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ORIGINAL PAPER

A genotype:phenotype approach to testing taxonomic hypotheses in hominids

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Abstract

Paleontology has long relied on assumptions about the genetic and developmental influences on skeletal variation. The last few decades of developmental genetics have elucidated the genetic pathways involved in making teeth and patterning the dentition. Quantitative genetic analyses have refined this genotype:phenotype map even more, especially for primates. We now have the ability to define dental traits with a fair degree of fidelity to the underlying genetic architecture; for example, the molar module component (MMC) and the premolar-molar module (PMM) that have been defined through quantitative genetic analyses. We leverage an extensive dataset of extant and extinct hominoid dental variation to explore how these two genetically patterned phenotypes have evolved through time. We assess MMC and PMM to test the hypothesis that these two traits reveal a more biologically informed taxonomy at the genus and species levels than do more traditional measurements. Our results indicate that MMC values for hominids fall into two categories and that *Homo* is derived compared with earlier taxa. We find a more variable, species-level pattern for PMM. These results, in combination with previous research, demonstrate that MMC reflects the phenotypic output of a more evolutionarily stable, or phylogenetically congruent, genetic mechanism, and PMM is a reflection of a more evolutionarily labile mechanism. These results suggest that the human lineage since the split with chimpanzees may not represent as much genus-level variation as has been inferred from traits whose etiologies are not understood.

Keywords Adaptive plateau · Dentition · Early *Homo* · Hominid evolution · Modularity

Introduction

With every discovery of a new hominid fossil comes intense scrutiny of its evolutionary relationship to other hominid taxa (e.g., Chen et al. 2019; Daura et al. 2017; Haile-Selassie et al. 2019; Harvati et al. 2019; Hershkovitz et al. 2018). Phylogenetic systematics is the most widely used approach for inferring these evolutionary relationships (Argue et al. 2017; Dembo et al. 2016; Mongle et al. 2019). This approach assesses a range of characters (i.e., traits) for each of the

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taxonomic units included in the analysis, forming a character matrix. From this matrix, analytical methods identify a nested hierarchy of taxonomic units with the most parsimonious pattern of primitive and derived characters. The result is presented as the most reasonable hypothesis to explain the evolutionary relationships among the taxonomic units included in the analysis. Two of the most essential decisions that go into this analytical method are as follows: (1) which fossils are clustered together as a species or population to form an operational taxonomic unit (OTU) and (2) the definition of the characters and the character states that are included in the matrix. We will first consider the definition of characters and then demonstrate what two genetically defined traits can reveal about the evolutionary history of the family Hominidae.

The characters employed in phylogenetic systematics are assumed to reflect genetically, developmentally, and functionally independent anatomical traits that can be discretely coded for each OTU (e.g., Dembo et al. 2015; Nevell and Wood 2008; Smith and Grine 2008; Strait and Grine 2004). Knowing that some error is included in these matrices due to our lack of knowledge about the underlying biology, many researchers have increasingly relied on the more-is-better approach. For example, previous analyses include a range from 99 to 380 characters within the primate dentition and skull (e.g., Dembo et al. 2015; Nevell and Wood 2008; Smith and Grine 2008; Strait and Grine 2004). The craniodental character matrices employed in these hominid phylogenetic analyses, while well-intentioned, are hindered by a lack of knowledge about the anatomy's biological etiology. The vertebrate skull is significantly influenced by pleiotropic, epistatic, epigenetic, and systemic effects (Square et al. 2017; Ziermann et al. 2019), calling into question the ability to define hundreds of developmentally, genetically, and functionally independent traits. While there have been repeated warnings over the last 30 years about the use of so many characters blind to their underlying genetic and developmental architectures (e.g., Hawks 2004; Hlusko 2004; Lovejoy et al. 1999, 2003; McCollum 1999; Trinkaus 1990), these cautions have largely gone unheeded because there was no immediate solution to the issues raised. Most paleoanthropologists agree that atomizing anatomical variation blind to the underlying biology is likely misleading, but until that biology is better understood and operationalized, there is no clear path forward.

Scientific knowledge of the developmental and genetic etiology of the dentition is now at the level that it can be operationalized for phylogenetic systematics. Before we describe how, we briefly review the deep understanding that biologists have gained about the relationship between genotype and phenotype for the mammalian dentition. Our insight comes from two distinct—and sometimes seemingly disparate—approaches, those that are gene-forward and those that are phenotype-back.

Research in developmental genetics takes a gene-forward approach to mapping the relationship between genotype and phenotype. Decades of dental developmental research on model organisms, such as mice, has been motivated by the goal to bioengineer teeth (Thesleff 2018). These developmental genetic studies have revealed that mesenchymal–epithelial interactions are involved at all stages of dental development, as are major gene signaling networks such as the WNT, BMP, FGF, SHH, and EDA pathways (reviewed in Balic 2019 and Balic and Thesleff 2015). At the earliest stage of tooth development (which occurs at embryonic day 11 in mice, E11), epithelial tissues in the dorsal region of the oral cavity initiate tooth development by migrating ventrally through the oral mesenchyme to points of *Shh* signaling, forming a concentrated band of epithelial cells called the dental lamina (Prochazka et al. 2015). By mouse E12, a cluster of epithelial cells forms an "initiation knot," the first of three subsequent signaling centers. The initiation knot is matched by a concentration of mesenchymal cells that take over the developmental potential, forming a localized placode that serves as a precursor to an individual tooth (reviewed in Balic 2019). The placodal epithelium is induced to differentially grow further into the mesenchyme, forming the tooth bud stage of development. Condensations of epithelial cells then form the second signaling center, the enamel knot (Balic 2019; Balic and Thesleff 2015; Thesleff and Jernvall 1997), and locally express signaling molecules that stimulate epithelial growth even more, forming cervical loops that demarcate the cap stage of tooth development. More specific differential epithelial growth shapes the tooth crown via the third stage of signaling centers—secondary enamel knots—that pattern the position and size of each cusp during the bell stage of development (Matalova et al. 2005). Computer modeling of the interactions among the signaling molecules involved in the enamel knots provides interesting recapitulation of the evolution of some dental morphologies (Harjunmaa et al. 2014; Salazar-Ciudad 2012; Salazar-Ciudad and Jernvall 2010), suggesting that we may well be close to understanding the G:P map for tooth morphogenesis. These advances in our understanding of how a tooth initiates and matures demonstrate how close we are to the ultimate goal of re-growing a patient's lost tooth (Li et al. 2019).

