

1 **Food mechanical properties and isotopic signatures in forest versus**
2 **savannah dwelling eastern chimpanzees**

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4 **Adam van Casteren^{1*}, Vicky M. Oelze^{2,3}, Samuel Angedakin³, Ammie K. Kalan³, Mohamed**
5 **Kambi³, Christophe Boesch³, Hjalmar S. Kühl^{3,4}, Kevin E. Langergraber⁵, Alexander K. Piel⁶,**
6 **Fiona A. Stewart⁶ & Kornelius Kupczik¹**

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8 ¹Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Max Planck
9 Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103, Leipzig, Germany

10 ²Anthropology Department, University of California Santa Cruz, 1156 High Street
11 Santa Cruz, CA 95064

12 ³Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher
13 Platz 6, D-04103, Leipzig, Germany

14 ⁴German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz
15 5e, 04103 Leipzig

16 ⁵School of Human Evolution and Social Change and Institute of Human Origins, Arizona State
17 University, Tempe, AZ, USA

18 ⁶School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK

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20 *Author for correspondence adam.vancasteren@gmail.com

21

22 **Abstract**

23 Chimpanzees are traditionally described as ripe fruit specialists with large incisors but relatively
24 small postcanine teeth, adhering to a somewhat narrow dietary niche. Field observations and
25 isotopic analyses suggest that environmental conditions greatly affect habitat resource
26 utilization by chimpanzee populations. Here we combine measures of dietary mechanics with
27 stable isotope signatures from eastern chimpanzees living in tropical forest (Ngogo, Uganda)
28 and savannah woodland (Issa Valley, Tanzania). We show that foods at Issa can present a
29 considerable mechanical challenge, most saliently in the external tissues of savannah woodland
30 plants compared to their tropical forest equivalents. This pattern is concurrent with different
31 isotopic signatures between sites. These findings demonstrate that chimpanzee foods in some
32 habitats are mechanically more demanding than previously thought, elucidating the broader
33 evolutionary constraints acting on chimpanzee dental morphology. Similarly, these data can
34 help clarify the dietary mechanical landscape of extinct hominins often overlooked by broad
35 C3/C4 isotopic categories.

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37

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39 Introduction

40 Diet is integral to understanding the behaviours and adaptations of extant and extinct primate
41 species alike. Nowhere is this more salient than in the evolution of the hominin tribe and the
42 emergence of modern day humans, as the majority of dietary inferences must be constructed
43 from a patchwork of fossilised craniodental remains. Food mechanics are likely a substantial
44 driver in the adaptation of the dental complex and the constraints that these place on the
45 efficiency of food processing. Understanding how the form of teeth relates to their function
46 therefore requires a synthesis of knowledge over both tooth structure and the mechanical
47 properties of the critical foods that resist being broken down¹.

48

49 In chimpanzees (*Pan troglodytes*), direct behavioural observation and indirect methods such as
50 isotopic and faecal analysis have allowed a rather in-depth knowledge of *what* their diets are
51 composed of²⁻¹⁰, and thus allow for some comparison with the putative diets of the earliest
52 hominins¹¹. However, in such studies, foods are still largely categorised in very broad terms
53 (e.g., fruits, leaves, bark) that do not faithfully track their mechanical properties¹². In addition,
54 accessing foods often includes the removal of external tissues with the teeth to access the
55 nutrients within. The mechanical properties of such tissues can vary substantially and can
56 instigate distinct oral feeding practices. Such processing is termed ingestion, which is often
57 facilitated by the anterior dentition and is distinct from mastication, where food is cyclically
58 processed by posterior dentition before being swallowed¹³. The mismatch between the
59 mechanical characteristics of foods and how they are processed orally often makes it difficult to
60 understand the physical conditions that foods exert on teeth and can lead to an

61 oversimplification of this vital interface. Therefore, comparative studies of ingestive behaviours
62 and food mechanical properties in large bodied apes, like chimpanzees, are essential to fully
63 understand relationships between craniodental form and function in fossil hominins.

64

65 Chimpanzees allow for an interesting comparison of feeding in two evolutionarily relevant
66 hominin habitats. The tropical forest is analogous to the original stem hominin habitat¹⁴, whilst
67 in comparison the savannah woodland mirrors the ecological conditions that drove later
68 hominin adaptation and the emergence of *Homo*¹⁵ (Figure 1). Currently our understanding of
69 chimpanzee dentition and its functional aspects are limited by a lack of data on the broader
70 dietary mechanical challenges faced species-wide^{16,17}. In fact, data on the mechanical
71 properties effectively hail from one tropical forest¹⁸, and it is doubtful these values accurately
72 reflect the dietary variance of the species. Unlike forest-dwelling chimpanzees, savannah
73 chimpanzees tend to incorporate and rely upon many non-fruit items¹⁹. Isotopic studies
74 conducted on chimpanzee populations have established the species firmly in the C₃ feeding
75 category, meaning that in all habitats chimpanzees primarily feed on tree products that utilise a
76 C₃ photosynthetic pathway²⁰⁻²³. Continued isotopic research has indicated that across
77 chimpanzee habitats, from rainforest to savannah, the values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ vary
78 significantly^{21,22}. These patterns are thought to occur because savannah chimpanzees rely
79 more on plant foods produced under drier environments with reduced canopy cover compared
80 to those of their forest counterparts. However, it remains unclear if utilising foods from
81 different environments affects food material properties in different chimpanzee populations
82 and how this is related to isotopic signatures.

83

84 Such a relationship could prove invaluable for reconstructing the diets of extinct hominins.

85 Early hominins, with the exception of *Homo*, show increasing craniodental robusticity over

86 time^{11,24}. Such morphological change is thought to represent, at least in part, adaptation to

87 more mechanically challenging foods^{25–29}. This seemingly correlates well with a broadening of

88 hominin diets over evolutionary time, as demonstrated by the incorporation of a greater

89 percentage of C₄ resources¹¹. However, the instigation of this adaptive morphology predates

90 the incorporation of large amounts of C₄ resources into the hominin diet^{11,24,30–32}. This may

91 indicate that the dietary mechanical pressures that predisposed early hominins to increased

92 craniodental robusticity are in fact to be found in C₃ as well as C₄ food resources of the mosaic

93 woodland environment.

