The functional significance of dental and mandibular reduction in *Homo*: a catarrhine perspective

Running title: Jaw reduction in hominins and catarrhines

Alessio Veneziano[1], Joel D. Irish[1,2], Carlo Meloro[1], Chris Stringer[3], Isabelle De Groote[1,3]

[1]School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, L3 3AF, UK

[2]Evolutionary Studies Institute and Centre for Excellence in PaleoSciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa

[3]Department of Earth Sciences, The Natural History Museum, London, SW7 5BD, UK

Corresponding author: Alessio Veneziano; veneziano.alessio@gmail.com; +44(0)7512389031

ABSTRACT

The reduction in dental size and mandibular robusticity is regarded as a major trend in human evolution, traditionally considered the result of the peculiar extra-oral food processing skills of *Homo*. The use of stone tools and fire would have allowed our ancestors to chew softer food in smaller bite size, thus relaxing the selective pressures to keep a large dentition and a robust lower jaw. This perspective assumes that differences in dental size and mandibular robusticity in hominins represent functional dissimilarities. This study uses a catarrhine comparative approach to test this fundamental assumption of the hypotheses on dental and mandibular reduction in *Homo*. A sample of extant catarrhines and fossil hominins was used to test for correlations between dental size, mandibular robusticity, and dietary proxies, the latter include diet quality, diet heterogeneity, feeding time, and microwear variables. The effects of phylogeny and body size were considered. Findings support the association between technological developments in *Homo* and reduction in incisor size and mandibular corpus robusticity, though not for premolar, molar size, and symphyseal robusticity. These results challenge the functional interpretation of postcanine reduction and symphyseal changes in the genus *Homo*.

KEYWORDS

Dental size; Lower jaw; Hominins; Human evolution; Comparative methods

1 | INTRODUCTION

Dental size and mandibular robusticity reduced during the evolution of the genus *Homo* (Brace, 1963; Chamberlain and Wood, 1985; McHenry and Coffing, 2000; Emes et al., 2011). Among hominins, differences in these features have been ascribed to dietary shifts or food processing. The big chewing surfaces, thick enamel and molar-like premolars of australopiths, in particular *Paranthropus* (Teaford and Ungar, 2000; Wood and Strait, 2004), are hypothesized to be the result of consumption of herbaceous vegetation and vegetal underground storage organs, following the transformation of forests into grasslands and savannahs (Kingston et al., 1994; WoldeGabriel, 1994). The genus *Homo* underwent a change in ecological niche probably linked to consumption of larger quantities of meat (Speth, 1989; Stanford and Bunn, 2001). It has been proposed that increased exploitation of this resource was made easier by improvements in food processing skills: the use of stone tools for slicing and pounding food items, and the ability to control fire for cooking (Wrangham, 2009; Zink and Lieberman, 2016) would have resulted in softening food texture. The food processing skills of *Homo* have been considered responsible for its reduction in mandibular robusticity and dental size (Brace, 1963; Calcagno and Gibson, 1988; Wrangham and Carmody, 2010; Zink and Lieberman, 2016).

From the above perspective, mandibular and dental reduction within *Homo* can be seen as the result of lowered functional requirements or natural selection (Brace, 1963; Calcagno and Gibson, 1988). Therefore, we should expect smaller, more gracile lower jaws in hominins adapted to consume foods that are intrinsically softer or that are made softer because of extra-oral food processing. This idea is based on the assumption that differences in size and robusticity in mandible and teeth reflect functional dissimilarities, thus adaptation. To validate this assumption, it is necessary to find an association between dental size, mandibular robusticity and proxies of diet or biomechanics in primates. If such an association is not detectable, then differences in dental size and robusticity among hominins do not necessarily represent functional adaptations.

Although adaptation does shape the morphology of the masticatory apparatus in primates (Meloro et al., 2015), other factors may overpower its effects. In the first place, species share ancestry because of their common evolutionary history, thus displaying traits that appear similar as a result of “phylogenetic inertia” (Cheverud et al., 1985; Blomberg and Garland, 2002). Second, a single species may appear or behave differently in different environments, or different species may respond similarly in the same environment, regardless of their morphological traits, because of phenotypic and behavioral plasticity (Chapman and Chapman, 1990; Brockman and Van Schaik, 2005; Lambert, 2009). In addition, changes in body size can alter the appearance of certain anatomical regions as a by-product of allometry (Mosimann, 1970). As a result of these and other factors acting on the lower jaw (Ross et al., 2012), the morphology of the masticatory apparatus may not be fully representative of a species’ diet.

Primates have been divided into four main feeding categories, i.e. frugivores, folivores, gummivores, and insectivores, depending on the main food source of each species (Nunn and Van Schaik, 2002). Meloro and colleagues (2015) found that primate mandibular morphology shows distinguishable feeding adaptations when a large sample of non-human primates is analyzed. Nevertheless, at smaller taxonomical scales differences among species appear unclear, in part because of plasticity and phylogenetic inertia. To state that the differences in dental size and mandibular robusticity among hominins have a functional meaning, it would be useful to test this assumption in catarrhines, both focusing on diet and food processing. Hominins belong to the catarrhine group, sharing several anatomical, physiological, developmental and behavioral features (Cachel, 2006), including the same dental formula (Swindler, 2002).

In this study, we assess the dependence among dental size, mandibular robusticity, and dietary proxies in the masticatory apparatus of catarrhines, to make inferences concerning the patterns of reduction observed within *Homo*. In particular, we test the hypotheses that, in catarrhines, (1) dental size and mandibular robusticity are mainly influenced by body size and phylogenetic constraints rather than diet and so, (2) these morphological traits cannot be used to interpret the dietary behaviors of fossil specimens. The results are crucial in reshaping the underlying basis of one of the major trends in human evolution. A phylogenetic comparative method was applied to study morphometric descriptors of mandible and teeth typically associated with the trend of reduction. These descriptors were compared to feeding and diet variables by controlling for the effect of body size and phylogeny.