However, from an evolutionary phylogenetic systematics perspective, these major gene signaling networks (e.g., WNT, BMP, FGF, SHH, and EDA pathways) represent a complicating factor for defining use-able traits and character states. While variation in the spatial expression of these pathways corresponds to differences in dental patterning across vertebrates (Lainoff et al. 2015; Moustakas et al. 2011), these networks are involved at essentially all stages of dental development, and significant shifts in their activities have effects that span far beyond individual teeth (reviewed in Balic and Thesleff 2015). For example, in mice, increased *Wnt* signaling

in the mesenchyme inhibits the sequential formation of teeth (Järvinen et al. 2018), whereas an increase in the activity of the ectodysplasin pathway results in larger and supernumerary teeth (Mustonen et al. 2003). Ectodysplasin's influence is even more pervasive; it also influences a suite of ectodermally derived structures, ranging from hair to mammary glands, that are often targets of selective pressures distinct from those acting on the dentition (Sadier et al. 2014; and for example, Hlusko et al. 2018). Due to the pleiotropic effects of these pathways, the dentition is difficult to parse into developmentally and genetically independent characters that will accord with the assumptions of phylogenetic systematics.

Quantitative genetic analyses are a phenotype-back approach that serves as a nice complement to developmental genetics. In quantitative genetics, researchers can identify and quantify pleiotropic effects on phenotypic variation using anatomical assessments that are commonly used by paleontologists. While the specific gene or base pair sequence underlying variation in these anatomies may not immediately be identified using this approach, the architecture of the genetic influences is discernible, i.e., the magnitude of genetic influence and patterns of genetic correlations. This information is extremely useful for paleontologists as it reframes how phenotypic variation is conceptualized. Most critically, results from quantitative genetic analyses of primate dental variation reveal that individual teeth are not genetically or developmentally independent structures, as they have long appeared to be. The size of the anterior teeth is genetically independent of the size of the postcanine dentition (Hlusko et al. 2011), but there is significant pleiotropy between the premolars and molars (Grieco et al. 2013; Hlusko et al. 2011). Furthermore, while molar width is genetically correlated with body size, molar length is not (Hlusko et al. 2006). We have also learned that different aspects of a tooth are underlain by different biological etiologies. For example, quantitative genetic analyses have revealed that minor shape variants on the crown are genetically independent of tooth size (Stojanowski et al. 2018). Detailed histological investigations have shown that genetic effects on enamel mineralization affect all teeth (Smith et al. 2017), but species-specific timing of enamel deposition can differ by tooth (Smith et al. 2007). These different patterns of pleiotropy highlight how important it is for paleontologists to understand anatomical variation as the output of underlying genetic/developmental processes.

Accordingly, hypotheses about the evolution of the dental arcade should focus on assessments of phenotypic variation that best reflect the underlying genetic architecture (Hlusko 2016; Hlusko et al. 2016). From the perspective of how the dentition is patterned by genetic effects (as described above), we know that it is variation in relative sizes of the teeth that will evolve over time and not the specific size of any one tooth. Our research group previously identified two traits that capture the output of two postcanine genetic patterning

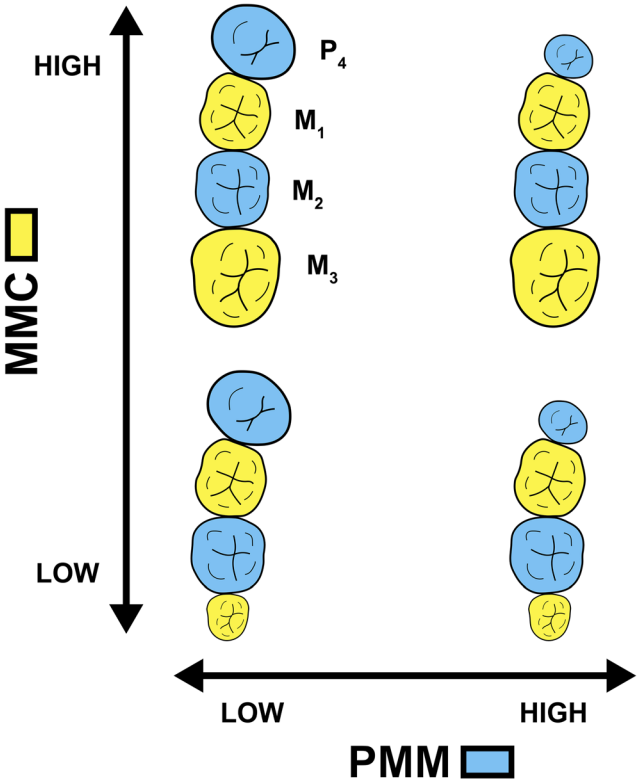

Fig. 1 Qualitative visualization of the molar module component (MMC) and premolar–molar module (PMM) phenotypic axes

mechanisms via ratios that reflect relative sizes of teeth in the submodules (Fig. 1; Hlusko et al. 2016). They are defined as

$$\text{Molar Module Component : MMC} = M_3L/M_1L$$
$$\text{Premolar–Molar Module : PMM} = M_2L/P_4L$$

where M and P refer to molar and premolar, respectively; subscripts denote the tooth position; and L refers to mesiodistal tooth crown diameter. The genetic variance that underlies the phenotypic variance in relative lengths of the premolars versus molars is reflected in the PMM (x-axis of Fig. 1; Hlusko et al. 2016). The MMC reflects the genetic variance that underlies the phenotypic variance within the molar submodule (y-axis of Fig. 1; Hlusko et al. 2016). These traits are heritable, uncorrelated, and independent of body size (Hlusko et al. 2016), making them ideal for elucidating the evolutionary history of the postcanine dentition independently from the evolution of body size, sex, the anterior dentition, etc.

Variation in MMC may well be due, in part, to genetic variation associated with the inhibitory cascade (IC) identified through developmental studies on mice (Kavanagh et al. 2007). However, the direct connection between MMC and the IC developmental mechanism has yet to be confirmed outside of the Murinae. Additionally, the IC alone has been

shown to be a poor model for the variation observed in molar size among primates (Roseman and Delezene 2019), and particularly hominoids (Carter and Worthington 2016). Therefore, we prefer to be conservative and use the term MMC rather than IC for this phenotype until the developmental causality is determined.

These two genetically patterned dental traits were recently assessed in a large sample of extant boreoeutherian mammals, for which a secure molecular phylogeny was available (Monson et al. 2019). Both MMC and PMM were found to have significant phylogenetic signal, supporting the taxonomic and phylogenetic utility of these traits in evolutionary analyses. Building on our primate genetic–neontological–paleontological research (Hlusko et al. 2016), the boreoeutherian research further demonstrated that MMC and PMM can be reliably used to understand phylogenetic relationships in fossil taxa. With the confidence derived from these other studies, we now apply the MMC and PMM traits to a detailed paleontological investigation of the evolutionary history of one mammalian family, the Hominidae.[1]

Material and methods

Sample

We calculated MMC and PMM from the mesiodistal measurements of the mandibular fourth premolar and first through third molars (data reported in Online Resource 2) for fossil hominid groups as well as African Miocene apes and extant apes ($n = 325$ total specimens). The African Miocene apes provide context for the phenotypic evolution of hominids and extant apes, as they record the range of variation known to have existed before the chimp:human last common ancestor. Extant apes provide a sense of the range of variation today.

