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

3 Running title: Jaw reduction in hominins and catarrhines

4

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20 ABSTRACT

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

36

37 KEYWORDS

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

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42 1 | INTRODUCTION

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

59 From the above perspective, mandibular and dental reduction within *Homo* can be seen as
60 the result of lowered functional requirements or natural selection (Brace, 1963; Calcagno and
61 Gibson, 1988). Therefore, we should expect smaller, more gracile lower jaws in hominins
62 adapted to consume foods that are intrinsically softer or that are made softer because of
63 extra-oral food processing. This idea is based on the assumption that differences in size and
64 robusticity in mandible and teeth reflect functional dissimilarities, thus adaptation. To

65 validate this assumption, it is necessary to find an association between dental size,
66 mandibular robusticity and proxies of diet or biomechanics in primates. If such an association
67 is not detectable, then differences in dental size and robusticity among hominins do not
68 necessarily represent functional adaptations.

69 Although adaptation does shape the morphology of the masticatory apparatus in primates
70 (Meloro et al., 2015), other factors may overpower its effects. In the first place, species share
71 ancestry because of their common evolutionary history, thus displaying traits that appear
72 similar as a result of “phylogenetic inertia” (Cheverud et al., 1985; Blomberg and Garland,
73 2002). Second, a single species may appear or behave differently in different environments,
74 or different species may respond similarly in the same environment, regardless of their
75 morphological traits, because of phenotypic and behavioral plasticity (Chapman and
76 Chapman, 1990; Brockman and Van Schaik, 2005; Lambert, 2009). In addition, changes in
77 body size can alter the appearance of certain anatomical regions as a by-product of allometry
78 (Mosimann, 1970). As a result of these and other factors acting on the lower jaw (Ross et al.,
79 2012), the morphology of the masticatory apparatus may not be fully representative of a
80 species’ diet.

81 Primates have been divided into four main feeding categories, i.e. frugivores, folivores,
82 gummivores, and insectivores, depending on the main food source of each species (Nunn and
83 Van Schaik, 2002). Meloro and colleagues (2015) found that primate mandibular morphology
84 shows distinguishable feeding adaptations when a large sample of non-human primates is
85 analyzed. Nevertheless, at smaller taxonomical scales differences among species appear
86 unclear, in part because of plasticity and phylogenetic inertia. To state that the differences in
87 dental size and mandibular robusticity among hominins have a functional meaning, it would

88 be useful to test this assumption in catarrhines, both focusing on diet and food processing.
89 Hominins belong to the catarrhine group, sharing several anatomical, physiological,
90 developmental and behavioral features (Cachel, 2006), including the same dental formula
91 (Swindler, 2002).

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

102

103

104 2 | METHODS

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

108

109

110 2.1 | The sample

111 The sample consists of mandibles of 56 species of non-hominin catarrhines inclusive of
112 Colobinae (n=7 species), Cercopithecinae (n=35), Hylobatidae (n=8), and Hominidae (n=6).
113 Hominin mandibles were also included, divided into six species and belonging to the genera
114 *Australopithecus* (n=2 species), *Paranthropus* (n=2) and *Homo* (n=2). Only adult individuals
115 were included, based on full eruption of the third molar. Except for fossil hominins, sex was
116 known and only female individuals were used. The inclusion of females only was dictated by
117 the need to reduce masticatory variability linked with sexual dimorphism. Male primates are
118 associated with the development of features for sexual display in the jaws (Harvey et al.,
119 1978; Plavcan, 2001), which may be misleading in the study of masticatory adaptation. For
120 the hominin species, sex allocation was obtained from Wood (2011) and Schwartz and
121 Tattersall (2005), although this information was not available for all individuals. Fossil
122 specimens for which sex was unknown were included to increase sample size. Fossil hominins
123 were included to increase sample size in regressions using microwear variables. A list of the
124 species included in the sample is shown in Table 1 and further specifications about the
125 sample are reported in the supplementary information (Tables S1 and S2).

