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Cover illustration: Collection of chimpanzee skulls in the Cleveland Museum of Natural History, Cleveland, Ohio, USA.

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Using machine learning to classify extant apes and interpret the dental morphology of the chimpanzee-human last common ancestor

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Machine learning is a formidable tool for pattern recognition in large datasets. We developed and expanded on these methods, applying machine learning pattern recognition to a problem in paleoanthropology and evolution. For decades, paleontologists have used the chimpanzee as a model for the chimpanzee-human last common ancestor (LCA) because they are our closest living primate relative. Using a large sample of extant and extinct primates, we tested the hypothesis that machine learning methods can accurately classify extant apes based on dental data. We then used this classification tool to observe the affinities between extant apes and Miocene hominoids. We assessed the discrimination accuracy of supervised learning algorithms when tasked with the classification of extant apes (n=175), using three types of data from the postcanine dentition: linear, 2-dimensional, and the morphological output of two genetic patterning mechanisms that are independent of body size: molar module component (MMC) and premolar-molar module (PMM) ratios. We next used the trained algorithms to classify a sample of fossil hominoids (n=95), treated as unknowns. Machine learning classifies extant apes with greater than 92% accuracy with linear and 2-dimensional dental measurements, and greater than 60% accuracy with the MMC and PMM ratios. Miocene hominoids are morphologically most similar in dental size and shape to extant chimpanzees. However, relative dental proportions of Miocene hominoids are more similar to extant gorillas and follow a strong trajectory through evolutionary time. Machine learning is a powerful tool that can discriminate between the dentitions of extant apes with high accuracy and quantitatively compare fossil and extant morphology. Beyond detailing applications of machine learning to vertebrate paleontology, our study highlights the impact of phenotypes of interest and the importance of comparative samples in paleontological studies.

Keywords: dentition, Miocene, fossils, Hominoidea, primates, supervised learning

INTRODUCTION

Paleontology is an important approach to the study of vertebrate evolution that enables quantitative and qualitative morphological comparisons between fossil and extant taxa (e.g., [Szalay and Delson 1979](#), [Patterson 1981](#), [Hartwig 2002](#)). Over the last several decades, machine learning has become an increasingly fine-tuned approach to pattern detection and classification ([Brown et al. 2000](#), [Bishop 2006](#), [Kotsiantis 2007](#), [Michalski](#)

[et al. 2013](#), [Alpaydin 2014](#), [Torkzaban et al. 2015](#)). In contrast to automated classification methods, machine learning relies on the ability of the model to 'learn', improving classification and generalization via quantitative repetition and adjustment through a training process ([Shalev-Shwartz and Ben-David 2014](#)). Within the biological sciences, these techniques have been applied to questions in cancer research ([Shipp et al. 2002](#), [Wang et al. 2005](#), [Belekar et al. 2015](#)), cognitive sciences ([Patel et al. 2015](#), [Weakley et al. 2015](#), [Caliskan et al. 2016](#), [Mohan et al. 2016](#)), informatics ([Vervier et al. 2015](#)), and animal

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call recognition (Acevedo et al. 2009, Armitage and Ober 2010, Skowronski and Harris 2016), to name a few (see also MacLeod 2007). Application of these methods to paleoanthropology is an ideal extension of the approach because machine learning provides three advantages: 1, allows the use of continuous data; 2, does not assume trait independence; and 3, reduces human bias.

One of the major drawbacks of character coding methods is that continuous data are rarely used without classification of the trait into discrete categories, reducing both the power of the method and the biological information of the phenotype (Mishler 1994, Lee and Bryant 1999). A classic example in paleontology is the subjective classification of continuous traits into categories like small, medium, and large (e.g., Ross et al. 1998). Machine learning eliminates this drawback by allowing the inclusion of continuous data in the analyses. Other methods often also require the assumption of independence between traits, an assumption that has been shown to be false with many phenotypes, particularly traits of the dentition, which have been shown to be highly correlated with other dental phenotypes as well as with skeletal phenotypes like body size (e.g., Hlusko 2004, Hlusko et al. 2006, Hlusko 2016, Monson et al. [in press]). In contrast, machine learning does not have any assumptions of trait independence in the methods, it can process highly multivariate data, and it has strong generalizing capabilities (e.g., Schmidhuber 2015). Additionally, machine learning reduces human bias by allowing for objective classification of taxa independent of *a priori* taxonomic assumptions or grouping aside from the training data used in the supervised learning stage of the analysis.

Given how contentious the research debates around the evolution and taxonomy of many clades can be, the proven efficacy of human-free machine learning can provide new insight to paleoanthropology. Machine learning and supervised learning methods have been applied to a series of paleontological questions, including analysis of Quaternary fossil pollen (Punyasena et al. 2012), landmark utility in classification analyses (Garriga et al. 2008, van Bocxlaer and Schultheiß 2010), taphonomic (Arriaza and Domínguez-Rodrigo 2016, Domínguez-Rodrigo and Baquedano 2018) and taxonomic studies (Polly and Head 2004). Our work is novel in using a large sample of extant and fossils individuals to test evolutionary questions of morphological similarity in the charismatic Superfamily Hominoidea using machine learning methods that rely on replication and training to increase generalizing capabilities.

We applied machine learning to the problem of selecting

an appropriate extant homologue for interpretation of fossil dental morphology. Despite decades of paleontological excavation, the origin of the hominid lineage (Family Hominidae, defined as all taxa on the human clade since the split from the chimpanzee clade [White et al. 2015]) remains a central and intriguing question. We have limited knowledge about the morphology of these early hominoids, as there are no known fossils of the chimpanzee-human last common ancestor (LCA), very few early fossils on the human side, and none older than the middle Pleistocene for the chimpanzee (McBrearty and Jablonski 2005, Wood and Harrison 2011). Likewise, the dental morphologies of currently known hominoids do not align with the expectations of ancestral state reconstruction (Gómez-Robles et al. 2013). As such, our knowledge of the LCA relies on what can be inferred from the limited fossil evidence, the Miocene possible ancestors, and the evolutionarily distant descendants.

Chimpanzees (*Pan Oken, 1815*) have long been used as a stand-in for the LCA because they are our closest living relative (Goodman 1999). However, with the discovery of *Ardipithecus* White et al., 1995, the applicability of the chimpanzee as an analogue for the LCA was seriously questioned (Suwa et al. 2009, White et al. 1994, 2009). This extinct genus, the best known of the earliest on the hominid lineage, has been recovered from sediments 6–4.4 million years in age (White et al. 2015). This taxon bears harbingers of an ancestor that lacked chimpanzee features such as knuckle-walking and tall, highly sexually dimorphic canines—strongly indicating that the LCA was distinct from both humans and chimpanzees (White et al. 2015). Despite this finding however, the certainty of *Ardipithecus*-derived insight to the LCA remains controversial (Wood and Harrison 2011). Discovery of the fossil remains of the LCA will be the ultimate means to elucidate its morphology, but in the meantime we bring to bear a significant advance in analytical approach.