94

95 To investigate the mechanical variance in chimpanzee diets, we measured the mechanical

96 properties of commonly-consumed plant foods of two communities inhabiting rather disparate

97 environments. This dataset was paired with carbon and nitrogen stable isotope data from

98 plants and hair to determine if isotopic differences were related to mechanical variance. We

99 hypothesised that even accounting for plant baseline, isotopic signatures will be distinct

100 between the two chimpanzee populations and the utilization of different biomes will promote

101 the oral processing of more mechanically challenging foods by the savannah chimpanzees of

102 Issa, Tanzania, compared to the rainforest population of Ngogo, Uganda.

103

104 Results

105

106 *Stable isotope data*

107 We found that with a mean of 3.0‰, the $\delta^{15}\text{N}$ plant values at Issa are lower than what is
108 commonly found in chimpanzee habitats. For Ngogo plants, Carlson³³ reported a mean of 4.5‰
109 (n = 246). A comparison between the $\delta^{15}\text{N}$ values of the two plant datasets controlling for
110 sample type (fruit or leaves) and plant species revealed these differences in $\delta^{15}\text{N}$ are significant
111 between Issa and Ngogo plant foods ($\chi^2=7.36$, df = 1, $p = 0.006$) (Figure 2a and b). However, the
112 same comparison between $\delta^{13}\text{C}$ plant values from Issa and Ngogo³³ revealed that on the broad
113 scale the sites were indistinguishable in carbon ($\chi^2=0.13$, df = 1, $p = 0.714$) (Figure 2a and b).
114 Samples of the sedge family *Cyperaceae* from Ngogo had a high mean $\delta^{13}\text{C}$ value of -11.6 ‰,
115 whereas the single grass sample we measured from Issa had a more typical C_4 plant value of -
116 15‰ (Table 1).

117

118 We obtained novel $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for a total of 51 hair sections (obtained from 11
119 individuals) from the Issa chimpanzees and 85 hair sections (obtained from 13 individuals) for
120 Ngogo. Means and standard deviation as well as fractionation factors between mean isotope
121 values of plants and chimpanzee hair isotope values ($\Delta_{\text{plant-hair}}$) are shown in Table 1.

122

123 Both data sets covered the different seasons of the year in an attempt to deliver an annual
124 isotopic spectrum of adult chimpanzees at both sites. Average temporal isotopic variation

125 within individual hair samples is moderate at Ngogo (0.32‰ in $\delta^{13}\text{C}$, 0.40‰ in $\delta^{15}\text{N}$) and also at
126 the savannah site of Issa (0.38‰ in $\delta^{13}\text{C}$, 0.46‰ in $\delta^{15}\text{N}$); this difference in variation between
127 sites is much smaller than the analytical error and thus not biologically meaningful. This
128 conformity between sites was not expected given the substantial differences in annual rainfall
129 patterns; as one would assume more striking effects of seasonality in the Issa population than
130 in Ngogo. Our model results (see methods for details) show that the differences between
131 chimpanzees from Ngogo and Issa were highly significant in the $\delta^{13}\text{C}$ values ($\chi^2 = 61.45$, $df = 1$, p
132 < 0.0001) and the $\delta^{15}\text{N}$ values ($\chi^2 = 80.67$, $df = 1$, $p < 0.0001$), with Issa chimpanzees being less
133 depleted in ^{13}C , and much lower in ^{15}N (Figure 2c, Table 1).

134

135 *Biomechanical data*

136 At both sites combined, we made 829 (Ngogo $n = 488$ and Issa $n = 341$) measurements of
137 toughness (R) and 557 (Ngogo $n = 321$ and Issa $n = 236$) measurements of elastic modulus (E)
138 on foods that were orally processed. These measurements included 17 plant species from
139 Ngogo (Table 2) that comprised all species observed above 1% of the feeding time of
140 chimpanzees during 36 hours of dry season focal feeding observations. These species feeding
141 times agreed well with long-term observations of the dry season at this site⁸. At Issa, 19 species
142 were tested, including samples from *Ficus*, *Saba* and *Garcinia* (Table 3) that are considered
143 year-round staple foods¹⁰. In the dry season at Issa, chimpanzees are thought to rely more on
144 the woodland plant genera, and our sample reflected this with the inclusion of 8 mainly
145 woodland species.

146

147 Values for R and E of orally processed foods overlapped between the two sites. However, there
148 was a noticeable difference, particularly in the range of the values. At Ngogo, toughness ranged
149 from 15 – 7694 Jm^{-2} , with 0.014 - 82 MPa for the elastic modulus, but at Issa, both toughness
150 and elastic modulus could be much higher: 6.7 – 28869.2 Jm^{-2} toughness and 0.013 – 799 MPa
151 for the elastic modulus. The data were then broken down into food tissue categories (Figure 3)
152 to help elucidate what may be driving the differences in food mechanics between sites. Values
153 within comparable categories had similar ranges in each location that fell within the values
154 previously published for primate food mechanical properties^{18,34,35}. The higher toughness
155 values at Issa were significant for fruit exocarp (Mann-Whitney U test, $W = 2633.5$, $p < 0.001$).
156 Lower values recorded for mesocarp at Issa were also significantly so ($W = 9934$, $p < 0.001$).
157 Similarly, values in leaf laminar tissues were significantly lower at Issa ($W = 2265$, $p = 0.007$), yet
158 there was no significant difference for the toughness of leaf midrib ($W = 2267$, $p = 0.1703$).
159 There were also differences in the recorded E of the comparable food tissues. The exocarps of
160 fruits from Issa were significantly stiffer than those from Ngogo ($W = 442.5$, $p < 0.001$), whilst
161 the fruit mesocarp from Issa was of a significantly lower stiffness than those of Ngogo ($W =$
162 97705 , $p < 0.001$). A similar relationship was observed for leaf laminar tissue ($W = 1157$, $p =$
163 0.005). Recorded values of both R and E demonstrate the most extreme disparity in the exterior
164 casings of fruits that must be breached to obtain nutrient rich mesocarp (see video S1). In Issa
165 exterior tissues such as fruit exocarp demonstrate considerably higher values than are seen in
166 other plant tissues.

167

168 Figure 4 provides a more in depth exploration of the external food casings. The Ngogo study
169 area is mostly covered by moist evergreen and semi-deciduous forest from which all the foods
170 in this study were sampled; therefore, all Ngogo exocarp data were pooled and labelled as
171 forest species. However, the external casings from Issa, a mosaic habitat with multiple biomes,
172 have been broken down into fruits from the gallery forest or fruits from the savannah
173 woodland species. Here it is clear that the largest differences in both *R* and *E* were found in
174 savannah woodland fruits. There was a significant difference between the three categories
175 (forest fruits, gallery forest fruits and savannah woodland fruits *R*, Kruskal Wallis test : $\chi^2 = 79.3$,
176 $p < 0.001$ and *E*, $\chi^2 = 78.8$, $p < 0.001$). A Dunn's test of multiple comparisons showed that all
177 categories were significantly different from each other in both toughness and stiffness.