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

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

144

145 2.2 | Morphological data

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

156 specimens for which data was collected virtually are indicated. A graphical representation of
157 alveolar lengths is shown in Figure 1.

158 Mandibular robusticity was measured as the robusticity index (Daegling, 1989), calculated as
159 the percent ratio between cross-section width and height ($W/H \times 100$) of the mandibular
160 corpus, measured at the symphysis (R_{sy}) and below the first (R_{m1}) and second molars (R_{m2}).
161 The cross-section of the symphysis was obtained as the intersection between the mandibular
162 surface and mid-sagittal plane. The cross-section of the mandibular corpus at molars was
163 obtained as the intersection between the mandibular surface and plane perpendicular to the
164 plane identified by the alveolar points surrounding molars. A graphical representation is
165 shown in Figure 1.

166

167 2.3 | Body size and diet proxies

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

175 Three different types of data were used as proxies of diet and biomechanics of mastication:
176 diet percentages, dental microwear and feeding duration. Except microwear, these data rely
177 on field observations of populations or captive animals. Microwear patterns principally refer

178 to the 'last' meal of an individual (Teaford and Oyen, 1989), thus reducing the observable
179 dietary spectrum. Although intrinsically affected by unknown levels of measurement error
180 (Freckleton, 2011), these data have been successfully used in other studies (Ross et al., 2009;
181 Scott et al., 2012; Jiménez-Arenas et al., 2014).

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

$$189 \quad DQ = 1s + 2r + 3.5a$$

190 where s represents the percentage of structural plant parts, r is the percentage of
191 reproductive plant parts, a is the percentage of animal matter in the diet, and the constants
192 1, 2 and 3.5 account for the relative energetic values per unit mass of s , r and a , respectively.

193 DH was calculated as the Simpson's diversity index (1-D), common in ecological studies
194 (Pielou, 1969):

$$195 \quad DH = 1 - \sum (n / N)^2$$

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

200 Dental microwear analysis is usually performed to infer aspects of diet in mammals and it has
201 been extensively applied to primates and hominins (Scott et al., 2012; Ungar et al., 2012).
202 Through time, microwear data have proven successful in discriminating among different diets
203 based on the mechanical properties of foods, such as hardness and toughness (Williams et
204 al., 2005; Scott et al., 2006; Ungar and Sponheimer, 2011). Indeed, some indices used to
205 describe microwear patterns have been shown to indicate the presence of hard and brittle
206 (such as seeds and some fruit parts) and tough (mostly leaves) foods in the diet (Scott et al.,
207 2006).

208 Here, microwear data include variables describing dental surface roughness (Area-Scale
209 Fractal Complexity, or Asfc) and anisotropy of surface properties (Length-scale anisotropy of
210 relief, or epLsar). Further details on these measurements can be found in Scott et al. (2006).

211 Dental microwear data was found for 18 species, including six hominin species, and are
212 available in Grine et al. (2012), Scott et al. (2012) and Ungar et al. (2012). The data are
213 consistent among the different literature sources.

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

218

219 2.4 | Catarrhine phylogeny

220 A phylogenetic tree built from genetic data of non-hominin catarrhines is used. This primate
221 molecular phylogeny is available from the online database 10ktrees (Arnold et al., 2010), and

222 is part of a larger project on mammalian phylogeny. For the hominin phylogeny, the topology
223 published by Dembo et al. (2015), based on a Bayesian statistical approach applied on a
224 matrix of morphological traits of hominins, was used. Paleontological data of First and Last
225 Appearance Datum (FAD and LAD) of fossil hominins were used to reconstruct plausible times
226 of divergence between taxa. Potts (2013) provides a list of FAD and LAD data from several
227 literature sources. Branch lengths were scaled to fit the time of divergence between *P.*
228 *troglydytes* and *H. sapiens* in the 10krees phylogenetic tree, by using the R package “ape”
229 (Paradis et al., 2004). The catarrhine and hominin trees were then merged. The catarrhine
230 phylogeny, including the hominin species used in this study, is shown in the supplementary
231 information (Figure S1).