We assessed the discrimination accuracy of three supervised learning algorithms when tasked with the classification of extant apes (n=175) using three types of data from the postcanine dentition (mandibular fourth premolar through third molar): linear (tooth crown mesiodistal length); 2-dimensional (tooth crown area: mesiodistal length x buccolingual width); and the morphological output of genetic patterning mechanisms (molar module component, MMC, and premolar-molar module, PMM; Hlusko et al. 2016). We next used the trained algorithms to classify a sample of fossil specimens, treated as unknowns (n=95). Using this large sample of extant and fossil data, we tested the hypothesis

that machine learning methods can accurately classify extant apes based on dental data. We then used this classification method to explore the affinities between dentitions of Miocene hominoid fossils and living apes.

MATERIALS AND METHODS

Materials

Our sample consists of dental data (dental length, dental area, and MMC and PMM ratios [Hlusko et al. 2016]) from four genera of extant primates (Hominoidea $n=175$; Table 1), as well as data from 13 fossil genera (Hominoidea $n=95$; Table 2). All mandibular postcanine dental lengths were included in the study, with the exception of the mandibular third premolar, which is highly sexually dimorphic due to the role it plays in sharpening the canines (Greenfield 1992). We used mesiodistal length for tooth length and mesiodistal length by buccolingual

Table 1. Extant sample size, by species. All data are from Suwa et al., (2009) and references therein except for the sample of *Homo sapiens*, which was measured by T.A.M.

Genus	Species	Sample Size	Repository
<i>Gorilla</i>	<i>gorilla</i>	41	CMNH
<i>Homo</i>	<i>sapiens</i>	42	PAHMA
<i>Pan</i>	<i>paniscus</i>	30	MRAC
<i>P.</i>	<i>troglodytes</i>	54	CMNH
<i>Pongo</i>	<i>pygmaeus</i>	8	CMNH
TOTAL		175	

width for dental area. In addition to the traditional linear metrics of dental length and area, we calculated MMC and PMM, two newly-defined ratios that reflect the output of two genetic mechanisms patterning tooth size variation in the primate postcanine dentition (Hlusko et al. 2016). MMC is calculated as the mesiodistal length of the third molar divided by the mesiodistal length of the first molar and is likely related to the inhibitory cascade defined in murine dentition (Kavanagh et al. 2007), and PMM is calculated as the mesiodistal length of the second molar divided by the mesiodistal length of the fourth premolar (Hlusko et al. 2016).

It is increasingly becoming evident that pleiotropic effects confound discrimination of fossil and extant taxa (Hlusko 2004, 2016, Hlusko et al. 2016, Ungar 2017). Whereas linear metrics of tooth size have shared genetic

(pleiotropic) effects with body size (Hlusko et al. 2006), MMC and PMM do not (Hlusko et al. 2016). The MMC and PMM phenotypes were originally defined by Hlusko et al. (2016) and validated using quantitative genetic analyses in extant primates. Because both dental area and the MMC and PMM ratios rely on calculations of length, all three dental data sets were analyzed separately to avoid replication of measurements.

The extant hominoid data include modern humans (*Homo sapiens* Linnaeus, 1758), gorillas (*Gorilla gorilla* Savage and Wymann, 1847), both species of chimpanzee (*Pan troglodytes* Elliot, 1913 and *Pan paniscus* Schwarz, 1929) and orangutans (*Pongo pygmaeus* Hoppius, 1763). The humans were measured by T.A.M. at the Phoebe A. Hearst Museum of Anthropology in Berkeley, CA, according to standardized protocols (see Grieco et al. 2013). All other extant data were derived from Suwa et al. (2009) and references therein. Gorillas differ from chimpanzees and orangutans in having skeletal and dental adaptations to a predominantly folivorous diet, many of which have effects on the size and shape of the postcanine dentition (e.g., Kay 1985). Gorillas, chimpanzees, and orangutans also differ in the relative proportions of their postcanine dentitions (size of the third molar relative to the second molar, relative to the first molar; Hlusko et al. 2016).

The fossil data were compiled via comprehensive literature review and through collaboration with G. Suwa and T. White (personal communication). All fossil data compiled from the literature are dental metrics taken from original specimens (unless otherwise noted in original text) according to standardized protocols (e.g., White 1977). We recognize that these data were collected by many different researchers across many different projects, and as such, some variation in method could affect the results of this study. However, dental metrics are a highly standardized and well-practiced method of data collection (e.g., Swindler 1976, 2002, Hillson 2005), and we rely on the scientific consistency and accuracy in reporting in all references used. The full list of references from which fossil data were compiled, as well as specimen numbers, sample sizes, and geologic information, is available in Table 2.

Dental data comprise the vast majority of all vertebrate fossil material, and have been well-studied, with analyses of tooth crown length and width linear data being central to paleontological research for many decades (e.g., Swindler 1976, Wood 1981, Ciochon and Holroyd 1992, Bermúdez de Castro et al. 2001, Hlusko et al. 2016). A huge body of phenotypic and genotypic information can be garnered from the study of teeth (Hillson 2005,

Table 2. Fossil sample size, specimen numbers, and reference information.