178

179 **Discussion**

180 Mechanical data from foods consumed by *P. troglodytes schweinfurthii* in Ngogo conformed
181 well to those of Vogel et al.¹⁸ measured from chimpanzee populations at Kanyawara. All Ngogo
182 data for toughness and stiffness remained at relatively low levels (Figure 3a and b). Similarities
183 between Kanyawara and Ngogo are not surprising, as both sites are within the Kibale National
184 Park, with foods comprising of comparable plant species. Indeed, there is up to 73% overlap in
185 feeding species between the two sites^{3,7}. Ngogo and Kanyawara provide an example of tropical
186 rainforest, and the chimpanzees at both sites have diets comprised largely of fleshy ripe fruits
187 even in times of reduced production^{3,8}. This pattern of high fruit consumption characterizes
188 chimpanzees inhabiting tropical and subtropical moist broadleaf forests²¹. In such biomes it is
189 likely that lower seasonality and higher fruit availability compared to savannah woodland sites

190 means that the majority of oral processing reduces the mechanical challenges to teeth. At Issa,
191 the mesocarp of fruit, leaf laminar tissue, and leaf midrib also manifested within this rather
192 narrow range (Figure 3a and b). These are all tissues that are likely masticated by molars and
193 then subsequently swallowed. Previous hypotheses surrounding the molar morphology of *Pan*
194 have suggested that gracile molars with thin enamel are a derived trait adapted for
195 comminuting large amounts of easy to process foods, along with some (possibly seasonal)
196 fracture resistant foods, such as foliage¹⁸. The loss of thick enamel is likely due to a relaxation of
197 selection pressures that necessitated strong durable crowns adapted to either hard and/or
198 abrasive food tissues. Our data go some way to supporting this hypothesis, demonstrating a
199 lack of variance in the mechanical properties of tissues likely masticated by chimpanzees across
200 our study sites.

201

202 Despite the overlap in masticated tissues, data from Issa presents a divergence from this
203 mechanical dietary uniformity. Substantial differences occur in both the toughness (Figure 4a)
204 and modulus (Figure 4b) in the external casing of savannah fruits at Issa. Such mechanically
205 challenging tissues will necessitate ingestive processing to access consumable tissues (see for
206 example Supplementary Movie 1). It is noteworthy that the mean values for these tissues, $R =$
207 1794.0 (s.d. 5435.2) J m^{-2} and $E = 50.1$ (s.d. 91.3) MPa, exceed those of Bornean orangutans ($R =$
208 1152.9 J m^{-2} and E of 3.08 MPa, respectively), which are generally considered to consume the
209 most mechanically challenging diet of all the great apes³⁶. At Issa, the highest values were
210 generated primarily by the woody valves of *Julbernardia* sp., which are comparable values to
211 other woody legume pods eaten by primates^{1,37} and the resilient outer exocarp of *Strychnos*

212 sp. (Table 3). The exocarp of other savannah species within our data set also demonstrated
213 generally higher toughness and stiffness estimates when compared to foods from rainforest,
214 gallery forest, and values obtained from the literature^{1,18,36} (Figure 3a and b). We know very
215 little about the mechanical properties of savannah plants, but these are likely to demonstrate a
216 greater variability, as such plant species must have different adaptations to water stress events.
217 All this would indicate that when feeding is more concentrated in the savannah woodland
218 habitats, as is the case at Issa during the dry season¹⁰, chimpanzees face external plant tissues
219 that are substantially more demanding than those encountered by their conspecifics within
220 Kibale National Park.

221

222 Whilst extractive and percussive foraging behaviours are reported in savannah chimpanzee
223 populations³⁸⁻⁴¹, the majority of plant foods are likely processed orally. In chimpanzees, oral
224 ingestive processing is done primarily by the anterior teeth^{2,38,42} (an example of such action can
225 be found in Supplementary Movie 1). These feeding behaviours coincide well with morphology,
226 as high forces and unique loading regimes are likely to be necessary in the husking of more
227 mechanically challenging foods, such as those demonstrated at Issa. Unlike basal Miocene apes
228 and later members of the human ancestral clade, chimpanzees have quite derived anterior
229 teeth, most obviously in the size and morphology of the incisors⁴³. Chimpanzee incisors are
230 characterised by their large broad spatulate shape^{16,42-44}, presenting a more procumbent
231 posture and sharp cutting edge, maintained through a thinning of the lingual enamel, which
232 may also reduce stress on the crown during ingestion⁴⁵. Uniquely amongst hominoids, the
233 lower incisors have converged to the morphology of the uppers⁴³. Both upper and lower

234 incisors therefore offer a large optimally angled cutting tool, well adapted for initiating and
235 propagating fracture in foods⁴⁶. Furthermore, each anterior tooth is anchored by a markedly
236 long and large tooth root⁴⁷, making them well equipped to deal with high forces that are likely
237 inflicted on these teeth during the ingestive processing of mechanically challenging foods. It
238 therefore appears that the anterior teeth of chimpanzees form the workhorse of the
239 chimpanzee dentition, and are well adapted to deal with mechanical challenges arising from
240 foods. These teeth are likely utilized to overcome the higher mechanical challenge presented by
241 the external casings of savannah plants within the Issa environment. Such external barriers
242 must be breached in order to gain access to internal nutrient tissues.

243

244 Isotopic signatures measured from chimpanzee hair samples show a significant difference
245 between sites in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}$ values: $\chi^2 = 61.45$, $df = 1$, $p < 0.0001$ and the $\delta^{15}\text{N}$
246 values $\chi^2 = 80.67$, $df = 1$, $p < 0.0001$). These differences become apparent in the substantial
247 differences in $\Delta_{\text{plant-hair}}$ isotope values, which show the behavioural difference in chimpanzee
248 habitat utilization when controlling for isotopic baseline effects in potential plant foods. For
249 $\delta^{15}\text{N}$, this discrepancy can be explained by the significant differences in the plant isotope
250 baselines between sites ($\chi^2=7.36$, $df = 1$, $p = 0.006$), which are probably driven by the isotope
251 values of non-fruit items such as leaves (see Table 1). This indicates that previous attempts^{20,21}
252 to explain the relatively low $\delta^{15}\text{N}$ values in the Issa chimpanzees in the absence of plant
253 baseline data require revision. Low $\delta^{15}\text{N}$ values in the Issa chimpanzees are best explained by
254 generally depleted plant baseline values in this woodland mosaic habitat, and not necessarily
255 by the chimpanzees' heavy consumption of nodulating (soil nitrogen fixating) plants. Moreover,

256 an overall depleted $\delta^{15}\text{N}$ signature seems to be more common in savannah chimpanzee sites
257 than previously assumed, as this low $\delta^{15}\text{N}$ pattern has also been observed at several other
258 savannah chimpanzee sites across Africa, including Kayan in Senegal²², as well as in several
259 unpublished datasets from West Africa (Oelze personal communication).