We gathered data for fossil groups from publications and for extant taxa from original specimens (see Table 1 for sample sizes and repositories). Following Hlusko et al. (2016), we collected only mandibular data, and we focused on the left side of the dentition, although right side data were used if the left was unavailable. The limited and unequal sample sizes across groups are a reflection of the fossil material available.

Given the controversy that surrounds the taxonomy of the included fossil assemblage, we describe in detail our terminology:

- There is debate as to whether or not the species *boisei* and *robustus* belong in *Australopithecus* or represent the genus *Paranthropus* (McCollum 1999; Ungar and Hlusko 2016; Wood and Schroer 2017). We refer to them as *Australopithecus boisei* and *Au. robustus* herein.
- It has been suggested that the recently named species *Australopithecus deyiremeda* (Haile-Selassie et al. 2015) is likely a junior synonym for *Australopithecus afarensis* (Wood and Boyle 2016). We follow this more conservative taxonomic classification here and include the single mandibular specimen with dentition from this hypodigm within *Australopithecus afarensis*.
- Considering the unstable nature of species definitions and identifications in early *Homo* taxa (Antón et al. 2014; Suwa et al. 2007), *Homo habilis* and *Homo rudolfensis* are pooled in all analyses as "Early *Homo*."
- *Homo erectus* is divided into African and Asian samples as a means of partitioning the large geographic span of this taxon. While each of these samples encompasses a broad temporal range, we have not further parsed this taxon into temporal categories in order to maintain more moderate sample sizes.
- *Homo sapiens* (Levant), which includes Skhul and Qafzeh specimens, is included as a separate group since these specimens have been noted as distinct from modern humans in various aspects of their anatomy (Thackeray et al. 2005; Trinkaus 2005).
- For the Miocene apes, following Hlusko et al. (2016), specimens from Kelley et al. (2002) described as *Equatorius africanus* are included here as *Kenyapithecus africanus* (following Pickford and Kunimatsu 2005), and specimens from Pickford et al. (2009) described as *Ugandapithecus major* are included here as *Proconsul major* (Harrison and Andrews 2009). *Ekembo heseloni* and *Ekembo nyanzae* are included here as distinct from *Proconsul* following recent systematic revision (McNulty et al. 2015).

Analytical methods

Statistical analyses were completed in the R statistical environment v3.2.2 (R Core Team 2015). We first calculated univariate descriptive statistics for MMC and PMM values for all taxa included in the study, using built-in functions in R. We next visualized the distribution of the MMC and PMM traits across taxa in boxplot and bivariate plot form, produced in R using the package *ggplot2* (*v1.0.1*; Wickham 2009). Our subsequent statistical tests fall into two main categories of analysis: species-level comparisons and genus-level comparisons.

In order to determine if MMC and PMM could discriminate between taxa at the species-level, we first employed the

[1] To maintain consistency with the traditional adaptive grade-based definition of the human clade, from here on we refer to all taxa on the human side of the chimpanzee/human divergence as the Hominidae.

Table 1 Number of specimens per group included in this study

	Number	Source/Repository
Pongo pygmaeus	10	Cleveland Museum of Natural History, Cleveland, Ohio, USA
Gorilla gorilla	41	Cleveland Museum of Natural History, Cleveland, Ohio, USA
Pan troglodytes	59	Cleveland Museum of Natural History, Cleveland, Ohio, USA
Pan paniscus	39	Royal Museum of Central Africa, Tervuren, Belgium
Homo sapiens (Modern)	27	Phoebe A. Hearst Museum of Anthropology, Berkeley, California, USA
Homo sapiens (Levant)[a]	2	Suwa et al. (2009)
Homo neanderthalensis[a]	15	Quam et al. (2001), Suwa et al. (2009), Trinkaus (1978), and Wolpoff (1979)
Homo heidelbergensis	26	Bermúdez de Castro (1993), Gabunia and Vekua (1995), Howell (1960), and Martinón-Torres et al. (2012)
Homo antecessor	1	Carbonell et al. (2005)
Homo floresiensis	1	Kaifu et al. (2015)
Homo erectus (Asia)	9	Kaifu et al. (2005), Lordkipanidze et al. (2013), Macaluso Jr. (2010), Rightmire (1990), and Weidenreich (1937)
Homo erectus (Africa)[a]	8	Arambourg and Hoffstetter (1963), Rightmire (1990), Suwa et al. (2009), Walker and Leakey (1993), Wood (1991), and Wood and Van Noten (1986)
Homo naledi[b]	3	Hawks et al. (2017)
Early *Homo*[a]	8	Leakey et al. (2012), Suwa et al. (2009), Villmoare et al. (2015), and Wood (1991)
Australopithecus robustus[a]	13	Suwa et al. (2009)
Australopithecus africanus[a]	5	Suwa et al. (2009)
Australopithecus boisei	5	Wood (1991)
Australopithecus garhi[a]	2	Suwa et al. (2009)
Australopithecus afarensis[a]	15	Haile-Selassie et al. (2015); Suwa et al. (2009), White et al. (2000)
Australopithecus anamensis	3	Ward et al. (2001)
Ardipithecus ramidus	3	White et al. (2015)
Kenyapithecus africanus	2	Kelley et al. (2002) and Pickford (1985)
Rangwapithecus gordoni	3	Cote et al. (2014) and Hill et al. (2013)
Ekembo nyanzae	5	Le Gros Clark (1952), Le Gros Clark and Leakey (1951), and Pickford et al. (2009)
Ekembo heseloni	6	Pickford et al. (2009)
Proconsul major	6	Le Gros Clark and Leakey (1951), Pickford et al. (2009), and Martin (1981)
Proconsul africanus	4	Le Gros Clark (1952); Le Gros Clark and Leakey (1951)
Limnopithecus legetet	1	Harrison (1981)
Micropithecus clarki	2	Harrison (1981)
Afropithecus turkanensis	1	Rossie and MacLatchy (2013)
Total	325	

[a] Includes data from Suwa and colleagues (Suwa et al. 2009) and references therein

[b] Includes data provided by L. Delezene

Wilcoxon rank-sum test, a non-parametric alternative to the two-sample *t* test, using built-in functions in R. This analytical approach enabled us to include all of the samples for which $n > 2$, regardless of the differences in sample size and variance. For the samples with $n > 20$, we then employed the Shapiro–Wilk normality test ($p > 0.05$) and Levene's test for homogeneity of variance across groups ($p > 0.05$) in R using the package *car* (*v2.1.0*; Fox and Weisberg 2011). Samples found to be normally distributed and with equal variances were also subjected to a two-sample *t* test, using built-in functions in R. Our goal for conducting this second set of analyses was to provide a parametric comparison for the non-parametric analysis conducted on the full set of data.