2 | METHODS

All of the research reported in this manuscript was based on specimens collected by museums prior to this study and adheres to the legal requirements of the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

2.1 | The sample

The sample consists of mandibles of 56 species of non-hominin catarrhines inclusive of Colobinae (n=7 species), Cercopithecinae (n=35), Hylobatidae (n=8), and Hominidae (n=6). Hominin mandibles were also included, divided into six species and belonging to the genera *Australopithecus* (n=2 species), *Paranthropus* (n=2) and *Homo* (n=2). Only adult individuals were included, based on full eruption of the third molar. Except for fossil hominins, sex was known and only female individuals were used. The inclusion of females only was dictated by the need to reduce masticatory variability linked with sexual dimorphism. Male primates are associated with the development of features for sexual display in the jaws (Harvey et al., 1978; Plavcan, 2001), which may be misleading in the study of masticatory adaptation. For the hominin species, sex allocation was obtained from Wood (2011) and Schwartz and Tattersall (2005), although this information was not available for all individuals. Fossil specimens for which sex was unknown were included to increase sample size. Fossil hominins were included to increase sample size in regressions using microwear variables. A list of the species included in the sample is shown in Table 1 and further specifications about the sample are reported in the supplementary information (Tables S1 and S2).

The data in this study consist of measurements collected on actual specimens and 3D virtual reconstructions. The virtual sample is available in CT, micro-CT scan, and photogrammetry formats. The data are recorded on one-half of the mandible, which allowed increasing sample size, in particular for fossil hominins. The non-hominin catarrhine material consists of virtual specimens from the online and museum databases of the Primate Research Institute at Kyoto University (KUPRI, Kyoto, Japan), the primate skeletal collection of the National Museum of Natural History (NMNH, Washington, US), the MorphoSource database at Duke

University (www.morphosource.org), and the Royal Museum for Central Africa (Tervuren, Belgium). Therefore, all of the data in non-hominin catarrhines were collected virtually. The fossil hominin sample includes measurements of both virtual and actual specimens. Much of the hominin data consists of dental and mandibular measurements available from the online “Human Origins Database” (Gordon and Wood, 2007), so were not recorded by our team. Some virtual specimens of fossil hominin are available from the National Museum of Kenya (NMK, Nairobi), Africanfossils archive (www.africanfossils.org), and Digital Archive of fossil hominoids (www.virtual-anthropology.com, Vienna, Austria). Other hominin specimens were digitally acquired from the cast collections of Liverpool John Moores University (UK) and anthropological museum “G. Sergi” (Rome, Italy), by digital reconstruction using photogrammetry, following the procedure described in Falkingham (2012).

2.2 | Morphological data

The data include dental size and robusticity of the mandibular corpus. Dental size for each tooth type was approximated as the alveolar length of incisors (I), premolars (P) and molars (M). Alveolar lengths were measured as the minimum chord distance between midpoints of the inter-alveolar septa for each tooth type. Alveolar length was used as a proxy for dental size to maximize sample size, because teeth are frequently missing *post mortem* in mandibles of museum specimens and fossils. For most fossil hominin, measurements of alveolar length were recorded on the actual specimen (“Human Origins Database”). A small part of fossil specimens were available in virtual format and alveolar length was measured in the Amira software package (version 5.4.5, FEI Visualization, Berlin). The complete list of fossil hominin specimens used is reported in the supplementary information (Table S2) where the specimens for which data was collected virtually are indicated. A graphical representation of alveolar lengths is shown in Figure 1.

Mandibular robusticity was measured as the robusticity index (Daegling, 1989), calculated as the percent ratio between cross-section width and height (W/H x 100) of the mandibular corpus, measured at the symphysis (Rsy) and below the first (Rm1) and second molars (Rm2). The cross-section of the symphysis was obtained as the intersection between the mandibular surface and mid-sagittal plane. The cross-section of the mandibular corpus at molars was obtained as the intersection between the mandibular surface and plane perpendicular to the plane identified by the alveolar points surrounding molars. A graphical representation is shown in Figure 1.

2.3 | Body size and diet proxies

Body weight in grams was used as a proxy for body size. For non-hominin catarrhines, values of female body weight averaged by species are available from the literature (Smith and Jungers, 1997; National Research Council US, 2003). Data collected on both wild and captive individuals were used. For hominin body weight, the most updated published estimations were adopted, averaged by species (McHenry and Berger, 1998; Jiménez-Arenas et al., 2014; Grabowski et al., 2015). A table of body weight values for hominins and other catarrhines is presented in the supplementary information (Table S3).

Three different types of data were used as proxies of diet and biomechanics of mastication: diet percentages, dental microwear and feeding duration. Except microwear, these data rely on field observations of populations or captive animals. Microwear patterns principally refer to the ‘last’ meal of an individual (Teaford and Oyen, 1989), thus reducing the observable dietary spectrum. Although intrinsically affected by unknown levels of measurement error (Freckleton, 2011), these data have been successfully used in other studies (Ross et al., 2009; Scott et al., 2012; Jiménez-Arenas et al., 2014).

Diet percentages refer to the relative amount of certain food type categories in the diet of a species (National Research Council US, 2003). Fruit/seed, plant soft materials, plant fibrous materials, tree gum, fungi and animal matter were used as food categories, assuming these groups account for the complete (100%) diet of each species. These percentages were used to calculate the diet quality index (DQ) and an index of diet heterogeneity (DH). The DQ was calculated using the equation in Sailer et al. (1985), previously applied in other works focusing on primate morphology (Allen and Kay, 2012):

$$DQ = 1s + 2r + 3.5a$$

where s represents the percentage of structural plant parts, r is the percentage of reproductive plant parts, a is the percentage of animal matter in the diet, and the constants 1, 2 and 3.5 account for the relative energetic values per unit mass of s, r and a, respectively. DH was calculated as the Simpson’s diversity index (1-D), common in ecological studies (Pielou, 1969):

$$DH = 1 - \Sigma (n / N)^2$$

Here n / N is the proportion of each food category in the diet. The Simpson’s diversity index is used to account for the prevalence of certain food types in the diet, so that DH becomes a measure of dietary specialisation. Diet percentages were found for 56 species of non-hominin catarrhines.