260

261 In this study, however, we focussed on the site specific signatures in $\delta^{13}\text{C}$, as they are highly
262 relevant for understanding paleodiets in the fossil record. Measurements of $\delta^{13}\text{C}$ can be
263 obtained from ancient dental enamel, whereas the analysis of $\delta^{15}\text{N}$ is limited to well preserved
264 organic material containing substantial amounts of nitrogen. The plant $\delta^{13}\text{C}$ values in our study
265 indicate that on a general scale, the isotopic variance between the two habitats is minimal.
266 However, chimpanzee hair isotope values significantly differ in $\delta^{13}\text{C}$. This evinces to two main
267 outcomes. Firstly, chimpanzees do not always simply resemble the isotopic characteristic of the
268 environment they inhabit, but they have feeding preferences and select microhabitats suitable
269 to meet their dietary demands. Our $\delta^{13}\text{C}$ data suggest that Issa chimpanzees do not feed solely
270 on plant foods (mainly ripe fruits and smaller quantities of leaves) derived from dense gallery
271 forest patches, but rely on ^{13}C enriched plants in the open areas of the woodland savannah,
272 which is concurrent with observational and faecal analysis at Issa^{4,10}. This is in line with isotopic
273 evidence reported from chimpanzees and their plant foods at the savannah site of Kayan in
274 Senegal²² and with what can be assumed from work at other savannah sites like Fongoli,
275 although respective $\delta^{13}\text{C}$ plant data are not yet available²³. Secondly, $\delta^{13}\text{C}$ values from hair
276 samples differed between sites, but this variance does not resemble the vast differences
277 reported between C_4 (savannah) and C_3 (forest) dependent fossil hominin species in East

278 Africa^{11,48}, primarily because no known population of chimpanzees has been found to habitually
279 consume C₄ plant foods²³. Yet it appears these smaller scale differences may have rather large
280 implications in the acquisition of food and the mechanical challenges encountered in
281 contrasting biomes. Such subtle differences could therefore be of interest to
282 paleoanthropologists reconstructing diets of the past.

283

284 A somewhat restrictive diet dominated by C₃ plants – as found in chimpanzees^{11, 49} – is often
285 assumed to be somewhat mechanically narrow, i.e., associated with easy to process fruits and
286 forest products. Our data indicate that this is not always the case. Plant tissues consumed by
287 chimpanzees that utilise a C₃ photosynthetic pathway can demonstrate pronounced mechanical
288 variance and challenges. Broad and easily observable isotopic categorisations based on
289 photosynthetic pathways are critical to our understanding of paleo-environments, but alone
290 these proxies may offer little indication of the finer scale mechanical behaviour of plant foods;
291 it is this which is likely to be driving the adaptations of the craniodental complex of African Plio-
292 Pleistocene fossil hominins.

293

294 Although discussion is ongoing concerning the exact paleoenvironment that the australopiths of
295 Pliocene East Africa inhabited, there is some consensus that this niche was either wooded
296 shrubland or wooded grassland, similar to the mosaic savannah woodland environment of
297 extant savannah chimpanzees^{15,50}. Fossil findings have also indicated that members of *Pan* have
298 long used these habitat types in sympatry with early *Homo*, a relationship with the human

299 lineage that may have endured since the divergence of *Pan* and hominins⁵¹. Middle Pliocene
300 australopiths such as *Ardipithecus ramidus* and *Australopithecus anamensis* possess remarkably
301 comparable isotopic signatures with savannah chimpanzees, suggesting they relied on a C₃
302 dominated diet^{49,52,53}. Whilst perhaps savannah chimpanzees are an imperfect morphological
303 analogy for these early hominins, there are some dental and gnathic similarities (e.g. increased
304 procumbancy and larger incisors) that appear somewhat reduced in later occurring Pliocene
305 hominins (such as *Au. afarensis*) and even more so in Pleistocene hominins (such as *Homo* and
306 *Paranthropus*)^{32,54,55}. The coupling of our mechanical and isotopic data suggests that savannah
307 dwelling members of *Pan* that utilize similar habitats and eat mechanically similar foods to our
308 earliest relatives could provide a reasonable extant analogue for exploring early hominin
309 feeding ecology. Further to this, our results indicate that there may have been a shift towards
310 more mechanically challenging foods associated with the hominin transition to exploiting more
311 wooded environments that likely predates the general hominin trend for increased C₄
312 consumption.

313

314 Our quantitative results of food mechanical properties indicate that many plant tissues
315 masticated by chimpanzees do inhabit a rather narrow dietary range and could be considered
316 rather easy to process. However, this does not comprehensively represent the extent of
317 chimpanzee diets, as harder to process plant tissues can represent substantial contributions to
318 the diets of some populations. We do not advocate that mechanically challenging food items in
319 the chimpanzee diet are only found in savannah environments or that chimpanzees routinely
320 process such foods at all savannah sites. Indeed, different chimpanzee populations have been

321 shown to use seemingly similar environments quite differently with regard to foraging habits²⁰.
322 Rather, we show that the possibility exists that in the resource limited savannah woodland
323 environment, chimpanzees choose different foods, some of which are more mechanically
324 challenging than has been considered the dietary norms for this species³⁶. Importantly, these
325 tissues are produced by C₃ plants, indicating that both C₃ and C₄ plants can manifest as
326 mechanically challenging plant tissues and both may be responsible for driving dental
327 adaptation. Mechanically challenging tissues, like the external casings of savannah plants, are
328 probably processed to a large extent with the anterior dentition. These teeth are likely to incur
329 larger and more variable forces than the postcanine teeth, as internal tissues that are
330 masticated present only a limited mechanical challenge. Understanding if there is a functional
331 driver behind morphological features of the teeth of chimpanzees and indeed fossil hominins
332 will require a further expansion of the current knowledge of both food mechanical properties
333 and ingestive behaviours on a pan-African scale to reduce our reliance of mechanical property
334 data from singular sites.

335

336 **Methods**

337 *The sites*

338 Two sites chosen for this study were the Ngogo Chimpanzee Project and the Greater Mahale
339 Ecosystem Research and Conservation Project (GMERC, formerly Ugalla Primate Project). Both
340 sites were investigated during the dry season, which in both vicinities is associated with a
341 decrease in fruit production and arguably presents a period of greater dietary stress for the
342 chimpanzee communities^{4,7}. Chimpanzee hair samples for isotope analysis were collected

343 opportunistically during a 12+ month study period at Ngogo (2012-2013) and Issa (2013-2014)
344 within the framework of the Pan African Programme (<http://panafrican.eva.mpg.de/>). They
345 represent the annual spectrum of isotope values at each site. At both sites, the samples
346 represent plants from both wet and dry seasons (as defined below).

347

348 Ngogo – The Ngogo study area is situated centrally in the Kibale National Park in south-western
349 Uganda^{7,56}. The park consists of an area of 795 km², dominated by moist evergreen, with some
350 seasonally deciduous, forest. Tree species are a transition between montane and lowland
351 forest^{7,56} (Figure 1a). The area receives high rainfall with the yearly average ranging from 1400 –
352 1600 mm. This is fairly evenly-distributed throughout the year, but dry seasons can be defined
353 as two low rainfall levels between June-July and December-February^{7,56}. The study area is
354 home to a chimpanzee population of close to 200 individuals that have been continuously
355 observed since 1995. The chimpanzees are well-habituated allowing direct observation of food
356 selection and feeding behaviours⁷.