We then pursued a set of analyses aimed at probing the genus-level questions posed by the visualization of the data. As for the species-level analyses, we employed both the Wilcoxon rank-sum test for the full data set and the two-sample *t* test when appropriate, as described above. In order to assess variance within (putative) genera and evaluate whether patterns differ between MMC and PMM, we

employed a non-parametric ANOVA, the Kruskal–Wallis rank sum test, using built-in functions in R.

As all of these sets of analyses are comprised of multiple comparisons, there is a concern about false positives. In addition to the statistics embedded in the analyses themselves, we also applied a Bonferroni adjustment and a Welch's ANOVA with a Games–Howell post hoc test (which is robust against variance differences and allows for samples of different sizes). The latter test was completed using the package *userfriendlyscience* (*v0.7.2*; Peters 2018) in R v3.5.1. That said, Bonferroni's adjustment is an extremely harsh correction. For example, with 231 comparisons (as we conduct for the species-level Wilcoxon rank-sum test), the significance would be set at $p < 0.0002165$ rather than $p < 0.05$. We present results from all three approaches—no correction for multiple tests, Bonferroni's adjustment, and Welch's ANOVA with the Games–Howell post hoc test. Statistical significance is a fairly arbitrary convention, in which the researcher imposes an artificial division between significant and non-significant *p*-values along a continuous range of values (Berger and Berry 1988; Johnson 1999). Here we follow general convention by placing our significance threshold at $p < 0.05$, but we focus more closely on the pattern of *p*-values across comparisons and less on the arbitrarily defined degree of statistical significance.

Results

Univariate descriptive statistics for MMC and PMM are presented in Tables 1 and 2 in Online Resource 1 and shown visually in boxplots (Fig. 2) and a bivariate plot (Fig. 3).

Results for MMC

From the visualization of MMC in Fig. 3, specimens in genus *Homo* primarily cluster at the lower part of the *y*-axis, and all other fossil specimens are in the upper portion. Figure 2 demonstrates this same pattern but also includes data from the extant great apes. We see that most of the Miocene apes and species within *Ardipithecus*, *Australopithecus*, and *Gorilla* fall at the higher range of MMC, whereas *Homo*, *Pan*, and *Pongo* have lower MMC values. Within *Homo*, *H. naledi* and Early *Homo* cluster near the values observed for all species of *Australopithecus* and *Ardipithecus* save for *Au. boisei*. The Wilcoxon rank-sum test reveals the statistical significance of this same pattern (Fig. 4), and the more stringent statistical significance standards reported in Figs. 1 and 2 in Online Resource 1 demonstrate the same pattern, though to varying degrees of statistical significance. The *Gorilla* MMC is distinct from Miocene apes and *Homo*, but not from *Ardipithecus*, *Australopithecus*, Early *Homo*, and *H. naledi* (as similarly reported elsewhere, Monson et al. 2018a). *Pongo* and *Pan* MMC means are distinct from the Miocene apes, *Ardipithecus*, *Australopithecus*, *Early Homo*, and *H. naledi*, but are not distinct from *Homo*.

We then pooled these data into groups that accord with these qualitative observations. We created a group for *Homo* that excluded Early *Homo* and *H. naledi* and compared this with Early *Homo* and *Australopithecus*. Wilcoxon rank-sum test results (Table 3 in Online Resource 1) also show the distinction in MMC between *Homo* and *Australopithecus*, and the similarity of Early *Homo* with *Australopithecus*.

Eight of our samples were large enough to probe using parametric tests, with sample sizes that range from $n = 20$ to $n = 82$ (Table 1; Table 4 in Online Resource 1). Shapiro–Wilk normality test results and Levene's test for homogeneity of variance identified six samples that could be employed in a two-sample *t* test (Tables 4 and 5 in Online Resource 1). Results from these analyses reveal the same pattern observed for the larger non-parametric series of analyses, with all samples being different save for *Homo sapiens* (modern) compared with *Pan paniscus* (Table 6 in Online Resource 1). Results from the Kruskal–Wallis rank sum test are also consistent with results from pairwise comparisons. The results reveal statistically significant differences across species within all pooled groups for MMC, except for *Australopithecus* and the group for *Homo* that excludes Early *Homo* and *H. naledi* (Table 7 in Online Resource 1).

Results for PMM

Turning to the PMM results, we see a more varied pattern across species within the same genus (Figs. 2 and 3). Within the fossil hominids, we see a gradual decrease in PMM from *Ardipithecus ramidus* to *Australopithecus anamensis* to *Au. afarensis*. Within *Homo*, *neanderthalensis* and *heidelbergensis* show comparatively higher PMM values, similar to those for *Ar. ramidus*, *Au. anamensis*, an *Au. afarensis* and generally above those of fossil and modern *H. sapiens*. At the opposite end of the PMM range, *Au. boisei* stands out as having low values among the fossil taxa, similar to *Pongo* among the extant apes. *Pan*, *Gorilla*, and modern *Homo* all have overlapping ranges of variation around a more moderate PMM mean. The Miocene apes reveal a considerable range of variation in PMM.

The Wilcoxon rank-sum test reveals that there is statistical significance to these observations (Fig. 4), and the parametric tests further bolster the pattern (Table 6 in Online Resource 1; see Figs. 1 and 2 in Online Resource 1 for results that address multiple testing). Results from the Kruskal–Wallis rank sum test also indicate a more variable pattern across congeneric species than observed for MMC. The results reveal statistically significant differences across species within all pooled groups for PMM (Table 7 in Online Resource 1). In contrast to MMC, variation in PMM across taxa/species does not appear to cluster in genus-level patterns.