Genus	Species	Specimen Nos.*	Sample Size	Epoch	Reference (Geologic)	Reference (Data Source)
<i>Afropithecus</i>	<i>turkanensis</i>	KNM-WK 24300	1	early Miocene	Harrison 2002	Rossie & MacLachy 2013
<i>Ankarapithecus</i>	<i>metei</i>	MTA 2125	1	late Miocene	Begun 2002	Begun & Güleç 1998
<i>Ardipithecus</i>	<i>ramidus</i>	ARA-1/128 ARA-1/300 ARA-6/500	3	late Miocene - early Pliocene	White 2002	G. Suwa & T.D. White (unpublished)
<i>Australopithecus</i>	<i>afarensis</i>	AL 266-1 AL 288-1i AL 330-5 AL 400-1a AL 417-1a-b LH-4 MAK-VP-1/12	7	Pliocene	White 2002	White et al. 2000, G. Suwa & T.D. White (unpublished)
<i>A.</i>	<i>africanus</i>	STS-52b Stw-14 Stw-384 Stw-404+407 Stw-498	5	Plio-Pleistocene	White 2002	G. Suwa & T.D. White (unpublished)
<i>A.</i>	<i>anamensis</i>	KNM-KP 29281 KNM-KP 29286	2	Pliocene	White 2002	Ward et al. 2001
<i>A.</i>	<i>bosei</i>	KNM-ER 729 KNM-ER 3230 Peninj 1	3	Pleistocene	White 2002	Wood 1991
<i>A.</i>	<i>garhi</i>	BOU-17/1	1	Plio-Pleistocene	White 2002	G. Suwa & T.D. White (unpublished)
<i>A.</i>	<i>robustus</i>	SK-23 SK-34 SK-6+100 SK-75+105+826a+843 +846a+SKW-14129a SK-858+861+883 SK-876 SKW-5 TM-1517b	8	Pleistocene	White 2002	G. Suwa & T.D. White (unpublished)
<i>Griphopithecus</i>	<i>alpani</i>	MTA 2253	1	early Miocene	Begun 2002	Güleç & Begun 2003
<i>Homo</i>	<i>antecessor</i>	ATD6-96	1	Pleistocene	Smith 2002	Carbonell et al. 2005
<i>H.</i>	<i>erectus</i>	KNM-ER 992 ZH G1 Sangiran 1b Sangiran 22 Thomas Quarry 1 Tighenif 1 Tighenif 2 Tighenif 3	8	Pleistocene	Smith 2002	Arambourg & Hoffstetter 1963, Rightmire 1990, Kaifu et al. 2005, Weidenreich 1937, Wood 1991, Wood & Van Noten 1986, Walker & Leakey 1993

Table 2 (continued). Fossil sample size, specimen numbers, and reference information.

Genus	Species	Specimen Nos.*	Sample Size	Epoch	Reference (Geologic)	Reference (Data Source)
<i>Homo</i>	<i>habilis (sensu lato)</i>	KNM-ER 1802 OH 13 OH 16 Omo 75-14	4	Pleistocene	Smith 2002	G. Suwa & T.D. White (unpublished)
<i>H.</i>	<i>heidelbergensis</i>	Arago XIII AT-300 I IV Mauer VI XII XV XVI XVIII XXII XXIII XXV XXVII	14	Pleistocene	Smith 2002	Bermúdez de Castro 1993, Gabunia & Vekua 1995, Howell 1960, Martín-Torres et al. 2012
<i>H.</i>	<i>neanderthalensis</i>	Amud mandible I Ehringsdorf Ehr F L Hortus V LaQuina mandible Spy I Spy II Tabun II VB I	8	Pleistocene	Smith 2002	Quam et al. 2001, T.D. White (unpublished)
<i>H.</i>	<i>sapiens (Levant)</i>	Qafzeh 3 Qafzeh 7	2	Pleistocene	Smith 2002	T.D. White (unpublished)
<i>Kenyapithecus</i>	<i>africanus</i>	KNM-MJ 5 KNM-TH 28860	2	middle Miocene	Ward & Duren 2002	Kelley et al. 2002, Pickford 1985
<i>Khoratpithecus</i>	<i>piriyai</i>	RIN 765	1	late Miocene	Chaimanee et al. 2004	Chaimanee et al. 2004
<i>Limnopithecus</i>	<i>legetet</i>	KNM-LG 1475	1	early Miocene	Harrison 2002	Harrison 1981
<i>Micropithecus</i>	<i>clarki</i>	KNM-CA 380	1	early Miocene - middle Miocene	Harrison 2002	Harrison 1981
<i>Ouranopithecus</i>	<i>macedoniensis</i>	RPI-79 RPI-84 RPI-88 RPI-89	4	late Miocene	Begun 2002	Koufos & de Bonis 2006
<i>Proconsul</i>	<i>africanus</i>	CMH 102 R 1948, 50	2	early Miocene	Harrison 2002	Le Gros Clark & Leakey 1951

Table 2 (continued). Fossil sample size, specimen numbers, and reference information.

Genus	Species	Specimen Nos.*	Sample Size	Epoch	Reference (Geologic)	Reference (Data Source)
<i>P.</i>	<i>heseloni</i>	KNM-RU 1674 KNM-RU 1706 KNM-RU 2087 KNM-RU 7290	4	early Miocene	Harrison 2002	Pickford et al. 2009
<i>P.</i>	<i>major</i>	KNM-LG 452 KNM-SO 396 BNMH-M 16648	3	early Miocene	Harrison 2002	Le Gros Clark & Leakey 1951, Pickford et al. 2009
<i>P.</i>	<i>nyanzae</i>	1942 mandible CMH 4 (KNM-RU 1676) KNM-RU 1947 R 1145. '50	4	early Miocene	Harrison 2002	Le Gros Clark 1952, Le Gros Clark & Leakey 1951, Pickford et al. 2009
<i>Rangwapithecus</i>	<i>gordoni</i>	KNM-KT 31234 KNM-SO 17500 KNM-SO 22228	3	middle Miocene	Begun 2002	Cote et al. 2014, Hill et al. 2013
<i>Sivapithecus</i>	<i>indicus</i>	GSP 15000	1	late Miocene	Kelley 2002	Pilbeam 1982
TOTAL			95			

*AL=Afar Locality, Ethiopia, **ARA**=Aramis, Ethiopia, **AT**=Atapuerca, Spain, **BOU**=Bouri, Ethiopia, **CMH**=Rusinga, Kenya, **GSP**=Geological Survey of Pakistan, Pakistan, **LH**=Laetoli Hominid, Tanzania, **MAK**=Makapansgat, South Africa, **OH**=Olduvai Hominid, Tanzania, **Omo**=Shungura Formation, Ethiopia, **RPI**=Ravin de la Pluie, Greece, **SK**=Swartkrans, South Africa, **SKW**=Swartkrans, South Africa, **STS**=Sterkfontein, South Africa, **Stw**=Sterkfontein, South Africa, **ZH**=Zhoukoudian, Beijing, China.

Swindler 2002), and the importance of the dentition to the field of paleontology has been well documented (Ungar 2017). As such, use of dental data in this study is not only justified but also highly appropriate and informative.

Analytical Methods

We began by assessing the relative accuracies of three different supervised learning algorithms on classifying teeth to extant genera using their morphological features. The models used are linear discriminant function analysis (LDA), support vector machines (SVM), and random forest (RF), implemented in the R statistical environment 3.2.3 (R Core Team 2015).

LDA is a parametric technique that attempts to predict a multiclass categorical outcome using a linear combination of predictor features (Rao 1948). It assumes features are normally distributed, homoscedastic, and represent a random sample from the population of interest. Machine learning LDA differs from traditional supervised discriminant function methods in allowing for adjustment of classification criteria based on the inclusion

of additional information during the training process (Tharwat et al. 2017).