Dental microwear analysis is usually performed to infer aspects of diet in mammals and it has been extensively applied to primates and hominins (Scott et al., 2012; Ungar et al., 2012). Through time, microwear data have proven successful in discriminating among different diets based on the mechanical properties of foods, such as hardness and toughness (Williams et al., 2005; Scott et al., 2006; Ungar and Sponheimer, 2011). Indeed, some indices used to describe microwear patterns have been shown to indicate the presence of hard and brittle (such as seeds and some fruit parts) and tough (mostly leaves) foods in the diet (Scott et al., 2006).

Here, microwear data include variables describing dental surface roughness (Area-Scale Fractal Complexity, or Asfc) and anisotropy of surface properties (Length-scale anisotropy of relief, or epLsar). Further details on these measurements can be found in Scott et al. (2006). Dental microwear data was found for 18 species, including six hominin species, and are available in Grine et al. (2012), Scott et al. (2012) and Ungar et al. (2012). The data are consistent among the different literature sources.

Data on feeding time (FT) (Ross et al., 2009) are used as a proxy of time spent in the activities related to mastication. FT does not account for foraging activities other than moving food into the mouth, chewing and swallowing, and derives from observations performed on wild animals. FT was available for 23 species of non-hominin catarrhines.

2.4 | Catarrhine phylogeny

A phylogenetic tree built from genetic data of non-hominin catarrhines is used. This primate molecular phylogeny is available from the online database 10ktrees (Arnold et al., 2010), and is part of a larger project on mammalian phylogeny. For the hominin phylogeny, the topology published by Dembo et al. (2015), based on a Bayesian statistical approach applied on a matrix of morphological traits of hominins, was used. Paleontological data of First and Last Appearance Datum (FAD and LAD) of fossil hominins were used to reconstruct plausible times of divergence between taxa. Potts (2013) provides a list of FAD and LAD data from several literature sources. Branch lengths were scaled to fit the time of divergence between *P. troglodytes* and *H. sapiens* in the 10ktrees phylogenetic tree, by using the R package "ape" (Paradis et al., 2004). The catarrhine and hominin trees were then merged. The catarrhine phylogeny, including the hominin species used in this study, is shown in the supplementary information (Figure S1).

2.5 | The correlation procedure

Each morphological variable was averaged by species. In each correlation, the sample was reduced to include only species available for the morphological trait, the phylogenetic tree and the dietary proxy tested. To test for the dependence between morphology and dietary proxies, Phylogenetic Generalized Least Squares (PGLS) was performed using Pagel's Lambda model of evolution (Pagel, 1999). Pagel's Lambda is a transformation of the Brownian Motion (BM), where the internal branch lengths of the tree are multiplied by the factor λ, which specifies the degree of phylogenetic signal in the data. If λ equals 0, data are completely independent on phylogeny; if it equals 1, then the correlation follows BM, meaning that traits evolve following a random walk after each event of speciation (neutral evolution), and phenotypic difference between taxa is proportional to the time of divergence from their common ancestor (Felsenstein, 1973).

Alveolar lengths (log-transformed) and robusticity indices were used as dependent variables, while the dietary proxies (scaled on variance) were considered as independent ones. To account for the effect of body size on the other variables, body weight (log-transformed) was included as a covariate (Christians, 1999). To improve interpretability and avoid over-parametrization and multicollinearity (Lehmann and Dunbar, 2009), each independent variable was analyzed separately. Each correlation was tested by linear regression. Regressions were not performed to find a predicting model for the mandibular and dental variables in relation to dietary proxies, but to detect the presence of a significant statistical effect of the independent variables on the dependent ones. The significance of each term was tested adopting a two-tailed 95% confidence level (α: 0.05). For regressions exhibiting a significant effect, a semi-partial R^2 was calculated as an indication of the variance explained by the sole independent variable. The semi-partial R^2 was calculated as the difference between the total R^2 (effect of independent variable and body weight) and R^2 relative to body weight only (Rasch et al., 2011). The regressions were performed using the R-package “phylolm” (Ho and Ané, 2014). The dependent and independent variables available for each species, and the number of species included in each correlation are reported in the supplementary information (Tables S1 and S4 respectively).

3 | RESULTS

Significant regressions are evident for several dependent variables, but not necessarily for every term of the correlation. Several regressions display R^2 values near zero; these results are not discussed here. The regression results are provided in Tables 2 and 3. Various levels of phylogenetic dependence are evident, as denoted by λ values ranging from 0 to 0.98. Only three of 35 regressions display significant effect of the independent variable; for these, semi-partial R^2 was calculated to separate contributions of body weight and the independent variable (Table 4). The variables of Diet Heterogeneity (DH) and Feeding Time (FT) are never associated with significant effects on any of the morphological traits investigated. In addition, postcanine alveolar lengths and robusticity index at symphysis and M_2 are not correlated with dietary proxies. Postcanine alveolar length is associated with changes in body weight and often with medium to high phylogenetic signals.

Diet Quality (p: 0.001) accounts for a positive linear effect on incisal alveolar length, indicated by a slope of 0.069. The adjusted R^2 statistics for the full model (including body weight and DQ) is 0.78 (Table 4); it reduces to 0.65 when only body weight is considered, thus indicating that DQ contributes to the variance of incisal alveolar length by 13% (semi-partial R^2: 0.13), although body weight has a larger effect. The λ phylogenetic signal for the regression between DQ and incisal alveolar length is 0.62. A significant positive correlation (slope: 0.17) exists between incisal alveolar length and the microwear variable Afsc (p: 0.033), with an adjusted R^2 of 0.72, a semi-partial contribution of 0.9 of Afsc (Table 4) and a negligible phylogenetic signal ($\lambda \approx 0$). Robusticity at M_1 is negatively associated with the variable epLsar (p: 0.022; adjusted R^2: 0.52; slope: -4.219; $\lambda \approx 0$), with epLsar contributing to the variance of the dependent variable by 37% (semi-partial R^2: 0.37). Figure 2 shows the scatterplots and relative lines of best fit for the three significant correlations.