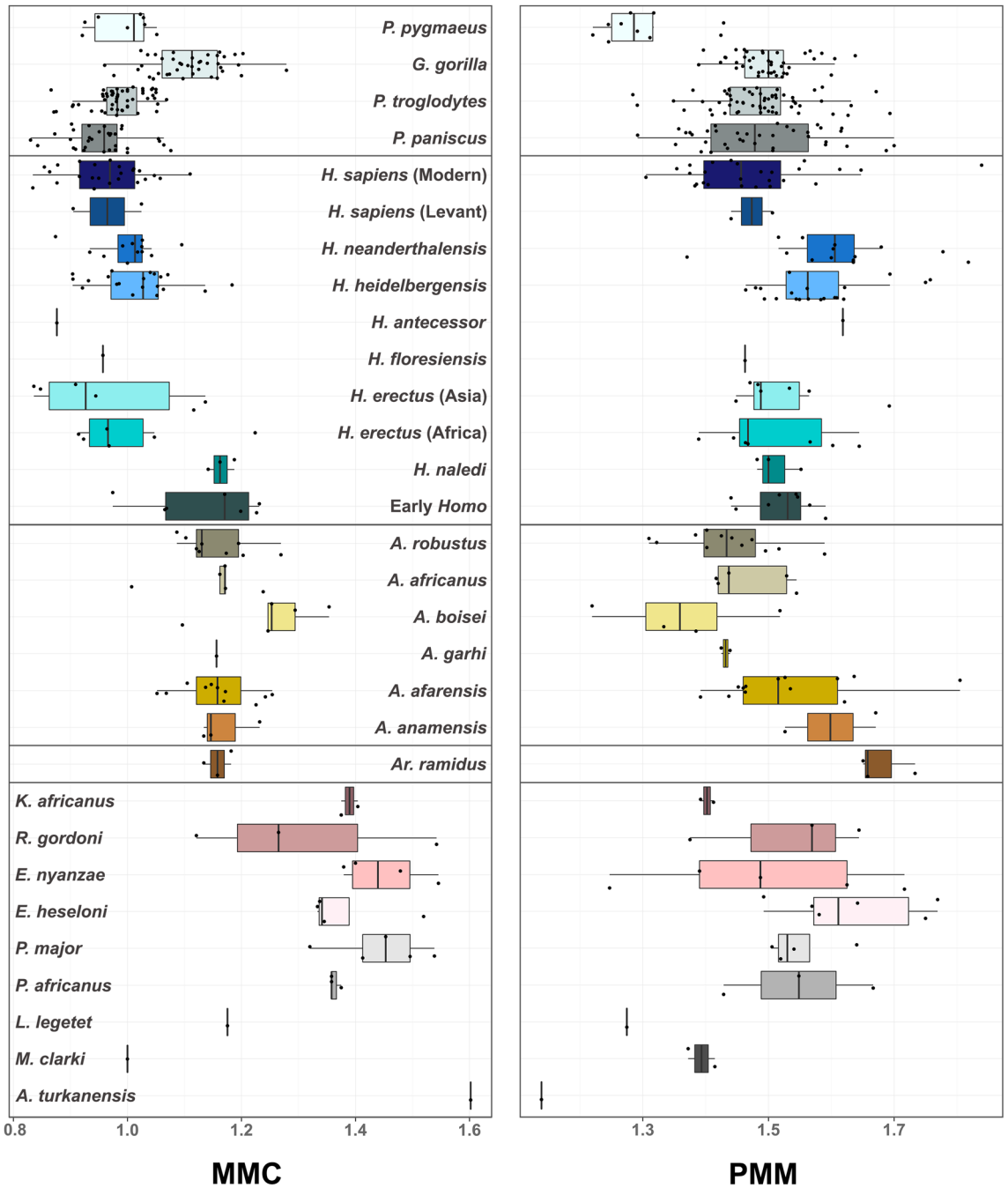

Fig. 2 Boxplots of the molar module component (MMC) and premolar–molar module (PMM) phenotypes, demonstrating the variation across extant apes, members of genus *Homo*, early hominids, and African Miocene apes. Note that MMC values are similar within genus *Homo* and within early hominids, with the exception of *Homo naledi* and early *Homo*, which align more closely with early hominids than with the other *Homo* groups. PMM values are recognizably less similar within *Homo* and early hominids than MMC values

Discussion

We tested the hypothesis that two traits, MMC and PMM—defined to reflect the output of two genetic mechanisms underlying variation in the primate postcanine dentition—would provide new insight into hominid evolution by revealing significant shifts in the output of those genetic mechanisms over geologic time. As would be predicted when analyzing two genetically independent traits (Hlusko et al. 2016), we find that PMM and MMC reveal different patterns of variation and evolution. Our results, taken together with previous findings from boreoeutherian mammals (Monson et al. 2019), suggest that MMC is relatively stable, by which we mean more congruent with phylogeny, whereas PMM is more evolutionary labile. We will focus our discussion first on MMC, a ratio that captures the relative size variation within the molar