Support vector machines (SVM) select linear separating hyperplanes between classes by maximizing the margin between the closest points belonging to different classes. We employed a radial basis function kernel to allow the computation of nonlinear feature boundaries (Boser et al. 1992). We optimized for SVM classification accuracy over a range of misclassification parameters spanning seven orders of magnitude (0.25–100,000).

The random forest is a decision-tree-based technique that constructs a large number of decision trees, each generated from bootstrapped random samples of the data, and generates predictions using a majority vote (Breiman 2001). Our random forest was comprised of 500 trees optimized for classification accuracy over a range of the number of random variables selected at each bootstrap (*mtry* parameter).

Accuracy for all models was assessed using 10-fold cross validation, and both mean and adjusted accuracies for each model are reported. Adjusted accuracies were

calculated as the sensitivity plus specificity, divided by two (Zeng et al. 2002, Tzanis et al. 2005). Because the scales and ranges of dental features were approximately equal, scaling and centering the data did not impact resulting classification accuracies, and so untransformed measures were used. The kappa (κ) statistic is a measurement of accuracy adjusted by the probability of agreement by chance alone (Cohen 1960). Kappa was calculated by comparing machine learning models using the resamples and summary commands in R (R Core Team 2015). We generated a list of the most important dental dimensions driving the classification with a variable importance analysis, run using the VarImp function in the *caret* package (Kuhn et al. 2012). Variable importance analysis is a standard output of the random forest model that averages error across variable permutations to calculate to what degree each variable influences the classification relative to the others, generating a rank list of importance, with the most important variable receiving a value of 100, and the least important variable receiving a value of zero (Liaw and Wiener 2002).

The LDA machine learning classification model classified extant apes with greatest raw accuracy of the three machine learning techniques, and high adjusted accuracy, and the output from this classification model was used in subsequent analysis of fossil specimens. While *a priori* taxonomic designations were used in the training data set, the extant ape species included in this study have been well agreed upon in the literature using extensive morphological, behavioral, and molecular data (Tuttle 2014).

We then included a large sample of fossil hominoids ($n=95$, Table 2), spanning 13 genera from Miocene to Pleistocene, to our extant sample of apes to test the hypothesis that the dentitions of fossil hominoids are morphologically more similar to extant chimpanzees than other apes. We assessed the agreement of each classifier on the predicted identities of fossil teeth using the following routine: we generated a random seed, which is used to partition training and test sets during cross-validation. We then trained the LDA model on the tooth features of extant genera and classified the fossil teeth using each classifiers' most accurate set of parameters. We repeated this process 50 times, generating 50 lists of genus predictions for fossil teeth per classifier. We then took the majority vote of each element of these lists to determine the extant genus to which a particular classifier most often assigned each fossil. While this method assumes that fossil taxa occupy the same morphospace as extant taxa, our goal here was to assess the best

supported extant homologue for the chimpanzee-human last common ancestor.

In order to visualize the relationships between the data and better interpret the classification boundaries drawn by the machine learning methods, we generated a principle components analysis (PCA) for the dental phenotypes using the *prcomp* function in *psych* (Revelle 2017). We then plotted all fossils and extant taxa over the classifiers' decision boundaries, first log-transforming, scaling, and centering the dental data for both fossil and extant genera. We decomposed these transformed features into principle components (PC) scores and plotted them on the first two PC axes. We then trained our classifiers on the PC scores of extant genera using the methods described previously. Next, we generated a grid of 160,800 regularly-spaced coordinates spanning the entire range of PC1 and PC2, and we classified each point on this grid to a particular extant genus. The decision boundaries for the LDA classifier were approximated using a contour line to trace around each region assigned to a particular genus. Over these decision regions, we plotted both the PC scores of extant genera and fossil teeth, with the expectation that the fossils most often disagreed-upon would lie at the boundaries of the classification regions and thus had features intermediate of the two (or more) conflicting assigned genera. We also computed and plotted 95% confidence intervals for the extant taxa using *stat_ellipse* in *ggplot2* (Wickham 2009).

Because there are only two measurements included in the comparison of MMC and PMM, we visualized variation in these ratios with bivariate plots using *qplot* in *ggplot* (Wickham 2009), excepting the machine learning classification output which requires PCA to plot the classification boundaries.

The R script for machine learning classification of extant specimens using the three models (LDA, SVM, and RF) and the classification of unknowns, here the fossil sample, is available for download from the Supplemental Material at <https://escholarship.org/uc/item/84d1304f>.

Institutional Abbreviations

BMNH: British Museum of Natural History, London, U.K.; **CMNH:** Cleveland Museum of Natural History, Cleveland, Ohio, U.S.A.; **KNM:** Kenya National Museum, Nairobi, Kenya; **MRAC:** Musée Royal de l'Afrique Centrale, Tervuren, Belgium; **MTA:** Maden Tetkik ve Arama Enstitüsü, Ankara, Turkey; **PAHMA:** Phoebe A. Hearst Museum of Anthropology, Berkeley, California, U.S.A.; **RIN:** Rajabhat Institute, Nakhon Ratchasima, Thailand; **TM:** Transvaal Museum, Pretoria, South Africa.

Table 3. Accuracy and Cohen's kappa of supervised learning techniques determined using 10-fold cross-validation. Abbreviations: *LDA*=Linear Discriminate Analysis, *RF*=Random Forest, *SVM*=Support Vector Machines, *SD*=standard deviation.

Model	Input Data	Accuracy	Adjusted Accuracy*	Accuracy SD	Kappa**	Kappa SD
<i>LDA</i>	Linear	0.94	0.96	0.07	0.90	0.11
	Area	0.97	0.94	0.05	0.95	0.08
	MMC & PMM	0.63	0.59	0.07	0.39	0.11
<i>RF</i>	Linear	0.92	0.94	0.07	0.88	0.11
	Area	0.96	0.96	0.04	0.94	0.07
	MMC & PMM	0.60	0.55	0.11	0.37	0.15
<i>SVM</i>	Linear	0.94	0.92	0.08	0.90	0.12
	Area	0.96	0.96	0.07	0.94	0.10
	MMC & PMM	0.61	0.65	0.08	0.29	0.14

*Adjusted accuracy was calculated as (selectivity + sensitivity)/2 (Tzanis et al. 2005).

**The kappa (κ) statistic is a measurement of accuracy adjusted by the probability of agreement by chance alone. $\kappa > 0.75$ indicates substantial agreement.