4 | DISCUSSION

Primarily involved in processing food, the lower jaw is clearly adapted to resist the stresses of mastication and incision, and evidence has been gathered to support the biomechanical interpretation of mandibular shape in primates (Hylander, 1979, 1985; Humphrey et al., 1999). In conformity with the assumption that differences in dental size and mandibular robusticity account for differences in biomechanical profiles of the lower jaw, the trend of mandibular and dental reduction in *Homo* (including modern humans) has been considered the effect of food texture alterations in the diet of our ancestors (Wrangham and Carmody, 2010; Zink and Lieberman, 2016). By means of its improved food processing skills, the genus *Homo* had the chance of modifying the mechanical properties of food, thus releasing the selective pressures on its own lower jaw. This hypothesis assumes a close link between feeding habits and lower jaw anatomy, particularly concerning dental size and mandibular robusticity. In this study, the association between feeding habits, dental size, and mandibular robusticity was tested to determine if such traits are sufficient to recognize a dietary signal in the trend of dental and mandibular reduction in *Homo*.

4.1 | Functional significance of lower jaw morphology in catarrhines

Across catarrhines, the link between dental, mandibular robusticity, and dietary adaptations seems elusive. Of the independent variables tested, most failed to predict size and robusticity (Tables 2 and 3), and significant effects of dietary proxies are evident in only a few cases. It is possible that changes in dental size and mandibular robusticity occur as a “threshold response” to modifications in diet or feeding regimen (Roff, 1996), rather than following continuous variability. This possibility would explain the absence of strong and consistent correlations in the data. Nevertheless, the diet variability of catarrhines makes it difficult to recognize dietary patterns that can be strictly categorized. In addition, part of the analyses performed here relies on the use of fossil hominin samples whose dietary habits were estimated by the same independent variables tested (microwear), therefore categorization is not applicable.

Variations in the size of incisors were associated with changes in microwear patterns when Asfc was used as predictor. Microwear variables record the patterns of dental wear due to contact with food and abrasion; they can reveal the hardness and toughness of the food items eaten (Scott et al., 2006). Asfc is higher in hard-feeding primates, which chew on seeds or hard parts of fruit items, and lower in species consuming leaves, which are regarded as tough plant material (Scott et al., 2006). Therefore, they are representative of food textural properties. As reported above, incisor alveolar length increases with Asfc. Although the data seem to cluster, small incisors appear associated with small values of Asfc (Figure 2). These results indicate that small incisors may be characteristic of species with a diet based on tough foods, such as leaves. Hylander (1975) observed that colobines are well adapted to a leaf-eating strategy and have small incisors relative to those of cercopithecines, which forage mostly on fruit. A similar pattern is suggested by the association between incisor alveolar length and diet quality (DQ), which revealed a positive effect of the latter on the former, with small DQ indices (typical of folivorous primates) associated with smaller incisors.

The regressions on mandibular robusticity produced the highest association between traits and dietary proxies, although only one correlation was significant (Table 3). Microwear (epLsar) displayed relatively high power in predicting robusticity at the level of first molar (Table 3). Studies on morphology of the mandibular corpus in primates suggested that robusticity might be involved in counteracting torsional and bending stresses during mastication (Daegling and Hylander, 1998). The results described above support previous interpretations that mandibular robusticity is linked to the mechanical properties of foods. Indeed, M_1 robusticity changes negatively with epLsar. Surprisingly, gracile mandibular corpora are associated with values of epLsar typical of folivorous primates (Scott et al., 2006), which contradicts previous results (Daegling and Hylander, 1998). Nevertheless, this result was controlled for both body size and phylogeny and considers a large range of catarrhine species. At least under the conditions here tested, robusticity of the mandibular corpus appears higher in primates that chew hard food items, and lower in tough food eaters.

Postcanine tooth size and symphyseal robusticity are not significantly influenced by any of the independent variables. The symphysis is thought to support biomechanical stresses of incisal biting in primates (Hylander, 1975; 1985; Daegling, 2001). Nevertheless, the robusticity index may not be enough to recognize such a role; other factors may be dominant, such as symphyseal three-dimensional shape and orientation. For postcanine size, it has been observed that folivorous catarrhines exhibit a larger postcanine dentition than frugivorous species (Kay, 1975), as an adaptation to breaking down tough plant material. In addition, postcanine megadontia was described in several primate species known to feed on hard objects (durophagy) (Daegling et al., 2011). Although enlarged premolars may provide adaptive advantages, some known durophagous species do not exhibit postcanine megadontia and species with enlarged premolars do not necessarily feed on hard objects (Daegling et al., 2011). Therefore, factors other than diet may influence postcanine tooth size. For example, Wood (1979) reports that molar crown area scales isometrically with body size in *Homo*, *Gorilla*, *Pan*, *Papio*, and *Colobus*. Willis and Swindler (2004) suggest that molar size differences across colobines may reflect phylogeny and variation in body size. In this work, both body size and phylogeny were taken into account and their effects isolated from that of dietary proxies. Our results show that premolar and molar size are mainly influenced by body size and phylogeny, rather than by dietary proxies (Table 2).