232

233 2.5 | The correlation procedure

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

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

262

263

264 3 | RESULTS

265 Significant regressions are evident for several dependent variables, but not necessarily for
266 every term of the correlation. Several regressions display R^2 values near zero; these results
267 are not discussed here. The regression results are provided in Tables 2 and 3. Various levels

268 of phylogenetic dependence are evident, as denoted by λ values ranging from 0 to 0.98. Only
269 three of 35 regressions display significant effect of the independent variable; for these, semi-
270 partial R^2 was calculated to separate contributions of body weight and the independent
271 variable (Table 4). The variables of Diet Heterogeneity (DH) and Feeding Time (FT) are never
272 associated with significant effects on any of the morphological traits investigated. In addition,
273 postcanine alveolar lengths and robusticity index at symphysis and M_2 are not correlated with
274 dietary proxies. Postcanine alveolar length is associated with changes in body weight and
275 often with medium to high phylogenetic signals.

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

288

289

290

291 4 | DISCUSSION

292 Primarily involved in processing food, the lower jaw is clearly adapted to resist the stresses of
293 mastication and incision, and evidence has been gathered to support the biomechanical
294 interpretation of mandibular shape in primates (Hylander, 1979, 1985; Humphrey et al.,
295 1999). In conformity with the assumption that differences in dental size and mandibular
296 robusticity account for differences in biomechanical profiles of the lower jaw, the trend of
297 mandibular and dental reduction in *Homo* (including modern humans) has been considered
298 the effect of food texture alterations in the diet of our ancestors (Wrangham and Carmody,
299 2010; Zink and Lieberman, 2016). By means of its improved food processing skills, the genus
300 *Homo* had the chance of modifying the mechanical properties of food, thus releasing the
301 selective pressures on its own lower jaw. This hypothesis assumes a close link between
302 feeding habits and lower jaw anatomy, particularly concerning dental size and mandibular
303 robusticity. In this study, the association between feeding habits, dental size, and mandibular
304 robusticity was tested to determine if such traits are sufficient to recognize a dietary signal in
305 the trend of dental and mandibular reduction in *Homo*.

306

307 4.1 | Functional significance of lower jaw morphology in catarrhines

308 Across catarrhines, the link between dental, mandibular robusticity, and dietary adaptations
309 seems elusive. Of the independent variables tested, most failed to predict size and robusticity
310 (Tables 2 and 3), and significant effects of dietary proxies are evident in only a few cases. It is
311 possible that changes in dental size and mandibular robusticity occur as a “threshold
312 response” to modifications in diet or feeding regimen (Roff, 1996), rather than following
313 continuous variability. This possibility would explain the absence of strong and consistent

314 correlations in the data. Nevertheless, the diet variability of catarrhines makes it difficult to
315 recognize dietary patterns that can be strictly categorized. In addition, part of the analyses
316 performed here relies on the use of fossil hominin samples whose dietary habits were
317 estimated by the same independent variables tested (microwear), therefore categorization is
318 not applicable.

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

333 The regressions on mandibular robusticity produced the highest association between traits
334 and dietary proxies, although only one correlation was significant (Table 3). Microwear
335 (epLsar) displayed relatively high power in predicting robusticity at the level of first molar
336 (Table 3). Studies on morphology of the mandibular corpus in primates suggested that

337 robusticity might be involved in counteracting torsional and bending stresses during
338 mastication (Daegling and Hylander, 1998). The results described above support previous
339 interpretations that mandibular robusticity is linked to the mechanical properties of foods.
340 Indeed, M_1 robusticity changes negatively with $epLsar$. Surprisingly, gracile mandibular
341 corpora are associated with values of $epLsar$ typical of folivorous primates (Scott et al., 2006),
342 which contradicts previous results (Daegling and Hylander, 1998). Nevertheless, this result
343 was controlled for both body size and phylogeny and considers a large range of catarrhine
344 species. At least under the conditions here tested, robusticity of the mandibular corpus
345 appears higher in primates that chew hard food items, and lower in tough food eaters.