357

358 Issa – The GMERC is located in the Issa valley that lies 100km east of Lake Tanganyika. The site
359 is a mosaic habitat dominated by savannah woodland (*Brachystegia* and *Julbernardia*) but
360 punctuated by evergreen gallery forests, swamps and grassland (Figure 1b). Seasonality is high
361 at Issa with two discrete seasons: a wet (October - April) and dry (May - September). The
362 annual rainfall is lower than at Ngogo, averaging 1220mm per annum with levels dropping to
363 <100 mm in the months of the dry season^{10,57,58}. Research on chimpanzees was first conducted

364 in this region in 2001-2003⁴, with a permanent research presence initiated in 2008 by the
365 GMERC that has since been maintained. The Issa community is considered semi-habituated;
366 current research is focused on a 85 km² study area where genetic analysis has identified 67
367 individuals^{57,58}.

368

369 *Sample collection for mechanical properties*

370 Ngogo - As the population is well habituated at this site it was possible to make direct
371 observations of what was consumed by individuals. This information was checked against the
372 substantial literature on chimpanzee diet in the Ngogo study area^{7,8,59} to confirm that the items
373 seen eaten were typical for the time of year and habitat. With such guidance, we determined
374 the most important foods to test by conducting day-long follows of chimpanzees, employing
375 the focal techniques used by Vogel et al.¹⁸. This entailed picking a focal animal from within the
376 group and recording their behaviour continuously for 10 min. After this period elapsed, another
377 individual was then selected and observed. This way one can garner observations across a large
378 group of individuals¹⁸.

379

380 Knowing what is being eaten allowed the selection of foods for measurements of the
381 mechanical properties of individual tissues either ingested or masticated by chimpanzees.
382 Samples were obtained by two main methods. Foods were either dropped by focal animals, this
383 may be because a plant tissue was not consumed, or it was dropped in the process of eating.
384 However to increase the number of samples for testing, food items were also acquired directly

385 from trees accessed using canopy access techniques⁶⁰ that chimpanzees had been observed
386 feeding in.

387

388 Issa - The semi habituated state of the population at Issa does not permit the kind of all-day
389 follows of chimpanzees used at Ngogo. Often finding groups of individuals can take some time
390 and the amount of time following is greatly reduced when compared to Ngogo. This means that
391 direct observations of feeding can be reduced to a matter of minutes per day. Therefore, direct
392 observations were used on an opportunistic basis and foods were collected following
393 confirmation that a certain food item was eaten by the chimpanzees. However, due to the low
394 levels of direct observations we also used information from over 4 years of dietary research
395 conducted at Issa which has identified the major food sources from faecal sieving and direct
396 observations alike¹⁰ this allowed us to target the most commonly consumed dry season foods.
397 In both sites, whenever foods were selected by humans, efforts were taken to match overt cues
398 of readiness of foods for consumption.

399

400 *Mechanical properties testing*

401 We measured two main mechanical properties that are particularly pertinent to the breakdown
402 of food: toughness and elastic modulus. We defined toughness as the energy needed to
403 propagate a crack through a material. An estimation of the energy needed to generate a new
404 surface is made and then this is divided by the actual surface area of one side of the crack. The
405 resulting value is termed R with the units of joules per meter squared (J m^{-2})^{1,61}. This is integral

406 to understanding how foods resist cracks being initiated and propagated by teeth: foods of
407 higher toughness will be more resilient and harder to breakdown during ingestion and
408 mastication. Toughness has been utilised as a dietary proxy in many studies of primate feeding
409 ecology and has helped understand the interface between teeth and foods¹. The elastic
410 (Young's) modulus (E) of a material is its resistance to reversible deformation, measured as the
411 stress (force per unit area) that produces a strain (a proportional change in dimensions). This
412 can be estimated from the slope of an initial linear region of a stress-strain curve and has units
413 that are usually given in the megapascal (MPa) range for foods consumed by chimpanzees and
414 other primates¹.

415

416 Whenever possible, foods were separated into broad plant anatomical categories, such as
417 exocarp and mesocarp for fruits, with leaves divided into laminar tissue vs. midrib/veins,
418 concordant with Vogel et al.^{18,62}. Samples of these tissues were tested individually. To deal with
419 anisotropy, tests were performed in the direction relevant to feeding. This was determined
420 from feeding remains or video evidence. If this was not possible, multiple orientations were
421 tested. All tests in this study were performed on a portable universal testing machine designed
422 for use in the field (Lucas Scientific FLS-1). This machine consists of a hand-cranked movable
423 crosshead and was equipped with a force transducer to measure the resultant forces and a
424 linear variable displacement transducer that measured accurately movements in the crosshead.
425 The equipment is powered by and interfaces with a laptop computer upon which custom built
426 software allows the calculations of the main material properties of foods. There are a multitude
427 of tests available to measure mechanical properties and the tester houses a range of

428 accessories and rigs that can be employed to measure *R* and *E*. Selection of a test depends
429 partly on the size and shape of food items and components and on how chimpanzees process
430 them. Below, we outline the tests that we used during this study.

431

432 Toughness Measuring this required the generation of a fracture. We utilised the displacement-
433 controlled action of blades for this purpose, measuring the force needed to propagate a crack
434 through a given area of material. Use of a blade allowed a fracture to be directed through a
435 heterogeneous specimen, such as a leaf for example, such that it accords with the types of
436 fracture seen on samples eaten by chimpanzees. One of the major causes of error in recording
437 toughness via this method is that the interface between blade and material will generate
438 friction and may lead to an overestimate of toughness if not separated out from fracture.
439 However, such friction can be estimated simply by running a second pass of the blade after a
440 fracture has been formed. The blade needs to pass through an identical displacement, with the
441 work recorded, being not that required to produce a new surface, but rather to overcome
442 frictional interactions. This second pass can be subtracted from the originally recorded energy
443 to give a more accurate figure of fracture toughness⁶¹.

444

445 Bulk food items, such as substantial pieces of fruit flesh, had their toughness estimated by
446 employing the wedge test. A sharp wedge (circa 15°) would be driven into a food specimen of
447 known dimensions for a known displacement, thus generating a crack within it. A second pass,
448 as described above, compensates for the influence of friction. The energy actually used in crack

449 formation, obtained by deducting the work done in the second pass from that in the first, was
450 then divided by the area of the newly created surface to obtain an estimate of the toughness⁶¹.
451 Sometimes the amount of testable material is too small to be wedged. Such tissues are sheet or
452 rod-like structures. When these circumstances arise, a single blade, or two crossing blades as in
453 a pair of scissors, was used to propagate a crack through a material of known dimensions. Again,
454 a second pass is used to compensate for friction between the blade and food or between the
455 two passing blades^{61,63}.