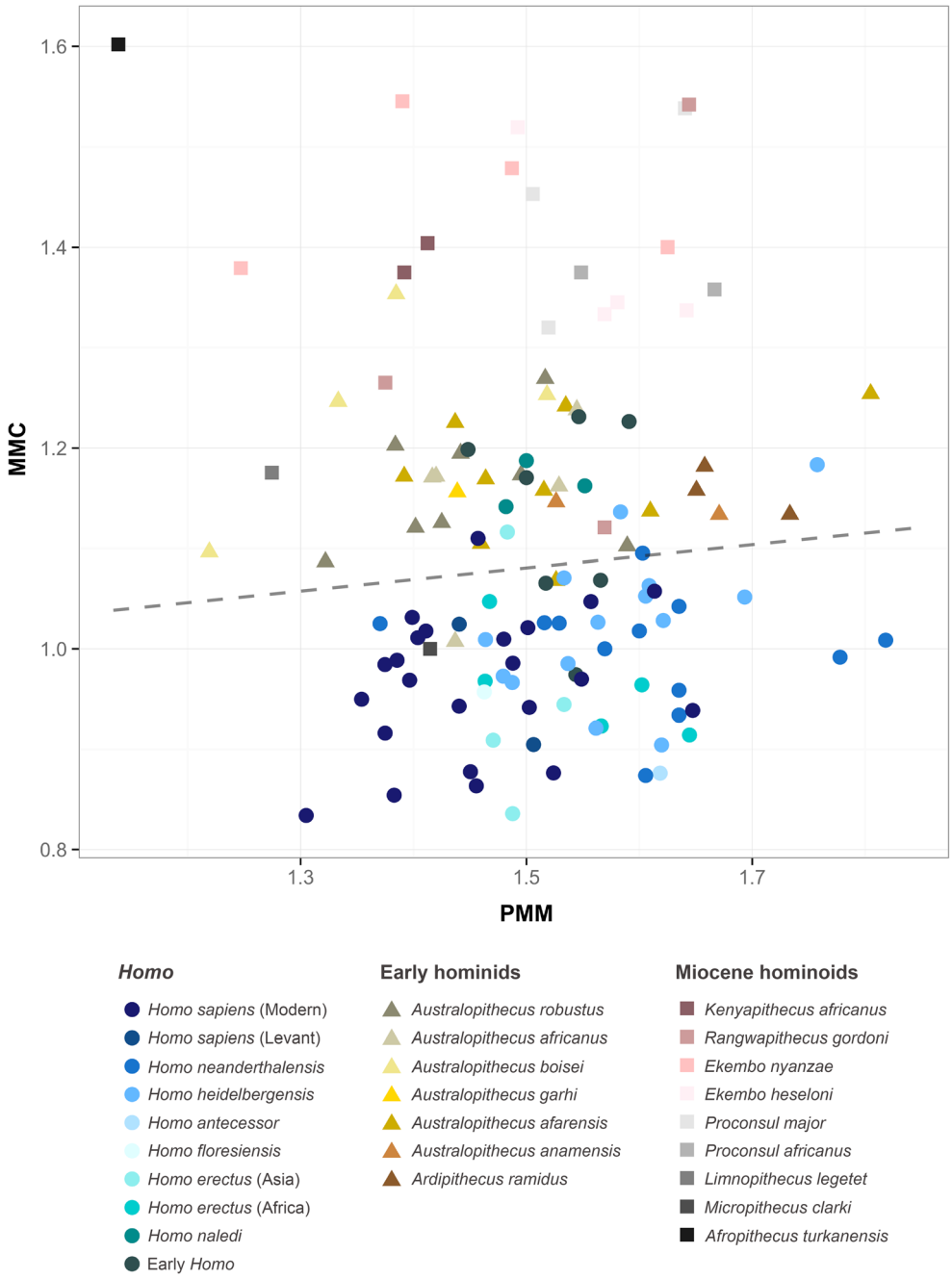

Fig. 3 Bivariate plot of the molar module component (MMC) and premolar–molar module (PMM) phenotypes for all fossil groups and extant modern humans. The phenotypes discriminate between *Homo*, early hominids, and the African Miocene apes. The dashed line is a qualitative indication of the separation between *Homo* and early hominids; the overlap between *Homo* and early hominids is due in large part to the position of *Homo naledi* and Early *Homo*

series, and then turn to PMM, which captures relative size variation between the premolar and molar modules. We then apply these results to three taxonomic questions within hominid evolution.

Evolutionary history of MMC

The hominid MMC decreases from the Late Miocene through to modern humans (Fig. 2; taxa are generally arranged from more recent toward the top to deeper in time toward the bottom). Paleontologists have not yet recovered a fossil record of the chimp:human last common ancestor. However, *Gorilla* MMC values are in the same range as the early hominids *Ardipithecus* and *Australopithecus*, suggesting that the last common ancestor likely had an MMC range similar to these taxa. A recent machine learning-based assessment of hominoid variation in PMM and MMC supports this inference (Monson et al. 2018a). While Miocene apes are more similar to *Pan* than *Gorilla* in absolute dental size and tooth area, they are more similar to *Gorilla* in terms of dental proportions. This similarity in MMC and PMM between Miocene taxa and *Gorilla* suggests that humans, chimpanzees, and orangutans

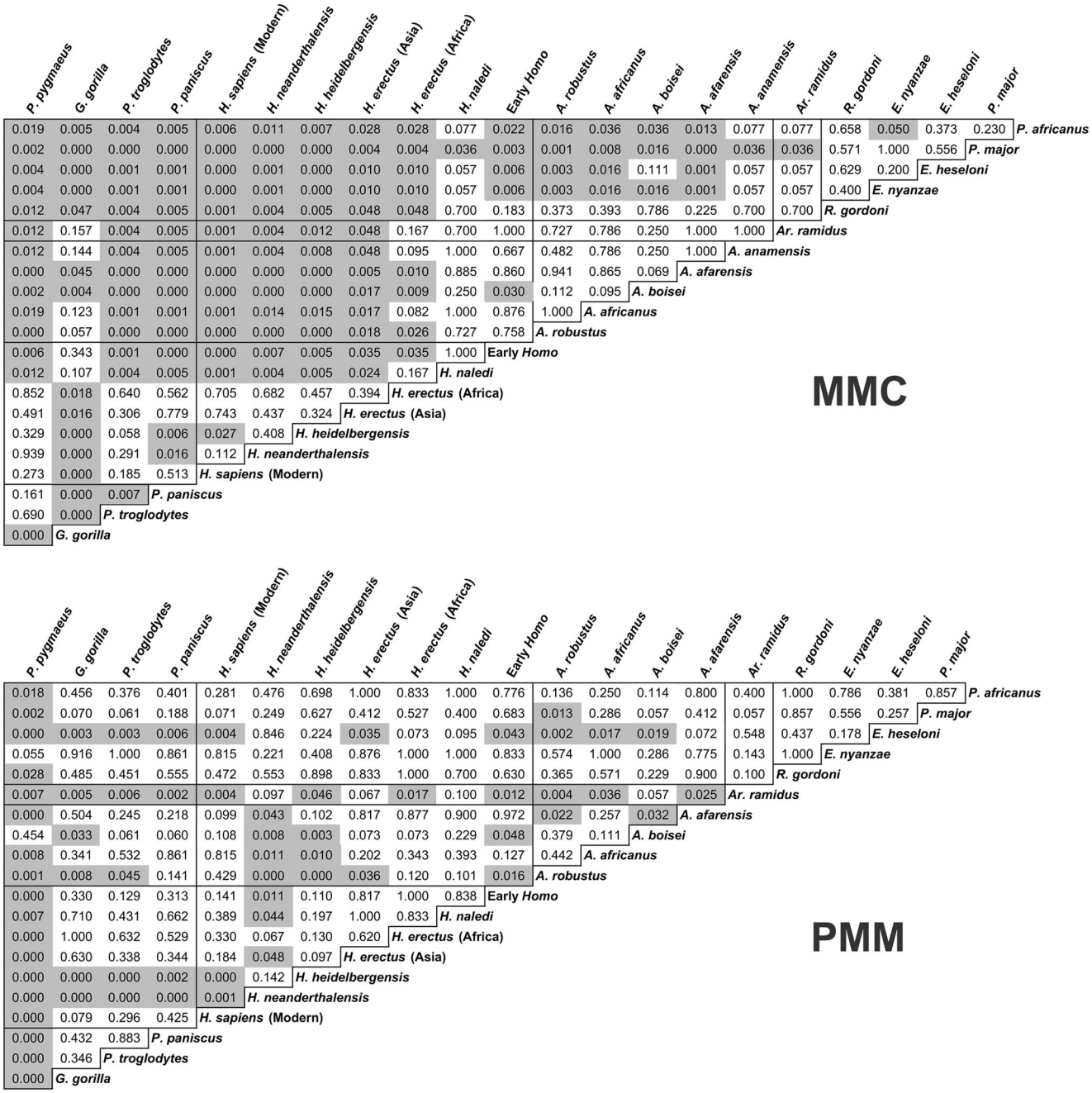

Fig. 4 Wilcoxon rank-sum test results for the molar module component (MMC) and premolar–molar module (PMM), visualized as pairwise comparison matrices. Only groups with $n > 2$ were included in this analysis. Pairs with significant differences ($p < 0.05$) are shaded gray

are derived in their dental proportions and that *Gorilla* is a better extant model for the chimp:human last common ancestor when considering postcanine proportions (Monson et al. 2018a).