Based on the preceding results, we cannot reject the hypothesis that factors other than diet can drive the evolution of certain morphological traits in the catarrhine mandible. This is the case for postcanine teeth, whose size seems to be influenced considerably by constraints related to phylogeny and body size. Nevertheless, the same hypothesis does not hold for incisors and mandibular robusticity, where diet and food mechanical properties may constitute an important evolutionary driver. Analogously, the hypothesis that masticatory traits cannot be used for inference in fossil species should not be generalized, having been confirmed for postcanine teeth but rejected for incisors and mandibular robusticity. The results suggest a complex, modular morphology of the catarrhine mandible and highlight the multifactorial nature of its evolution. In addition, we recommend caution in interpreting the dietary habits of fossil catarrhine species based only on dental size and mandibular robusticity.

4.2 | Implications for mandibular and dental reduction in *Homo*

In light of what was observed across catarrhines, links between diet and anatomy are difficult to find; as well, attempting to estimate the diet of a fossil hominin based on its masticatory morphology may prove to be misleading and inaccurate. Nevertheless, certain features, such as mandibular robusticity and incisor size, seem to be correlated with dietary proxies.

Based on our results, mandibular robusticity is associated with food mechanical properties. Therefore, it is plausible to hypothesize that the extra-oral food processing skills of *Homo* allowed modifying the mechanical properties and size of foods prior to mastication, leading to changes in robusticity. Softening would result in reduction of the force needed to break down hard foods. Therefore, gracilization of the mandibular corpus by relaxation of selective pressures on mastication (Calcagno and Gibson, 1988; Wrangham and Carmody, 2010) is not contradicted by this work. As a result, the link between extra-oral food processing skills and changes in mandibular robusticity in *Homo* is not impossible, although not demonstrated by our analysis.

The presence of small incisors in certain groups of catarrhines was confirmed to be an indicator of low diet quality and folivory. Nevertheless, small incisors may not be the result of a folivorous diet itself, but rather the effect of reduced incisal preparation of food. Hylander (1975) suggested that a correlation exists between incisal size in anthropoid primates and size of the food items eaten. Large items need extensive preparation before placing them in the mouth, while small fruits, seeds, and leaves can be chewed without pre-processing. As an example, papionins include both large food items and leaves in their diets, which they process with their anterior teeth (Hylander, 1975; Whitehead and Jolly, 2000). Papionins often use incisal preparation, benefitting from thick enamel that minimizes the effect of dental wear (Jolly, 1970; Hylander, 1975). Colobines, which rely on smaller food items, have smaller teeth relative to body size and do not exhibit the enamel adaptations observed in papionins, because their incisors do not undergo extensive wear. The same mechanism is plausible, although not proven, for explaining incisal reduction in the genus *Homo*. Use of lithic tools during the Pleistocene reduced food size and toughness by slicing, crushing, and pounding (Zink and Lieberman, 2016), thus assigning to the hands the job previously accomplished by incisors.

These findings show that the relationship between anatomy and dietary proxies is often overwhelmed by factors such as body size and phylogeny. The results suggest that non-biomechanical factors may have been involved in the reduction of postcanine tooth size and symphyseal robusticity. Nevertheless, the patterns observed across catarrhines demonstrate a link between incisor size, mandibular robusticity, and food mechanical properties. This association is fundamental to the hypotheses that consider food processing to explain the onset of dental and mandibular reduction in *Homo*. Although this study does not prove that improvements in extra-oral food processing and the consequent food softening caused some masticatory traits to reduce in *Homo*, it does show that such a link is not impossible. Therefore, this study does not reject the hypothesis of a relationship between hominin technological developments and physical changes in their masticatory apparatus.

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Table 1 The species used in the analyses. The taxonomic authority and the number of individuals are reported. The fossil hominin specimens are listed in the supplementary information.

Colobinae	Authority	N		Cercopithecinae	Authority	N
Colobus guereza	Rüppell, 1835	1		*Allenopithecus nigroviridis*	Pocock, 1907	1
Colobus polykomos	Zimmermann, 1780	2		*Cercocebus agilis*	A. Milne-Edwards, 1886	1
Piliocolobus badius	Kerr, 1792	1		*Cercocebus atys*	Audebert, 1797	1
Presbytis melalophos	Raffles, 1821	2		*Cercocebus galeritus*	Peters, 1879	1
Procolobus verus	Van Beneden, 1838	2		*Cercocebus torquatus*	Kerr, 1792	1
Trachypithecus cristatus	Raffles, 1821	4		*Cercopithecus albogularis*	Sykes, 1831	1
Trachypithecus obscurus	Reid, 1837	2		*Cercopithecus ascanius*	Audebert, 1799	1
				Cercopithecus campbelli	Waterhouse, 1838	1
				Cercopithecus mitis	Wolf, 1822	1
Hominidae				*Cercopithecus nictitans*	Linnaeus, 1766	2
Gorilla beringei	Matschie, 1903	6		*Cercopithecus petaurista*	Schreber, 1774	2
Gorilla gorilla	Savage, 1847	9		*Chlorocebus sabaeus*	Linnaeus, 1766	1
Pan paniscus	Schwarz, 1929	1		*Erythrocebus patas*	Schreber, 1774	1
Pan troglodytes	Blumenbach, 1775	15		*Lophocebus albigena*	Gray, 1850	1
Pongo abelii	Lesson, 1827	5		*Lophocebus aterrimus*	Oudemans, 1890	1
Pongo pygmaeus	Linnaeus, 1760	10		*Macaca arctoides*	I. Saint-Hilaire, 1831	2
				Macaca assamensis	McClelland, 1840	3
				Macaca cyclopis	Swinhoe, 1863	2
Hylobatidae				*Macaca fascicularis*	Raffles, 1821	3
Hoolock hoolock	Harlan, 1834	2		*Macaca fuscata*	Blyth, 1875	3
Hylobates agilis	F. Cuvier, 1821	1		*Macaca leonina*	Blyth, 1863	1
Hylobates klossii	Miller, 1903	1		*Macaca maura*	Schinz, 1825	1
Hylobates lar	Linnaeus, 1771	5		*Macaca mulatta*	Zimmermann, 1780	2
Hylobates muelleri	Martin, 1841	1		*Macaca nemestrina*	Linnaeus, 1766	3
Nomascus concolor	Harlan, 1826	2		*Macaca pagensis*	Miller, 1903	2
Nomascus leucogenys	Ogilby, 1840	3		*Macaca radiata*	É. Saint-Hilaire, 1812	3
Symphalangus syndactylus	Raffles, 1821	6		*Macaca silenus*	Linnaeus, 1758	2
				Macaca sinica	Linnaeus, 1771	2
				Macaca sylvanus	Linnaeus, 1758	1
Hominins				*Macaca thibetana*	A. Milne-Edwards, 1870	1
Australopithecus afarensis	Johanson & White, 1978	12		*Mandrillus sphinx*	Linnaeus, 1758	1
Australopithecus africanus	Dart, 1925	5		*Papio anubis*	Lesson, 1827	1
Homo ergaster	Groves & Mazak, 1975	10		*Papio hamadryas*	Linnaeus, 1758	2
Homo habilis	L. Leakey, 1964	5		*Papio papio*	Desmarest, 1820	1
Paranthropus boisei	M. Leakey, 1959	31		*Theropithecus gelada*	Rüppell, 1835	2
Paranthropus robustus	Broom, 1938	4				