RESULTS

The three supervised learning algorithms classify extant apes with greater than 95% accuracy with the four 2-dimensional area measurements, and greater than 92% accuracy with the four linear measurements (Table 3), a result that relies heavily on the absolute size differences between taxa. Adjusted accuracies for classification are also greater than 90%. With the MMC and PMM phenotypes, raw accuracy classification decreases to 60–63%, and adjusted accuracy decreases to 55–65%. However, it is surprising that the algorithms can classify so well using only two data points for each individual, in comparison to the four used in the linear or 2-dimensional analyses. The reduction in classification accuracy results either from the use of only two data points for each individual, or more likely, from the similarity in tooth size proportions between chimpanzees and humans once the effects of body size are removed, as is the case when using the MMC and PMM ratios. When assessing the importance of the dental data for classification, variable importance analysis identifies dental length of the first molar, area of the first molar, and the MMC phenotype, respectively, to be the most important traits used in the classification of the extant apes (Table 4). This result supports that MMC differentiates extant and fossil apes with greater power than PMM, and aligns with previous findings of higher heritability in MMC relative to PMM (Hlusko et al. 2016).

When comparing fossil ape to extant ape morphology using machine learning, the dental metric data tend to be most often classified as *Pan* using dental length and area measurements for the majority of the Miocene apes, and as *Gorilla* using the MMC and PMM ratios (Table 5, Fig.

1; see results for *Afropithecus* Leakey and Leakey, 1986, *Griphopithecus* Abel, 1902, *Kenyapithecus* Leakey, 1961, *Limnopithecus* Hopwood, 1933, *Micropithecus* Fleagle and Simons, 1978, *Proconsul* Hopwood, 1933, *Rangwapithecus* Andrews, 1974, and *Sivapithecus* Pilgrim, 1910). Likewise, *Ouranopithecus macedoniensis* de Bonis and Melentis, 1978 is exclusively classified as *Gorilla* using the MMC and PMM phenotypes, but the results for dental

Table 4. Variable importance of the dental traits in classifying extant apes. Abbreviations: M=molar, P=premolar, L=length, A=area, 2-D=two-dimensional, *GP Phenotypes*=genetic patterning phenotypes (MMC and PMM). All dental data are from mandibular dentitions.

Dental Data	Variable Importance
<i>Linear Metrics</i>	
M ₁ L	100.00
M ₂ L	34.659
M ₃ L	2.278
P ₄ L	0.00
<i>2-D Metrics</i>	
M ₁ A	100.00
M ₂ A	39.09
M ₃ A	25.26
P ₄ A	0.00
<i>GP Phenotypes</i>	
MMC	100.00
PMM	0.00

Table 5. Predictions of the machine learning classification under linear discriminant analysis. Abbreviations: **LDA**=linear discriminant analysis, **Pred.**=prediction, **MMC**=molar module component, **PMM**=premolar-molar module. Cells containing extant classification predictions are color-coded: **blue**=*Pan* (chimpanzee), **green**=*Gorilla* (gorilla), **pink**=*Homo* (human), **yellow**=*Pongo* (orangutan), **white**=NA (not available).

Fossil Specimen ID	Species	LDA Pred. Linear	LDA Pred. Area	LDA Pred. MMC & PMM
KNM-WK 24300	<i>Af. turkanensis</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
MTA 2125	<i>An. metei</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
ARA-1/128	<i>Ar. ramidus</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
ARA-1/300	<i>Ar. ramidus</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
ARA-6/500	<i>Ar. ramidus</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
AL 266-1	<i>Au. afarensis</i>	<i>Pongo</i>	<i>Gorilla</i>	<i>Gorilla</i>
AL 288-1i	<i>Au. afarensis</i>	<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>
AL 400-1a	<i>Au. afarensis</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
AL 417-1a, b	<i>Au. afarensis</i>	<i>Homo</i>	<i>Homo</i>	<i>Gorilla</i>
AL 330-5	<i>Au. afarensis</i>	<i>Homo</i>	<i>Homo</i>	<i>Gorilla</i>
LH-4	<i>Au. afarensis</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
MAK-VP-1/12	<i>Au. afarensis</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
STS-52b	<i>Au. afarensis</i>	<i>Pongo</i>	<i>Pongo</i>	<i>Pan</i>
Stw-14	<i>Au. afarensis</i>	<i>Gorilla</i>	NA	<i>Gorilla</i>
Stw-384	<i>Au. afarensis</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
Stw-404+407	<i>Au. afarensis</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
Stw-498	<i>Au. afarensis</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
KNM-KP 29281	<i>Au. anamensis</i>	<i>Homo</i>	<i>Homo</i>	<i>Gorilla</i>
KNM-KP 29286	<i>Au. anamensis</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Gorilla</i>
KNM-ER 729	<i>Au. boisei</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
KNM-ER 3230	<i>Au. boisei</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
Peninj 1	<i>Au. boisei</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
BOU-17/1	<i>Au. garhi</i>	<i>Gorilla</i>	NA	<i>Gorilla</i>
SK-23	<i>Au. robustus</i>	<i>Gorilla</i>	<i>Pongo</i>	<i>Gorilla</i>
SK-34	<i>Au. robustus</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
SK-6 + 100	<i>Au. robustus</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
SK-75+105+826a+843 + 846a+SKW-14129a	<i>Au. robustus</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
SK-858+86+ 883	<i>Au. robustus</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
SK-876	<i>Au. robustus</i>	<i>Gorilla</i>	NA	<i>Gorilla</i>
SKW-5	<i>Au. robustus</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
TM-1517b	<i>Au. robustus</i>	<i>Pongo</i>	<i>Pongo</i>	<i>Gorilla</i>
MTA 2253	<i>Gr. alpani</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
ATD6-96	<i>H. antecessor</i>	<i>Pan</i>	<i>Pan</i>	<i>Pan</i>
KNM-ER 992	<i>H. erectus</i>	<i>Homo</i>	<i>Pan</i>	<i>Pan</i>

Table 5 (continued). Predictions of the machine learning classification under linear discriminant analysis. Abbreviations: **LDA**=linear discriminant analysis, **Pred.**=prediction, **MMC**=molar module component, **PMM**=premolar-molar module. Cells containing extant classification predictions are color-coded: **blue**=*Pan* (chimpanzee), **green**=*Gorilla* (gorilla), **pink**=*Homo* (human), **yellow**=*Pongo* (orangutan), **white**=NA (not available).