There is a distinct shift to lower MMC values first observed with *Homo erectus* that persists through later populations in the genus *Homo*. Although we have not yet identified the specific genetic mechanism that underlies MMC, variation in this trait may well reflect major shifts in dietary adaptation (e.g., Kavanagh et al. 2007) or possibly systemic effects such as ontogenetic variation in growth rates (e.g., Monson et al. 2018b). Either way, based on our current understanding of MMC, it is not unreasonable to interpret these clusters of MMC values as a reflection of adaptive niches, or adaptive plateaus (e.g., White et al. 2015).

Prior studies of hominid evolution concluded that there is no clear adaptive shift between *Australopithecus* and early *Homo* (Kimbel and Villmoare 2016). Consequently, these scientists conclude that the rank of genus is a necessary unit for classification but essentially irrelevant to evolutionary theory.

Foley et al. (2016) suggest that the apparent lack of a transition between *Australopithecus* and *Homo* could be due to the incorrect placement of the boundary between genera. Indeed, Wood and Collard (1999b) recommend transferring early *Homo* taxa to *Australopithecus* on the basis of a shared adaptive strategy. An adaptive shift could also be elusive because the investigation of the anatomical variation in previous studies does not accurately capture the output of the evolving genetic mechanism(s). By using a G:P mapped trait, our analysis of MMC supports the hypothesis that there is a distinction between *Australopithecus* and *Homo* (Foley et al. 2016; Wood and Collard 1999b). We find that the Early *Homo* sample reflects the earlier MMC niche and therefore may be more appropriately designated *Australopithecus*. A previous attempt to apply "rules" about the inhibitory cascade to hominid evolution similarly interpreted *Homo* as distinct from other hominids, although their use of 2-dimensional crown area (rather than G:P defined ratios) incorporated the pleiotropic effects of body size into their analysis, leading to a more convoluted set of results (Evans et al. 2016).

While we see MMC as a highly informative trait, we want to be clear that genus definitions cannot rely on one trait alone. For example, *Ardipithecus*, *Australopithecus*, and *Gorilla* have indistinguishable MMC values, but simultaneously have dramatically different locomotory repertoires (Tuttle and Watts 1985; Ward 2013; White et al. 2015). The similarity of their MMC values indicates that the different adaptive niches these genera occupy/ied did not drive a differentiation in the genetic mechanism that influences the relative sizes of the molars. Different phenotypes can, and often do, yield different conclusions about boundaries and relationships between hominid genera (Strait et al. 1997; Wood and Collard 1999a). As we learn more about the relationship between genotype and phenotype, and hone our paleontological studies to rely more on traits that have a higher fidelity to the underlying genetic architecture, the seemingly mosaic nature of evolution will shift from a conundrum to a rich source of paleobiological insight (Hlusko 2004, 2016).

Evolutionary history of PMM

In contrast to the stability we observe for MMC, variation in PMM appears to capture the influence of a more evolvable mechanism. In early hominids, PMM values decrease over time, from *Ardipithecus ramidus* at the older end to *Australopithecus anamensis* ➔ *Australopithecus afarensis* ➔ *Australopithecus garhi* at the younger end, likely evidence of an evolving lineage (Asfaw et al. 1999; Kimbel et al. 2006; Leakey et al. 1998; White et al. 2009). In later *Homo*, PMM values increase in the *Homo erectus* ➔ *Homo heidelbergensis* ➔ *H. neanderthalensis* lineage (following the phyletic relationships of Arsuaga et al. 2014 and Meyer et al. 2016), resulting in a statistically significant difference from modern humans. These two trends suggest that PMM (reflecting variation between the premolar and molar modules) may permit division of niche space on a different and more evolvable phenotypic axis relative to MMC, perhaps in some cases between contemporaneous, sympatric species that may be competing for resources (i.e., Schroer and Wood 2015a).

Application to phylogenetic quandaries

The distinct evolutionary patterns of MMC and PMM are not surprising given that they capture the phenotypic output of two genetically independent modules (Grieco et al. 2013; Hlusko et al. 2011; Hlusko and Mahaney 2009; Gómez-Robles and Polly 2012). Genetic modularity is known to influence the evolutionary trajectory of a lineage (Goswami and Polly 2010; Marroig et al. 2009; Schluter 1996, 2000). As we further understand the genetic underpinnings of MMC and PMM, both may prove to be informative of paleobiology, the mode and pace of evolution, and at different levels of taxonomic classification. Even at this early stage of discovery through G:P mapping, there are several taxonomic puzzles within hominid evolution to which our analyses of MMC and PMM provide insight and intrigue.

Paranthropus or *Australopithecus*?

Variation in MMC can be brought to bear on the long-standing debate of how to classify the two dentally robust species, *boisei* and *robustus*. There is considerable debate as to whether or not the robust masticatory features and megadontia of these two species are shared derived characters (synapomorphies) or reflect convergence (homoplasy) (Ungar and Hlusko 2016; Wood and Schroer 2017). The answer to this question determines whether we place these two species in their own genus *Paranthropus* or keep them in *Australopithecus*. For PMM, we see that both *boisei* and *robustus* differ significantly from other species of *Australopithecus*. But for MMC, we find no statistically significant differences between the six species of *Australopithecus* included in our analysis, including *boisei* and *robustus* (Fig. 4). However, *robustus* and *boisei* do differ to some degree in their MMC values. *Au. robustus* falls well within the observed ranges of variation for other species of *Australopithecus*, while *boisei* MMC values are noticeably higher. Given how stable MMC is over evolutionary time across the hominid taxa sampled here, and the primates published previously (Hlusko et al. 2016), this observation suggests that the megadontia is underlain by similarity in PMM but potentially different MMC niches. However, we must be mindful of the small sample sizes (Table 1), which may inadequately sample variation in these fossil species and create an artificial distinction between them. Looking to

taxa with larger samples, such as modern *H. sapiens*, we observe a much greater PMM range relative to most fossil *Homo* samples, which is most likely an effect of more thorough sampling. Nonetheless, given the limited available data, *Au. boisei* appears to deviate from its congeneric species in both PMM and MMC, whereas *Au. robustus* only differs in PMM. As mentioned above, it may be that these differences between the two robust species reflect variation in growth rates during ontogeny, perhaps an indication of variation in dietary niche; the precise underlying cause of these differences remains unclear until the specific genetic loci influencing MMC and PMM are identified.