Table 2 Correlations between tooth alveolar lengths and dietary proxies.

		DQ[a]	DH[b]	Asfc[c]	epLsar[d]	FT[e]
I	Intercept	-0.791	0.129	-0.849	-0.348	-0.613
	slope X[†]	0.069	0.025	0.17	-0.074	0.057
	slope B[‡]	0.311	0.21	0.312	0.263	0.29
	Adj. R^2	0.783	0.631	0.724	0.599	0.713
	λ[§]	0.622	0.907	0	0	0.207
	p X	< 0.01**	0.163	0.033*	0.385	0.241
	p B	< 0.01**	< 0.01**	< 0.01**	< 0.01**	< 0.01**
P	Intercept	-0.034	0.172	0.126	0.166	0.146
	slope X	0.024	0	0.044	0.011	0.003
	slope B	0.283	0.26	0.266	0.261	0.264
	Adj. R^2	0.783	0.76	0.846	0.83	0.807
	λ	0.817	0.843	0	0	0.834
	p X	0.13	0.981	0.254	0.772	0.9
	p B	< 0.01**	< 0.01**	< 0.01**	< 0.01**	< 0.01**
M	Intercept	0.019	0.011	0.731	0.861	-0.188
	slope X	-0.001	-0.006	0.028	-0.027	0.001
	slope B	0.347	0.347	0.28	0.268	0.37
	Adj. R^2	0.604	0.59	0.771	0.77	0.589
	λ	0.976	0.978	0	0	0.761
	p X	0.956	0.661	0.503	0.522	0.97
	p B	< 0.01**	< 0.01**	< 0.01**	< 0.01**	< 0.01**

[†] Independent variable

[‡] Body weight (covariate)

[§] Pagel’s Lambda (phylogenetic signal)

[a] Diet Quality

[b] Diet Heterogeneity

[c] Area-Scale Fractal Complexity (Microwear)

[d] Length-scale anisotropy of relief (Microwear)

[e] Feeding Time

Table 3 Correlations between mandibular robusticity indices and dietary proxies.

		DQ[a]	DH[b]	Asfc[c]	epLsar[d]	FT[e]
Rsy	Intercept	7.14	3.583	23.46	23.271	35.352
	slope X[†]	-0.726	-0.557	-1.179	-0.572	-0.675
	slope B[‡]	4.42	4.811	3.085	3.127	1.352
	Adj. R^2	≈ 0	≈ 0	≈ 0	≈ 0	≈ 0
	λ[§]	0.398	0.356	0	0	0
	p X	0.568	0.611	0.709	0.861	0.72
	p B	0.037*	0.011*	0.262	0.283	0.572
Rm1	Intercept	38.476	62.727	35.344	8.529	45.251
	slope X	3.207	-0.945	1.23	-4.219	-0.896
	slope B	1.992	-0.778	2.31	5.204	1.157
	Adj. R^2	≈ 0	-0.106	0.139	0.518	-0.154
	λ	0.542	0.609	0.757	0	0.463
	p X	0.026*	0.453	0.399	0.037*	0.751
	p B	0.421	0.746	0.531	0.016*	0.767
Rm2	Intercept	62.844	64.4	111.44	100.14	72.073
	slope X	0.428	-1.539	0.136	-1.21	-2.84
	slope B	-0.52	-0.764	-5.387	-4.169	-1.334
	Adj. R^2	≈ 0	≈ 0	≈ 0	≈ 0	≈ 0
	λ	0.482	0.452	0.913	0.878	0.644
	p X	0.73	0.143	0.918	0.563	0.307
	p B	0.805	0.677	0.231	0.342	0.744

[†] Independent variable

[‡] Body weight (covariate)

[§] Pagel's Lambda (phylogenetic signal)

[a] Diet Quality

[b] Diet Heterogeneity

[c] Area-Scale Fractal Complexity (Microwear)

[d] Length-scale anisotropy of relief (Microwear)

[e] Feeding Time

Table 4 Semi-partial R^2 calculated for the regressions showing significant effect of the independent variables. The semi-partial R^2 is the difference between the R^2 of the full regression (including independent variable and covariate) and the R^2 of the regression with the covariate only. It represents the contribution of the sole independent variable to the variance of the dependent variable.