Fossil Specimen ID	Species	LDA Pred. Linear	LDA Pred. Area	LDA Pred. MMC & PMM
ZH G1	<i>H. erectus</i>	<i>Homo</i>	<i>Homo</i>	<i>Pan</i>
Sangiran 1b	<i>H. erectus</i>	<i>Homo</i>	<i>Homo</i>	<i>Gorilla</i>
Sangiran 22	<i>H. erectus</i>	<i>Pan</i>	<i>Homo</i>	<i>Pan</i>
Thomas Quarry 1	<i>H. erectus</i>	<i>Homo</i>	<i>Homo</i>	<i>Pan</i>
Tighenif 1	<i>H. erectus</i>	<i>Homo</i>	<i>Homo</i>	<i>Pan</i>
Tighenif 2	<i>H. erectus</i>	<i>Homo</i>	<i>Homo</i>	<i>Pan</i>
Tighenif 3	<i>H. erectus</i>	<i>Homo</i>	<i>Homo</i>	<i>Pan</i>
KNM-ER 1802	<i>H. habilis (sensu lato)</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
OH 13	<i>H. habilis (sensu lato)</i>	<i>Homo</i>	<i>Homo</i>	<i>Gorilla</i>
OH 16	<i>H. habilis (sensu lato)</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
Omo 75-14	<i>H. habilis (sensu lato)</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Pan</i>
Arago XIII	<i>H. heidelbergensis</i>	<i>Homo</i>	<i>Pongo</i>	<i>Pan</i>
AT-300	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
I	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Homo</i>	<i>Pan</i>
IV	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Homo</i>	<i>Pan</i>
Mauer	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Homo</i>	<i>Gorilla</i>
VI	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Pan</i>	<i>Pan</i>
XII	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
XV	<i>H. heidelbergensis</i>	<i>Homo</i>	<i>Pan</i>	<i>Pan</i>
XVI	<i>H. heidelbergensis</i>	<i>Homo</i>	<i>Pan</i>	<i>Pan</i>
XVIII	<i>H. heidelbergensis</i>	<i>Homo</i>	<i>Pan</i>	<i>Pan</i>
XXII	<i>H. heidelbergensis</i>	<i>Homo</i>	<i>Homo</i>	<i>Gorilla</i>
XXIII	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Homo</i>	<i>Gorilla</i>
XXV	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Homo</i>	<i>Pan</i>
XXVII	<i>H. heidelbergensis</i>	<i>Pan</i>	<i>Homo</i>	<i>Gorilla</i>
Amud mandible I	<i>H. neanderthalensis</i>	<i>Pan</i>	NA	<i>Pan</i>
Ehringsdorf Ehr F	<i>H. neanderthalensis</i>	<i>Homo</i>	NA	<i>Pan</i>
L Hortus V	<i>H. neanderthalensis</i>	<i>Pan</i>	NA	<i>Pan</i>
LaQuina mandible	<i>H. neanderthalensis</i>	<i>Pan</i>	NA	<i>Pan</i>
Spy I	<i>H. neanderthalensis</i>	<i>Pan</i>	NA	<i>Pan</i>
Spy II	<i>H. neanderthalensis</i>	<i>Homo</i>	NA	<i>Pan</i>
Tabun II	<i>H. neanderthalensis</i>	<i>Homo</i>	NA	<i>Pan</i>
VB 1	<i>H. neanderthalensis</i>	<i>Homo</i>	<i>Homo</i>	<i>Pan</i>
Qafzeh 3	<i>H. sapiens (Levant)</i>	<i>Homo</i>	NA	<i>Pan</i>

Table 5 (continued). Predictions of the machine learning classification under linear discriminant analysis. Abbreviations: **LDA**=linear discriminant analysis, **Pred.**=prediction, **MMC**=molar module component, **PMM**=premolar-molar module. Cells containing extant classification predictions are color-coded: **blue**=*Pan* (chimpanzee), **green**=*Gorilla* (gorilla), **pink**=*Homo* (human), **yellow**=*Pongo* (orangutan), **white**=NA (not available).

Fossil Specimen ID	Species	LDA Pred. Linear	LDA Pred. Area	LDA Pred. MMC & PMM
Qafzeh 7	<i>H. sapiens</i> (Levant)	<i>Homo</i>	NA	<i>Pan</i>
KNM-MJ 5	<i>Ke. africanus</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-TH 28860	<i>Ke. africanus</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
RIN 765	<i>Kh. piriyai</i>	<i>Gorilla</i>	NA	<i>Gorilla</i>
KNM-LG 1475	<i>L. legetet</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-CA 380	<i>M. clarki</i>	<i>Pan</i>	<i>Pan</i>	<i>Pan</i>
RPI-79	<i>Ou. macedoniensis</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
RPI-84	<i>Ou. macedoniensis</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
RPI-88	<i>Ou. macedoniensis</i>	<i>Homo</i>	<i>Homo</i>	<i>Gorilla</i>
RPI-89	<i>Ou. macedoniensis</i>	<i>Gorilla</i>	NA	<i>Gorilla</i>
CMH 102	<i>Pr. africanus</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
R 1948, 50	<i>Pr. africanus</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-RU 1674	<i>Pr. heseloni</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-RU 1706	<i>Pr. heseloni</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-RU 2087	<i>Pr. heseloni</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-RU 7290	<i>Pr. heseloni</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-LG 452	<i>Pr. major</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-SO 396	<i>Pr. major</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Gorilla</i>
BNMH-M 16648	<i>Pr. major</i>	<i>Gorilla</i>	<i>Gorilla</i>	<i>Gorilla</i>
1942 mandible	<i>Pr. nyanzae</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
CMH 4 (KNM-RU 1676)	<i>Pr. nyanzae</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-RU 1947	<i>Pr. nyanzae</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
R 1145. '50	<i>Pr. nyanzae</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-KT 31234	<i>R. gordonii</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-SO 17500	<i>R. gordonii</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
KNM-SO 22228	<i>R. gordonii</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>
GSP 15000	<i>S. indicus</i>	<i>Pan</i>	<i>Pan</i>	<i>Gorilla</i>

length and dental area are majority *Homo*.

Uniquely among the Miocene fossil sample, *Micropithecus clarki* Fleagle and Simons, 1978 is classified as *Pan* with 100% agreement using dental length, area, and the MMC and PMM ratios. On the opposite end of the spectrum, *Ankarapithecus metelai* Ozansoy, 1957 is classified as *Gorilla* with 100% agreement using dental length, area, and the MMC and PMM ratios. *Khoratpithecus piriyai* Chaimanee et al., 2004 is also classified as *Gorilla* with

100% agreement using dental length, and the MMC and PMM phenotypes (dental areas are not available for this taxon).