456

457 Modulus Measuring the modulus of primate foods has become far easier in recent years with
458 the onset of developments in indentation methods (for more detail, see Talebi et al³⁵ and van
459 Casteren et al.,⁶⁴). Blunt indentation uses hemispherical indenters to measure the modulus of a
460 material quickly and with very little sample preparation. All blunt indent tests follow basic load
461 relaxation conditions: a material is loaded slowly at a consistent rate for around 10s and the
462 resultant “force ramp” is recorded. After 10s, the displacement is then held constant whilst
463 measuring decay of the load for a further 90s or until the load becomes constant. A curve is
464 fitted to this relaxation behaviour allowing the calculation of an instantaneous (E_i) and infinite
465 (E_∞) elastic modulus. These terms effectively represent the upper and lower bounds of a
466 material’s elastic resistance and the ratio of the two values (E_∞/E_i) indicates the rate sensitivity
467 of a material. Whilst neither of these values is an ideal representation of what happens in the
468 mouth for this particular study, we consider E_i to be a more useful measure when considering
469 ingestion and mastication and is used primarily in this investigation⁶⁴.

470

471 We used two types of blunt indent test for this study. The first, a bulk indent test, used a large
472 hemispherical probe (of 3.6 mm radius) for measuring the modulus of bulk food items, like fruit
473 flesh. A sample must be cut so that is stable and has a flat surface normal to the probe. Care
474 must be taken that the sample is sufficiently thick ($\geq 2\text{mm}$) and that the indent does not exceed
475 10% of the sample thickness to avoid influence of the substrate on which it rests⁶⁴. The second
476 test is a membrane test that can be used on sheet-like materials like leaves and, in some cases,
477 a peel-like exocarp of a fruit. A test specimen was clamped between two transparent plates
478 that have aligned circular holes, 2 mm in radius, in their centre. A hemispherical probe of
479 0.25mm radius is then used to measure the modulus of a specimen - laminar leaf tissue or
480 some external fruit peels by pressing down on a specimen exactly in the centre of the exposed
481 disc of tissues. In this test, the total deformation needed to be less than the total thickness of
482 the specimen being tested to avoid error. After testing, the material was checked for visible
483 damage to ascertain if there was damage due to cellular collapse; such test results were
484 discarded³⁵. Both these blunt indentation tests followed the basic load relaxation method
485 described above.

486

487 Some foods cannot be indented because their shape and size does not allow for this, e.g.
488 specimens in the form of rods. In these cases, we resorted to more traditional compression
489 tests where possible. Cylinders of material of known dimension were compressed and the
490 modulus calculated as the slope of the initial region of the stress strain graph⁶⁵. For woody
491 material, or that arranged in a rod-like manner, 4-point bending tests were used to calculate

492 the modulus. This is where a beam of known dimensions is bent and the elastic modulus
493 estimated from the elastic phase of this bending behaviour⁶⁵.

494

495 *Stable isotope sampling and analysis*

496 For this study we analysed 11 hair samples from the chimpanzees at Issa, and 13 hair samples
497 from the Ngogo chimpanzees in Kibale. Chimpanzee hair samples exported from Uganda and
498 Tanzania were done so following the regulations set out in the Convention on International
499 Trade in Endangered Species of Wild Fauna and Flora (CITES). CITES Permit No. UG003042
500 (Uganda) and CITES Permit No. 28753 (Tanzania). Samples consist of at least 10-15 hairs each
501 and were obtained non-invasively from fresh or recent nests (nest decay stage 1 or 2, see
502 Kouakou et al.⁶⁶) (Supplementary Table 1), which were associated to four distinct nests groups
503 at Issa and to five nest groups in Ngogo. By focussing on nest groups we tried to ensure the
504 sampling of different members of a chimpanzee party with the aim to minimize potential errors
505 easily introduced by pseudoreplication⁶⁷. Hair samples were prepared following the procedure
506 outlined in detail by Oelze⁶⁸, with an emphasis on removing potential infant hairs and lipid
507 contaminants from the material used for isotope analysis. All hair used contained root bulbs in
508 the telogen stage and was cut sequentially in 5 or 10 mm long sections as weight for analysis
509 allowed (< 3.5mg). Each hair yielded multiple isotope measurements with hair section isotope
510 values reflecting the previous two weeks (5 mm) or one month (10 mm) of diet if human hair
511 growth rates are used as a proxy. As a result, each complete hair sample reaches several
512 months back into time and covers on average six previous months of chimpanzee dietary
513 behaviour⁶⁸.

514

515 Plant carbon isotope data from Ngogo were available due to the extensive work of Bryce
516 Carlson and could be extracted from the literature³³. Although several peer-reviewed
517 publications contain the carbon data from his work, we decided to refer to his PhD dissertation,
518 as it contains both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data on Ngogo plants, reporting means for samples for which
519 multiple samples had been collected. Ngogo plant samples were collected in the different
520 seasons of 2009 and 2010 and represent the top 40 plant foods known to be preferred by the
521 Ngogo chimpanzees^{33,69}. To ease the comparison with the Issa plant data, we considered only
522 the data obtained from fruits and leaves (n=184, reported mean isotope values n=34, see
523 Supplementary Table 2), including fruits, seeds, pulp and grasses but excluding roots, bark,
524 flowers and piths. These plant samples were selected based on the chimpanzees' feeding
525 preferences and thus encompass the different levels of the canopy as exploited by the Ngogo
526 chimpanzees, including ground and high canopy foods^{69,70}. In Issa we collected a small selection
527 of representative plant samples (n=32) for stable isotope analysis in the wet and dry seasons of
528 2015 and 2016. We focussed on plant foods assumed to be essential for the Issa chimpanzees
529 based on the literature¹⁰, feeding signs, and the presence of the tree species in the GMERC's
530 phenology inventory. Thus food plant samples were predominantly obtained from miombo
531 woodland and gallery forest habitat types and much less so from open savannah areas. All Issa
532 plant materials are represented by bulk fruits (exocarp, mesocarp, seeds) and leaves, but also
533 by one sample of grass from the open savannah (Supplementary Table 3). As in Ngogo, plant
534 sampling followed evidence of chimpanzees' feeding selection and thus encompasses samples
535 from the different layers of the canopy. Ripe fruit and leaves were predominantly collected

536 after being dropped to the ground by various animals feeding in the canopy, whereas some
537 mature leaves and terrestrial herbs such as *Aframomum* sp. and the unidentified grass were
538 collected from the subcanopy level. Both datasets are slightly over representative of fruit over
539 leaves, which we consider to resemble chimpanzee feeding preferences. Plant samples
540 exported from Tanzania were done so with the permission of the Tanzanian Chamber of
541 Commerce, Industry and Agriculture (Permit No. A025760) and adhered to Phytosanitary
542 conditions for export (Phytosanitary certificate No. 215903). All plant materials were thoroughly
543 dried, homogenized to a fine powder in a pebble mill, and ~2 mg were weighed into tin
544 capsules for isotopic measurement.

