: Results of character displacement analysis. Two pairs of sympatric Gorilla and Pan populations were compared to one pair of allopatric Gorilla and Pan (i.e. G. b. beringei and P. paniscus) in three different versions of the analysis: macromorphological variables alone, DNE scores alone, and a combination of both.

A. Macromorphological variables

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Dₜ</th>
<th>Dₘ</th>
<th>Dₕ-Dₘ</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. g. gorilla and P. t. troglodytes</td>
<td>0.031</td>
<td>0.015</td>
<td>0.016</td>
<td>0.229</td>
</tr>
<tr>
<td>G. b. graueri and P. t. schwarifurthii</td>
<td>0.042</td>
<td>0.011</td>
<td>0.031</td>
<td>0.046</td>
</tr>
<tr>
<td>All sympatric Gorilla and sympatric Pan</td>
<td>0.017</td>
<td>0.024</td>
<td>-0.007</td>
<td>0.672</td>
</tr>
</tbody>
</table>

B. DNE scores

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Dₜ</th>
<th>Dₘ</th>
<th>Dₕ-Dₘ</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. g. gorilla and P. t. troglodytes</td>
<td>115.959</td>
<td>59.788</td>
<td>56.171</td>
<td>0.051</td>
</tr>
<tr>
<td>G. b. graueri and P. t. schwarifurthii</td>
<td>142.993</td>
<td>21.822</td>
<td>121.170</td>
<td>0.006</td>
</tr>
<tr>
<td>All sympatric Gorilla and sympatric Pan</td>
<td>115.791</td>
<td>35.053</td>
<td>80.739</td>
<td>0.033</td>
</tr>
</tbody>
</table>

C. Combined analysis (macromorphological variables & DNE scores)

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Dₜ</th>
<th>Dₘ</th>
<th>Dₕ-Dₘ</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. g. gorilla and P. t. troglodytes</td>
<td>109.425</td>
<td>18.331</td>
<td>91.093</td>
<td>0.014</td>
</tr>
<tr>
<td>G. b. graueri and P. t. schwarifurthii</td>
<td>141.299</td>
<td>39.216</td>
<td>102.083</td>
<td>0.015</td>
</tr>
<tr>
<td>All sympatric Gorilla and sympatric Pan</td>
<td>131.190</td>
<td>21.679</td>
<td>109.511</td>
<td>0.026</td>
</tr>
</tbody>
</table>
Table 5: Pairwise comparison of hominin taxa, depicting which were likely sympatric (Sym, likely), probably sympatric (Sym, prob), geographically separated (Geog sep), temporally separated (Temp sep), or geographically and temporally separated (none-of-the-above).

<table>
<thead>
<tr>
<th></th>
<th>Australopithecus afarensis</th>
<th>Australopithecus africanus</th>
<th>Australopithecus anamensis</th>
<th>Australopithecus bahrelghazali</th>
<th>Australopithecus deyiremeda</th>
<th>Australopithecus garhi</th>
<th>Homo sp. early</th>
<th>Kenyanthropus platyops</th>
<th>Paranthropus</th>
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</thead>
<tbody>
<tr>
<td><strong>Australopithecus</strong></td>
<td></td>
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<tr>
<td>afarensis</td>
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<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
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<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
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<tr>
<td>anamensis</td>
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<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
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<tr>
<td>bahrelghazali</td>
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<td></td>
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<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
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<td>deyiremeda</td>
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<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
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<td>garhi</td>
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<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
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<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
<td>Geog sep</td>
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<tr>
<td>Homo sp. early</td>
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<td>Geog sep (prob)</td>
<td>Geog sep (prob)</td>
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<td>Geog sep (prob)</td>
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<td>Geog sep (prob)</td>
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<td>Geog sep</td>
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<tr>
<td>Species</td>
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<td>above</td>
<td>(prob)</td>
<td>prob</td>
<td>of-the-above</td>
<td>likely</td>
<td>sep</td>
<td>likely</td>
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<td>Geog sep</td>
<td>Temp sep</td>
<td>none-of-the-above</td>
<td>Temp sep</td>
<td>Sym, prob</td>
<td>Geog sep</td>
<td>Sym, likely</td>
<td>Temp sep</td>
</tr>
</tbody>
</table>
Figure 4

Tree 1
- G. g. gorilla
- G. b. graueri
- G. b. beringei
- P. paniscus
- P. t. schweinfurthii
- P. t. troglodytes
- P. p. pygmaeus

Tree 2
- G. g. gorilla
- G. b. graueri
- G. b. beringei
- P. paniscus
- P. t. schweinfurthii
- P. t. troglodytes
- P. p. pygmaeus

Tree 3
- G. g. gorilla
- G. b. graueri
- G. b. beringei
- P. paniscus
- P. t. schweinfurthii
- P. t. troglodytes
- P. p. pygmaeus

Tree 4
- G. g. gorilla
- G. b. graueri
- G. b. beringei
- P. paniscus
- P. t. schweinfurthii
- P. t. troglodytes
- P. p. pygmaeus
Click here to download Supplementary Material: ESM 1_DNE 10000 triangles.xlsx
Click here to download Supplementary Material: ESM 2_character displacement raw data.csv
Click here to download Supplementary Material: ESM3_ape locations and sex.xlsx
Click here to download Supplementary Material: ESM4_character displacement single indeces.xlsx