Like many of the fossil specimens, *Ardipithecus* is classified as *Pan* using dental length, and as *Gorilla* using the MMC and PMM ratios. In contrast, *Australopithecus robustus* Broom, 1938 is almost exclusively classified as *Gorilla* by the machine learning LDA model (Fig. 1). The other *Australopithecus* specimens have less agreement

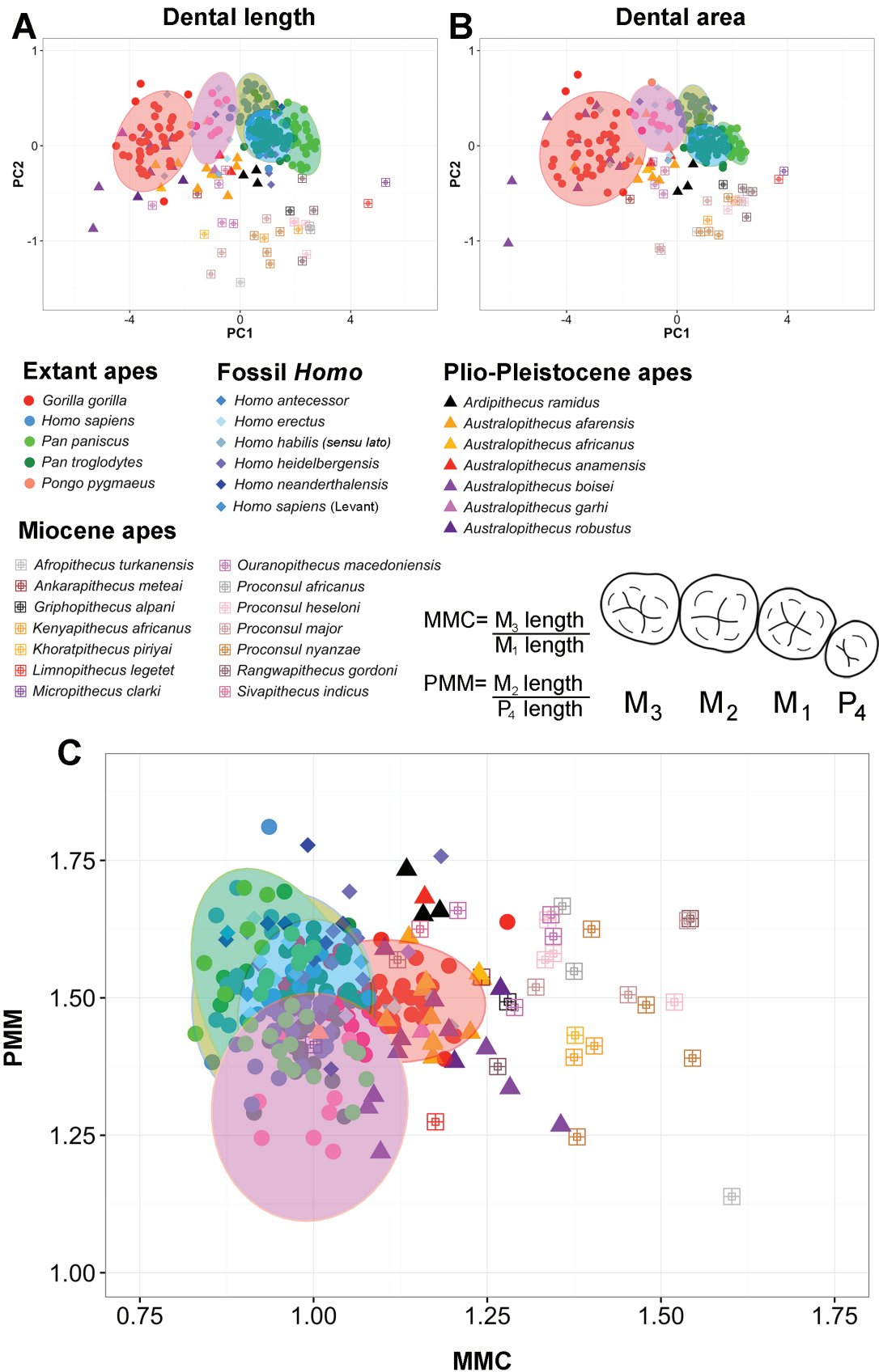


Figure 2. Caption at the top of next page.

Figure 2. The distribution of fossil and extant taxa in multidimensional space. **Circles**=extant taxa, **diamonds**=fossil *Homo*, **triangles**=Plio-Pleistocene fossil taxa, **crossed square**=Miocene fossil taxa. Ellipses represent 95% confidence intervals. PCs computed using specific taxonomy are slightly different than PCs computed using generic taxonomy (Fig. 1). Equations for calculating MMC and PMM ratios are detailed in the figure next to a diagram of generalized mandibular primate dentition. M₃ is mandibular third molar, M₂ is mandibular second molar, M₁ is mandibular first molar, P₄ is mandibular fourth premolar. **A.** PCA comparing dental length across the fossil and extant samples. PC1 comprises 93.2% of the variation, and PC2 comprises 3.8% of the variation. **B.** PCA comparing dental area across the fossil and extant samples. PC1 comprises 95.4% of the variation, and PC2 comprises 2.6% of the variation. Note how the Miocene taxa are distinct from the Plio-Pleistocene and extant taxa in **(A)** and **(B)**. **C.** Bivariate plot comparing the MMC and PMM ratios across the fossil and extant samples.

boundary of *Pan* set by the supervised learning model (Fig. 1, Table 5), but it is difficult to confidently argue that the Miocene taxa are morphologically more similar to *Pan* than *Gorilla* because they are practically equidistant in PC space despite the classification boundary (Figs. 1, 2A). This same result is also seen for the 2-dimensional data (Fig. 2B, Table 5).

Use of the MMC and PMM phenotypes provides a different result (Fig. 2C). Miocene apes are more similar

to extant gorillas in dental proportions and are almost exclusively classified as *Gorilla* (Table 5). We also qualitatively document a strong trajectory through bivariate space that correlates with evolutionary time, from Miocene apes to Plio-Pleistocene hominids to extant apes, including humans (Fig. 3). This trend captures a linear decrease in MMC from Miocene to present which characterizes almost all taxa sampled, further emphasizing the relatively greater importance of MMC compared to