545

546 All stable isotope measurements were performed in a Flash 2000 – HAT elemental analyser
547 (Thermo Fisher Scientific, Waltham, USA) coupled via ConFlo IV (Thermo Fisher Scientific,
548 Waltham, USA) with a MAT 253 mass spectrometer (Thermo Fisher Scientific, Waltham, USA) at
549 the commercial stable isotope laboratory IsoDetect in Leipzig, Germany. The stable isotope
550 ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are expressed as the ratio of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$
551 ratios, respectively, using the delta (δ) notation in parts per thousand or permil (‰) relative to
552 the international standard materials Vienna PeeDee Belemite (vPDB) and atmospheric N_2 . The
553 analytical error calculated from repetitive measurements of international (USGS25, USGS40 and
554 USGS41 for N; IAEA-CH6, IAEA-CH7 and IAEA-CH3 for C) and lab-internal standards (caffeine,
555 methionine) included in each run is less than 0.2 ‰ (2σ) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. To assure analytical
556 quality we excluded all hair isotope data with atomic C:N ratios outside the acceptable 2.6 to
557 3.8 range⁷¹.

558

559 For statistical analysis we used R (version 3.4.1, R Development Core Team 2017. We tested the
560 response variables $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in plant samples by running two separate mixed models with
561 Gaussian error structure containing the fixed effect of 'site', and the control predictor 'plant
562 sample', as well as the random effect of 'plant species', accounting for multiple measurements
563 per taxon in the datasets used. We excluded the C_4 grass samples from both plant datasets in
564 our analysis due to low sample size for this control variable. We calculated p-values for both
565 models by comparing a full model against a null model excluding the fixed effect of 'site' with
566 the function ANOVA. To compare the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in chimpanzee hair between sites,
567 we also tested each isotope value as a response in a linear model with Gaussian error structure.
568 In both models we included the main effect of 'site' and the random effect of 'hair sample' to
569 account for the fact that we conducted several measurements per hair sample and thus per
570 individual. We obtained model results by running an ANOVA with the full model and a null
571 model excluding the main effect. For all the four above models, various diagnostic plots of the
572 residuals against fitted values confirmed normal distribution of residuals in the models. We
573 tested variance inflation factors and found no issues with collinearity. Model stability was
574 tested by running each model again by excluding single observations one at a time and
575 comparing the respective model results. Stability tests showed no sign of influential cases.

576

577 **Data availability**

578 The data that support the findings of this study are available from the corresponding author
579 upon reasonable request.

580

581 **References**

- 582 1. Lucas, P. W. *Dental Functional Morphology: How Teeth Work*. (Cambridge University
583 Press, 2004).
- 584 2. Suzuki, A. An ecological study of chimpanzees in a savanna woodland. *Primates* **10**, 103–
585 148 (1969).
- 586 3. Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P. & Isabirye-Basuta, G. Social ecology
587 of Kanyawara chimpanzees: implications for understanding the costs of great ape groups
588 in *Great Ape Societies* (eds. McGrew, W. C., Marchant, L. F. & Nishida, T.) 45 – 57
589 (Cambridge University Press, 1996).
- 590 4. Hernandez-Aguilar, R. A. Ecology & Nesting Patterns of Chimpanzees (*Pan Troglodytes*) in
591 Issa, Ugalla, Western Tanzania. (University of Southern California, 2006).
- 592 5. Morgan, D. & Sanz, C. M. Chimpanzee feeding ecology and comparisons with sympatric
593 gorillas in the Goulougo Triangle, Republik of Congo in *Feeding Ecology in Apes and*
594 *Other Primates* (eds. Hohmann, G., Robins, M. M. & Boesch, C.) (Cambridge University
595 Press, 2006).
- 596 6. Pruett, J. D. Feeding ecology of savanna chimpanzees at Fongoli, Senegal in *Feeding*
597 *Ecology in Apes and Other Primates* (eds. Hohmann, G., Robins, M. M. & Boesch, C.)

- 598 (Cambridge University Press, 2006).
- 599 7. Watts, D. P., Potts, K. B., Lwanga, J. S. & Mitani, J. C. Diet of Chimpanzees (*Pan*
600 *troglodytes schweinfurthii*) at Ngogo , Kibale National Park , Uganda , 1 . Diet
601 Composition and Diversity. *Am. J. Primatol.* **74**, 114–129 (2012).
- 602 8. Watts, D. P., Potts, K. B., Lwanga, J. S. & Mitani, J. C. Diet of Chimpanzees (*Pan*
603 *troglodytes schweinfurthii*) at Ngogo , Kibale National Park , Uganda , 2 . Temporal
604 Variation and Fallback Foods. *Am. J. Primatol.* **74**, 130–144 (2012).
- 605 9. Lindshield, S., Danielson, B. J., Rothman, J. M. & Pruett, J. D. Feeding in fear? How adult
606 male western chimpanzees (*Pan troglodytes verus*) adjust to predation and savanna
607 habitat pressures. *Am. J. Phys. Anthropol.* **163**, 480–496 (2017).
- 608 10. Piel, A. K. *et al.* The diet of savanna-woodland chimpanzees (*Pan troglodytes*
609 *schweinfurthii*) at Issa , Ugalla , western Tanzania. *J. Hum. Evol.* **112**, 57–69 (2017).
- 610 11. Sponheimer, M. *et al.* Isotopic evidence of early hominin diets. *Proc. Natl. Acad. Sci.* **110**,
611 10513–10518 (2013).
- 612 12. Coiner-Collier, S. *et al.* Primate dietary ecology in the context of food mechanical
613 properties. *J. Hum. Evol.* **98**, 103–118 (2016).
- 614 13. Wright, B. W. Craniodental biomechanics and dietary toughness in the genus *Cebus*. *J.*
615 *Hum. Evol.* **48**, 473–492 (2005).
- 616 14. Potts, R. Paleoenvironmental basis of cognitive evolution in great apes. *Am. J. Primatol.*
617 **62**, 209–228 (2004).

- 618 15. Cerling, T. E. *et al.* Woody cover and hominin environments in the past 6 million years.
619 *Nature* **476**, 51–56 (2011).
- 620 16. Deane, A. First contact: Understanding the relationship between hominoid incisor
621 curvature and diet. *J. Hum. Evol.* **56**, 263–274 (2009).
- 622 17. Klukkert, Z. S., Teaford, M. F. & Ungar, P. S. A dental topographic analysis of
623 chimpanzees. *Am. J. Phys. Anthropol.* **148**, 276–284 (2012).
- 624 18. Vogel, E. R. *et al.* Functional ecology and evolution of hominoid molar enamel thickness:
625 *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *J. Hum. Evol.* **55**, 60–74
626 (2008).
- 627 19. Lindshield, S. M. Multilevel analysis of the foraging decisions of western chimpanzees
628 (*Pan troglodytes verus*) and resource scarcity in a savanna environment at Fongoli,
629 Senegal. (Iowa State University, 2014).
- 630 20. Schoeninger, M. J., Moore, J. & Sept, J. M. Subsistence strategies of two ‘savanna’
631 chimpanzee populations: The stable isotope evidence. *Am. J. Primatol.* **49**, 297–314
632 (1999).
- 633 21. Schoeninger, M. J., Most, C. A., Moore, J. J. & Somerville, A. D. Environmental variables
634 across *Pan troglodytes* study sites correspond with the carbon, but not the nitrogen,
635 stable isotope ratios of chimpanzee hair. *Am. J. Primatol.* **78**, 1055–1069 (2015).
- 636 22. Oelze, V. M. *et al.* Comparative isotope ecology of African great apes. *J. Hum. Evol.* **101**,
637 1–16 (2016).