	Semi-partial R^2	R^2 body weight	Total R^2
I[a] – DQ[b]	0.13	0.65	0.78
I – Asfc[c]	0.09	0.63	0.72
Rm1[d] – epLsar[e]	0.37	0.15	0.52

[a] Incisor alveolar length

[b] Diet Quality

[c] Area-Scale Fractal Complexity (Microwear)

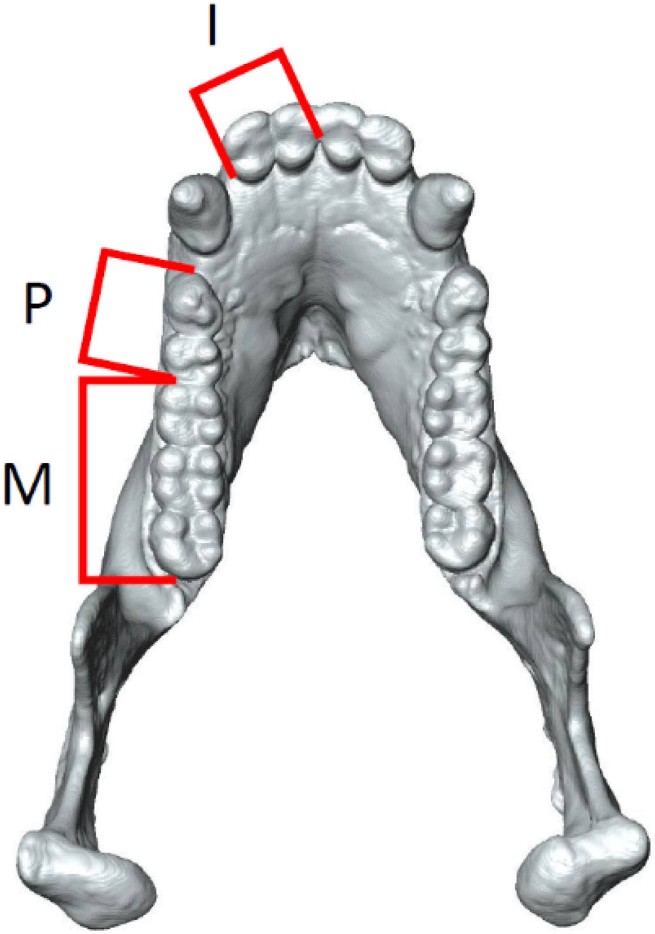
[d] Robusticity index at first molar

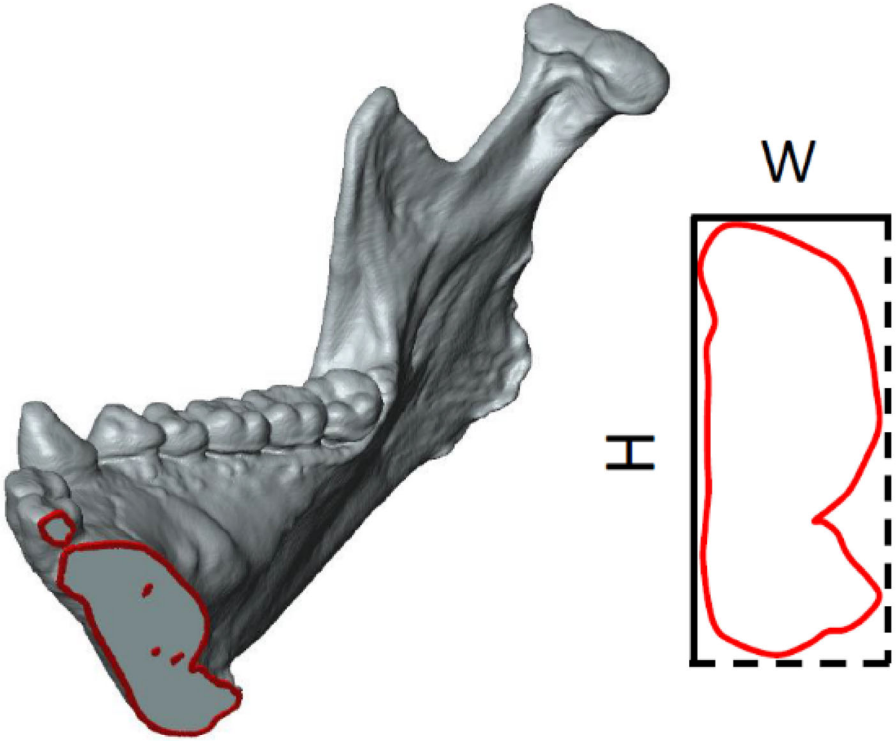
[e] Length-scale anisotropy of relief (Microwear)