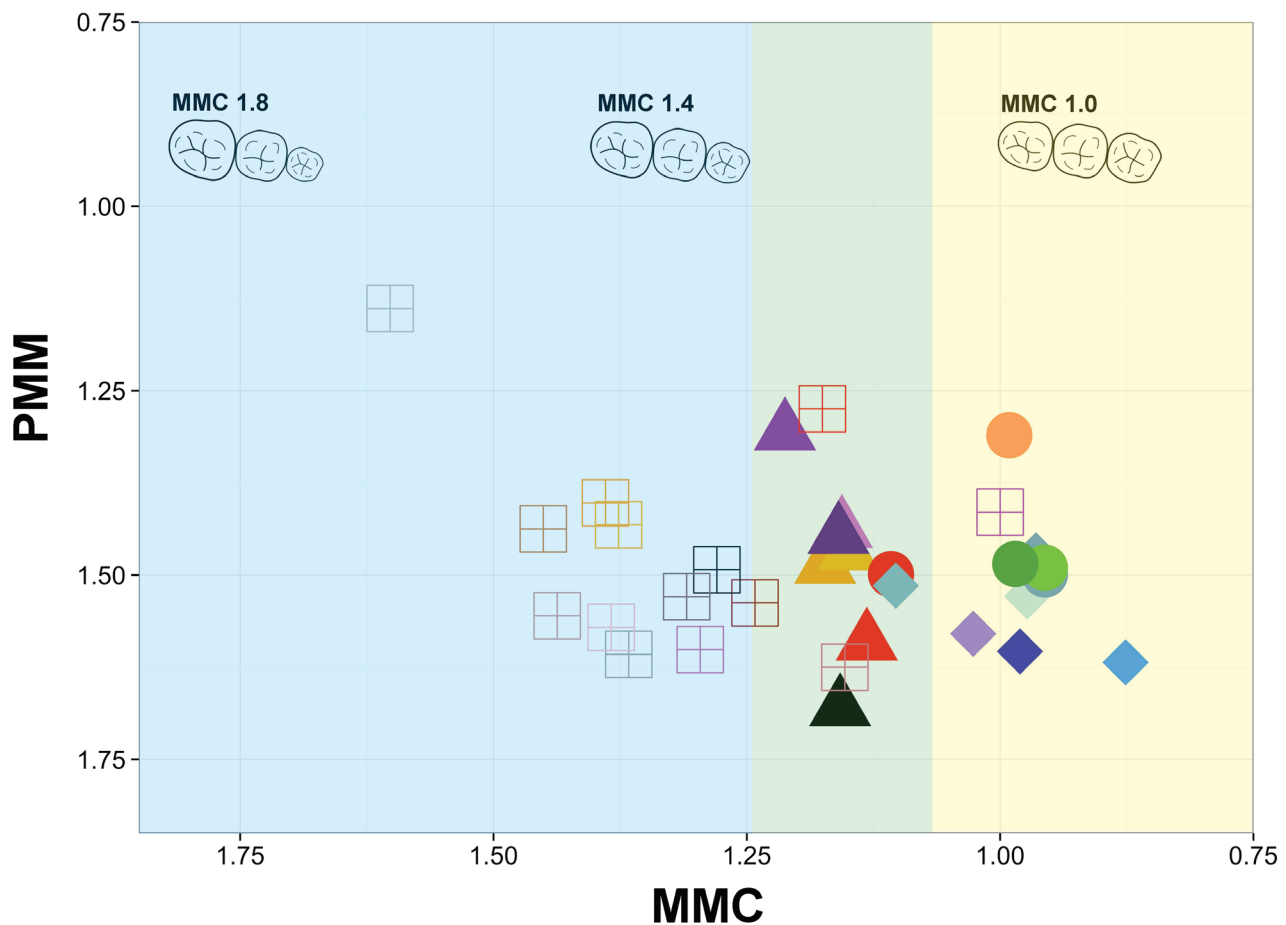


Figure 3. Bivariate plot of MMC and PMM ratios. All taxa are represented by the species average. **Circles**=extant taxa, **diamonds**=fossil *Homo*, **triangles**=Plio-Pleistocene fossil taxa, **crossed squares**=Miocene fossil taxa. Difference in shape size is an artifact of R. See Figure 2 for species legend. **Blue shading**=Miocene, **green shading**=Pliocene, **yellow shading**=Pleistocene. Note the linearly decreasing values of MMC through time. Outliers to the pattern include *Limnopithecus*, *Rangwapithecus*, *Micropithecus*, *Homo habilis*, and *Gorilla*. Sample MMC ratios with figurative tooth proportions (M₃, M₂, M₁) are overlaid on the plot.

PMM in characterizing primate variation (Fig. 3). Of the extant apes, gorillas retain more ancestral MMC and PMM values, as evidenced by their morphological similarity to Miocene taxa (Figs. 2C, 3). Pliocene taxa (*Australopithecus*), are also similar to gorillas in dental proportions (Fig. 3). Fossil taxa do not have PMM and MMC values comparable to modern humans until genus *Homo* in the Pleistocene (Fig. 3). Chimpanzees and humans, as well as orangutans (*Pongo*), are morphologically derived relative to Miocene taxa, and this is why the machine learning methods fail to classify fossil taxa as chimpanzee using the MMC and PMM ratios.

Chimpanzees and humans shared a last common ancestor approximately five to nine million years ago, in the Miocene (Goodman 1999, Raaum et al. 2005, Steiper and Young 2006, Langergraber et al. 2012). Postcanine tooth size proportions of fossil hominoids in our sample (e.g., *Afropithecus*, *Kenyapithecus*, *Proconsul*) are more similar to those of extant gorillas than chimpanzees or humans, as are the dentitions of many Pliocene taxa, suggesting that the last common ancestor of chimpanzees and humans likely also had dental proportions more similar to gorillas. The fossil evidence, interpreted through machine learning classification methods, suggests that humans and chimpanzees likely converged in their MMC and PMM values, evolving independently from a dental morphology that was much more similar to living gorillas.

The similarity between extant *Homo* and *Pan* postcanine dentitions has long been interpreted as a result of shared common ancestry (Johanson 1973, Begun 1994, 2004, Lucas et al. 2008). However, our machine learning approach reveals that the relative sizes of the postcanine teeth of putative LCAs were much more like extant gorillas, suggesting that similarities in postcanine tooth proportions in extant *Pan* and *Homo* postcanine dentitions are the result of parallel evolution.

Gorillas have evolved many tooth crown features specialized for folivory (Glowacka et al. 2016), but retain a more primitive pattern of dental proportions. Given that the divergence of humans and chimpanzees occurred in the late Miocene, and that Miocene apes are much more similar to *Gorilla* in dental proportions, we assert that gorillas are the more appropriate extant model for the African ape LCA in terms of the relative sizes of the postcanine teeth. This similarity in dental proportions likely has implications for the interpretation of dietary adaptation and possibly phylogenetic relationships in Miocene apes, including the chimpanzee-human last common ancestor. Overall, our results also further highlight the well-known dramatic reduction in morphological variation when

Miocene apes are compared to extant apes.

Machine learning is a powerful tool that can accurately classify extant species based on dental metrics as well as be used to explore evolutionary hypotheses that rely on interpretations of fossil morphology. However, machine learning still depends heavily on human decisions, and we emphasize here the importance of carefully considering which phenotypes to use as input based on which will best capture the underlying biological mechanisms being explored, and the importance of considering appropriate comparative samples.

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