While cladistic analyses continue to cluster these two species together exclusively (supporting the genus level distinction as *Paranthropus*), research that approaches the anatomical variation from a genetic/developmental perspective consistently reaches the opposite conclusion. For example, Schroer and Wood (2015b) tested predictions based on the inhibitory cascade hypothesis and similarly concluded that the megadontia of these two species is a convergence rooted in different developmental bases. A developmentally based approach to palatal structure also concluded that *boisei* and *robustus* represent convergence (McCollum 1999). Megadontia may well be an evolutionary path of least resistance that offers a common solution to a variety of different selective pressures (Ungar and Hlusko 2016). As the evidence of convergence continues to build, the insight gained from our analysis of MMC and PMM further supports the conclusion that *boisei* and *robustus* are most appropriately classified in the genus *Australopithecus*.

Homo or *Australopithecus*?

There is also considerable debate regarding the classification of the small-bodied hominid from Indonesia, *Homo floresiensis* (Brown et al. 2004), and its systematic relationship to modern humans (Falk et al. 2007; Gordon et al. 2008; Hershkovitz et al. 2007; Martin et al. 2006; Morwood et al. 2005; Oxnard et al. 2010; Richards 2006). Following recent additional discoveries (van den Bergh et al. 2016), and a revised chronology that places these hominids on the islands prior to the documented arrival of modern humans (Sutikna et al. 2016), two main hypotheses for the evolutionary origins of *Homo floresiensis* have been proposed: (1) *Homo floresiensis* descended from the larger-bodied *Homo erectus*, undergoing an extreme reduction in size, or (2) *Homo floresiensis* descended from an earlier, smaller-bodied hominid, such as *Homo habilis* or a late member of *Australopithecus* (Argue et al. 2006; van den Bergh et al. 2016). We find that the *Homo floresiensis* MMC value is indistinguishable from *Homo erectus* and falls outside of the range of Early *Homo* and all species of *Australopithecus*. This alignment indicates that *Homo floresiensis* presents the derived MMC condition of the genus *Homo*.

Variation in MMC adds a surprising twist to the taxonomic affinity of *Homo naledi* (Berger et al. 2015). In MMC values, *H. naledi* aligns with Early *Homo* and *Australopithecus*, nearly outside the range of other members of *Homo*. This suggests that *H. naledi*, like Early *Homo*, may be more consistent with the ancestral MMC niche. This is surprising given the most recent geological age estimate of 236–335 ka (Dirks et al. 2017) and demonstrates our earlier point that classification should rely on multiple traits. The small sample size for *H. naledi* MMC values also makes any interpretation tentative at best.

The issue of rank equivalency

As we conclude, there is one additional implication of our research that merits discussion: the widely recognized dilemma within clade-based phylogenetic nomenclature that "equal ranks imply only exclusivity, not comparability" (Kuntner and Agnarsson 2006:777). Primates provide a few excellent examples of why a distinction between rank exclusivity and comparability is important. For example, current taxonomic practice is for the Linnaean Family Hylobatidae to refer to the gibbons and siamangs, and Hominidae to refer to all of the great apes—from the suspensory Asian orangutans to the knuckle-walking African gorillas and chimpanzees to the globally dispersed, bipedal, technology-dependent humans (Rowe and Myers 2016; Watts 2012). While these clades are equal in terms of systematic exclusivity, they clearly encompass very different degrees of adaptation. The amount of adaptive breadth across the great apes even exceeds the adaptive variation within the Cercopithecidae, the Family that includes all genera involved in the last six million years of the Old World Monkey radiation (Frost et al. 2011; Jablonski and Frost 2010). While a discussion about the loss of equivalency at the Family level needs to be had at some point, we raise this point here in order to focus attention on how genetically defined phenotypes can bring us toward establishing rank equivalency at least at the level of genera.

Linnaean rank equivalency may seem like an academic point, but this is an issue that should not be dismissed lightly given that evolutionary and conservation biologists widely assume that it exists at numerous hierarchical levels. This assumption is evident in pervasive rank-comparison statements, taxon counts, and analyses that rely on comparability across a particular rank (e.g., Kuntner and Agnarsson 2006). These analyses extend beyond the realm of neontology and conservation studies to impact our understanding of biodiversity and ecology in the past. Paleoecological inferences are often based on vertebrate faunal lists without consideration

of issues introduced by a lack of rank equivalency across the taxa being counted and compared (Bobe 2011; Curran and Haile-Selassie 2016; Patterson et al. 2017; Reed 2008; Su and Harrison 2015).

While taxonomy is rife with such conundrums, there is a strong argument for maintaining Linnaean binomial nomenclature (Kuntner and Agnarsson 2006:776). There is a convincing case as to why species should not be held to the rule of monophyly, as speciation is often reticulate and complex (Rogers and Gibbs 2014; Zinner et al. 2011). As just one example, recent findings from molecular genomics reveal complexity in species formation within cercopithecid monkeys (Detwiler 2019; Fan et al. 2018; Roos et al. 2019a, b; Wall et al. 2016) and highlight that species distinctions are highly labile and complicated by interbreeding (Rogers et al. 2019; Svardal et al. 2017). But how much variability should be accepted at the generic level? These studies (and others, e.g., Burrell et al. 2009; Osterholz et al. 2008) make apparent that genomics has had difficulty grappling with genus-level polyphyly and has not yet provided a clear solution to defining the boundaries of genera via genetic similarity, at least not in a way that reflects adaptive similarity (Di Fiore et al. 2015; Rogers et al. 2019; Svardal et al. 2017). Evolutionary biology is therefore at a crossroads: should we define genera to convey information about adaptive regime or prioritize taxonomic exclusivity in a way that species cannot?

As biologists continue to make gains in mapping the relationship between genotype and phenotype (Hlusko et al. 2016; Pigliucci 2010; Wagner and Zhang 2011), these insights can be incorporated into taxonomy to bring biological comparability back into our taxonomic ranks. We have demonstrated that these insights are now operational and that they enable us to utilize the genus as an adaptively informative taxon.

Conclusion

Biological organisms are not found with taxonomic labels affixed; it is the task of the researcher to classify organisms based on the available evidence. Whereas the neontologist has many lines of evidence from which they can draw taxonomic classifications (physiology, behavior, pelage, etc.), the paleontologist is reliant on a much more restricted dataset, primarily bones and teeth. We have shown that the use of anatomical traits developed through quantitative genetic analyses reveals novel patterns within the evolutionary history of the hominid dentition. The molar module component (MMC) is a relatively stable trait that may well reflect genus-level shifts in adaptation. The premolar–molar module (PMM) is more evolutionarily labile, providing insight to species-level distinctions. Our results demonstrate the promise of employing genetically defined traits, such as MMC and PMM, to classifying organisms in a more biologically informed way, and to elucidating their evolutionary histories.

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Data availability All data are included in the supplementary materials (Online Resource 2).

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