346 Postcanine tooth size and symphyseal robusticity are not significantly influenced by any of
347 the independent variables. The symphysis is thought to support biomechanical stresses of
348 incisal biting in primates (Hylander, 1975; 1985; Daegling, 2001). Nevertheless, the
349 robusticity index may not be enough to recognize such a role; other factors may be
350 dominant, such as symphyseal three-dimensional shape and orientation. For postcanine size,
351 it has been observed that folivorous catarrhines exhibit a larger postcanine dentition than
352 frugivorous species (Kay, 1975), as an adaptation to breaking down tough plant material. In
353 addition, postcanine megadontia was described in several primate species known to feed on
354 hard objects (durophagy) (Daegling et al., 2011). Although enlarged premolars may provide
355 adaptive advantages, some known durophagous species do not exhibit postcanine
356 megadontia and species with enlarged premolars do not necessarily feed on hard objects
357 (Daegling et al., 2011). Therefore, factors other than diet may influence postcanine tooth
358 size. For example, Wood (1979) reports that molar crown area scales isometrically with body
359 size in *Homo*, *Gorilla*, *Pan*, *Papio*, and *Colobus*. Willis and Swindler (2004) suggest that molar
360 size differences across colobines may reflect phylogeny and variation in body size. In this

361 work, both body size and phylogeny were taken into account and their effects isolated from
362 that of dietary proxies. Our results show that premolar and molar size are mainly influenced
363 by body size and phylogeny, rather than by dietary proxies (Table 2).

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

376

377 4.2 | Implications for mandibular and dental reduction in *Homo*

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

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

391 The presence of small incisors in certain groups of catarrhines was confirmed to be an
392 indicator of low diet quality and folivory. Nevertheless, small incisors may not be the result of
393 a folivorous diet itself, but rather the effect of reduced incisal preparation of food. Hylander
394 (1975) suggested that a correlation exists between incisal size in anthropoid primates and
395 size of the food items eaten. Large items need extensive preparation before placing them in
396 the mouth, while small fruits, seeds, and leaves can be chewed without pre-processing. As an
397 example, papionins include both large food items and leaves in their diets, which they
398 process with their anterior teeth (Hylander, 1975; Whitehead and Jolly, 2000). Papionins
399 often use incisal preparation, benefitting from thick enamel that minimizes the effect of
400 dental wear (Jolly, 1970; Hylander, 1975). Colobines, which rely on smaller food items, have
401 smaller teeth relative to body size and do not exhibit the enamel adaptations observed in
402 papionins, because their incisors do not undergo extensive wear. The same mechanism is
403 plausible, although not proven, for explaining incisal reduction in the genus *Homo*. Use of
404 lithic tools during the Pleistocene reduced food size and toughness by slicing, crushing, and

405 pounding (Zink and Lieberman, 2016), thus assigning to the hands the job previously
406 accomplished by incisors.

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

418

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431

432

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- 595

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

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

^aDiet Quality

^bDiet Heterogeneity

^cArea-Scale Fractal Complexity (Microwear)

^dLength-scale anisotropy of relief (Microwear)

^eFeeding 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. R²	≈ 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. R²	≈ 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. R²	≈ 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)

^aDiet Quality

^bDiet Heterogeneity

^cArea-Scale Fractal Complexity (Microwear)

^dLength-scale anisotropy of relief (Microwear)

^eFeeding 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

^aIncisor alveolar length

^bDiet Quality

^cArea-Scale Fractal Complexity (Microwear)

^dRobusticity index at first molar

^eLength-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 ($W/H \times 100$).

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