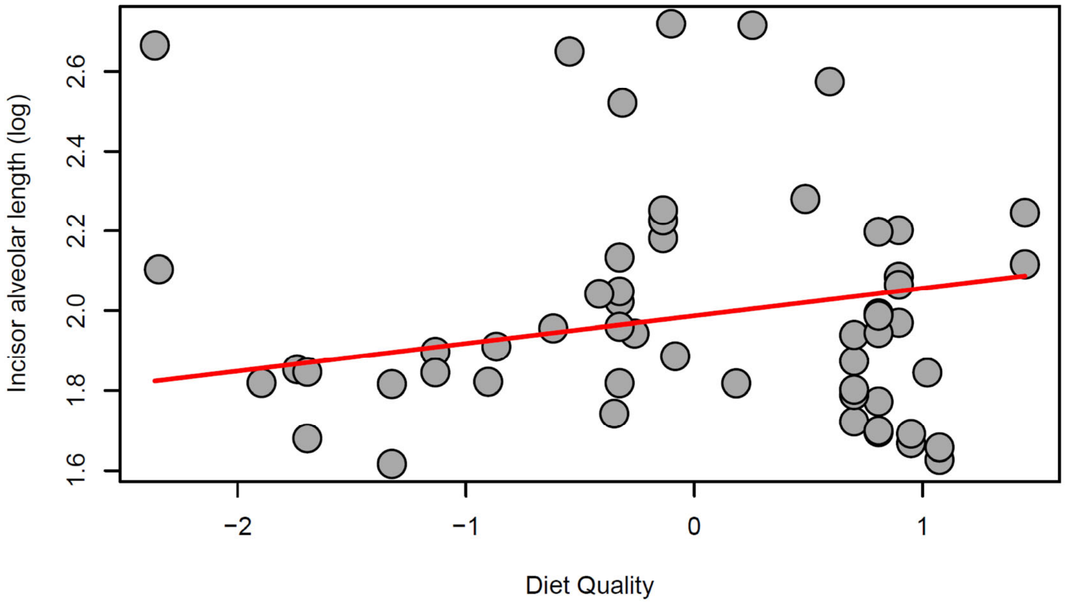
FIGURE LEGENDS

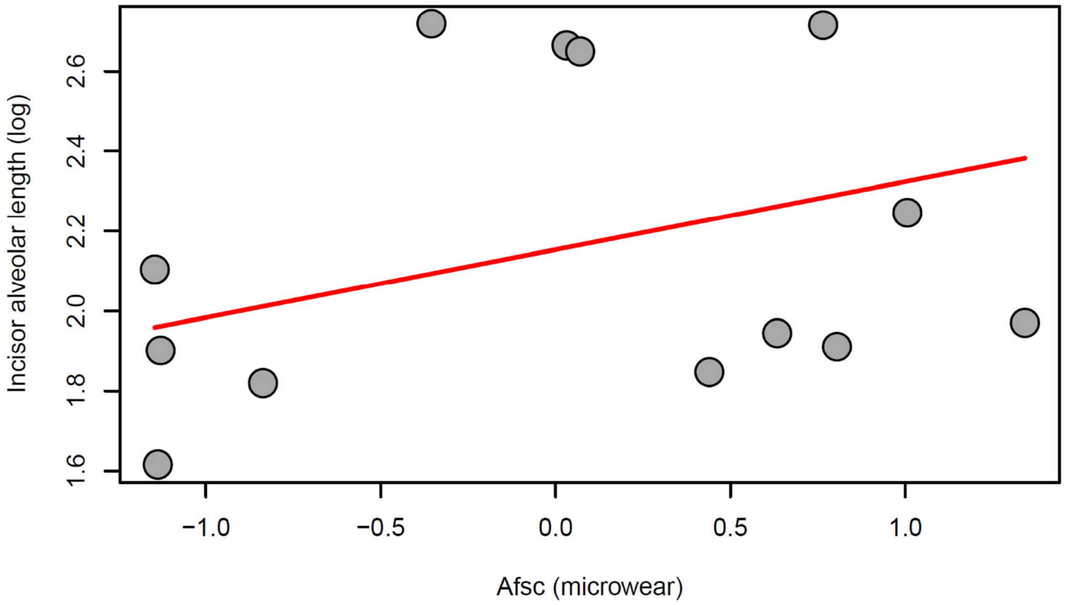
Figure 1 Morphological data used in the analyses shown on the mandible of a female *Pan troglodytes*. Alveolar lengths (left) of incisors (I), premolars (P) and molars (M), measured as the minimum chord distances between midpoints of the interalveolar septa. Robusticity indices (right) measured at the symphysis and at the first and second molars (not shown). The height (H) and width (W) of the symphysis and corpus cross-sections were used to calculate the robusticity index (W/H x 100).

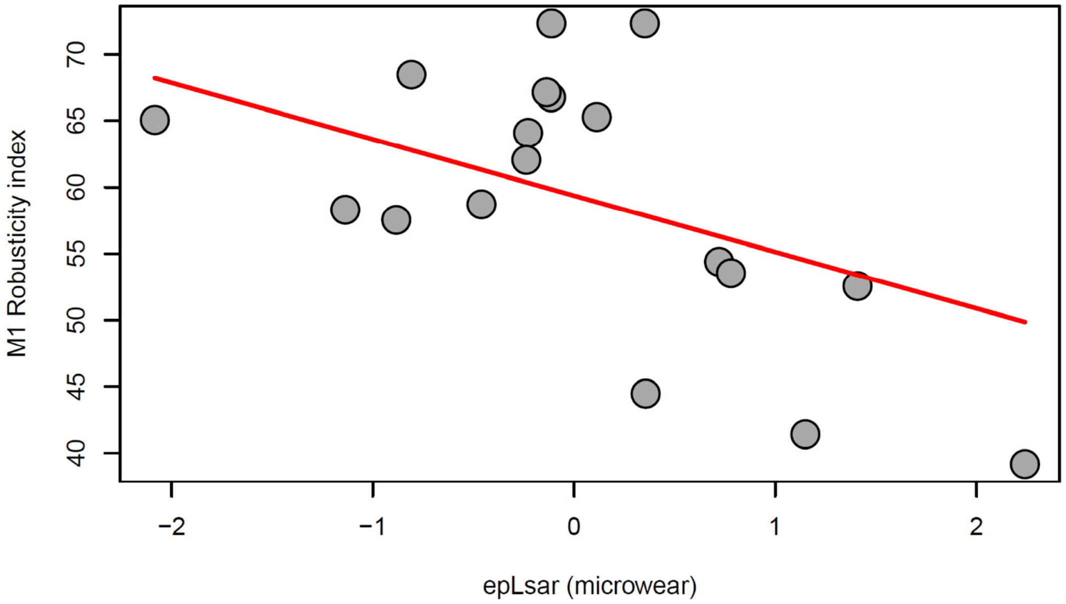
Figure 2 Scatterplots of the regressions showing significant effect of the independent variables. The regression line (red) was corrected for the effect of body weight and phylogeny


I
P
M


W
H


Incisor alveolar length (log)
1.6
1.8
2.0
2.2
2.4
2.6
−2
−1
0
1
Diet Quality


Incisor alveolar length (log)
1.6
1.8
2.0
2.2
2.4
2.6
−1.0
−0.5
0.0
0.5
1.0
Afsc (microwear)


M1 Robusticity index
40
45
50
55
60
65
70
−2
−1
0
1
2
epLsar (microwear)