- 638 23. Sponheimer, M. *et al.* Do 'savanna' chimpanzees consume C4 resources? *J. Hum. Evol.*
639 **51**, 128–33 (2006).
- 640 24. White, T. D. *et al.* Asa Issie, Aramis and the origin of *Australopithecus*. *Nature* **440**, 883–
641 889 (2006).
- 642 25. Teaford, M. F. & Ungar, P. S. Diet and the evolution of the earliest human ancestors.
643 *Proc. Natl. Acad. Sci. U. S. A.* **97**, 13506–13511 (2000).
- 644 26. Jolly, C. J. The Seed-Eaters : A New Model of Hominid Differentiation Based on a Baboon
645 Analogy. *Man* **5**, 5–26 (2009).
- 646 27. Strait, D. S. *et al.* The feeding biomechanics and dietary ecology of *Australopithecus*
647 *africanus*. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 2124–2129 (2009).
- 648 28. Strait, D. S. *et al.* Viewpoints: diet and dietary adaptations in early hominins: the hard
649 food perspective. *Am. J. Phys. Anthropol.* **151**, 339–355 (2013).
- 650 29. Lucas, P. W., Constantino, P. J., Wood, B. & Lawn, B. Dental enamel as a dietary indicator
651 in mammals. *Bioessays* **30**, 374–385 (2008).
- 652 30. Levin, N. E., Haile-Selassie, Y., Frost, S. R. & Saylor, B. Z. Dietary change among hominins
653 and cercopithecids in Ethiopia during the early Pliocene. *Proc. Natl. Acad. Sci.* **112**,
654 12304–12309 (2015).
- 655 31. Ward, C. V, Leakey, M. G. & Walker, a. Morphology of *Australopithecus anamensis* from
656 Kanapoi and Allia Bay, Kenya. *J. Hum. Evol.* **41**, 255–368 (2001).
- 657 32. Ward, C., Leakey, M. & Walker, A. The new hominid species *Australopithecus anamensis*.

- 658 *Evol. Anthropol. Issues, News, Rev.* **7**, 197–205 (1999).
- 659 33. Carlson, B. Reconstructing Diet from the Ground Up: Isotopic Dietary Ecology of
660 Chimpanzees at Ngogo, Kibale National Park, Uganda. (Emory, 2011).
- 661 34. Constantino, P. J., Lucas, P. W., Lee, J. J.-W. & Lawn, B. R. The influence of fallback foods
662 on great ape tooth enamel. *Am. J. Phys. Anthropol.* **140**, 653–60 (2009).
- 663 35. Talebi, M. G. *et al.* Membrane–plate transition in leaves as an influence on dietary
664 selectivity and tooth form. *J. Hum. Evol.* **2016**, (2016).
- 665 36. Taylor, A. B., Vogel, E. R. & Dominy, N. J. Food material properties and mandibular load
666 resistance abilities in large-bodied hominoids. *J. Hum. Evol.* **55**, 604–616 (2008).
- 667 37. McGraw, W. S. *et al.* Feeding and oral processing behaviors of two colobine monkeys in
668 Tai Forest, Ivory Coast. *J. Hum. Evol.* **98**, 90–102 (2015).
- 669 38. McGrew, W. C. Manual Laterality in Anvil Use: Wild Chimpanzees Cracking Strychnos
670 Fruits. *Laterality Asymmetries Body, Brain Cogn.* **4**, 79–87 (1999).
- 671 39. Pruett, J. D. & Bertolani, P. Savanna Chimpanzees, *Pan troglodytes verus*, Hunt with
672 Tools. *Curr. Biol.* **17**, 412–417 (2007).
- 673 40. Gaspersič, M. & Pruett, J. D. Savanna chimpanzees (*Pan troglodytes verus*) and baobab
674 fruits (*Adansonia digitata*): Investigation of percussive technology among three
675 chimpanzee communities in southeastern Senegal. *Folia Primatol.* **79**, 332–333 (2008).
- 676 41. Bogart, S. L. & Pruett, J. D. Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at
677 Fongoli, Senegal. *Am. J. Phys. Anthropol.* **145**, 11–20 (2011).

- 678 42. Hylander, W. L. Incisor size and diet in anthropoids with special reference to
679 Cercopithecidae. *Science* **189**, 1095–1098 (1975).
- 680 43. Pickford, M. Incisor-molar relationships in chimpanzees and other hominoids:
681 Implications for diet and phylogeny. *Primates* **46**, 21–32 (2005).
- 682 44. White, T. D., Lovejoy, C. O., Asfaw, B., Carlson, J. P. & Suwa, G. Neither chimpanzee nor
683 human, *Ardipithecus* reveals the surprising ancestry of both. *Proc. Natl. Acad. Sci.* **112**,
684 4877–4884 (2015).
- 685 45. Kupczik, K. & Chattah, N. L. T. The adaptive significance of enamel loss in the mandibular
686 incisors of cercopithecine primates (mammalia: Cercopithecidae): A finite element
687 modelling study. *PLoS One* **9**, e97677; 10.1371/journal.pone.0097677 (2014).
- 688 46. Dominy, N. J. *et al.* How chimpanzees integrate sensory information to select figs. *J. R.*
689 *Soc. Interface Focus* **6**, 20160001; 10.1098/rsfs.2016.0001 (2016).
- 690 47. Kupczik, K. & Dean, M. C. Comparative observations on the tooth root morphology of
691 *Gigantopithecus blacki*. *J. Hum. Evol.* **54**, 196–204 (2008).
- 692 48. Ungar, P. S. & Sponheimer, M. The diets of early hominins. *Science* **334**, 190–193 (2011).
- 693 49. Alemseged, Z. Stable isotopes serving as a checkpoint. *Proc. Natl. Acad. Sci.* **112**, 12232–
694 12233 (2015).
- 695 50. White, T. D. *et al.* Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus*
696 *ramidus*. *Science* **326**, 87–93 (2009).
- 697 51. McBrearty, S. & Jablonski, N. G. First fossil chimpanzee. *Nature* **437**, 105–108 (2005).

- 698 52. White, T. D. *et al.* *Ardipithecus ramidus* and the Paleobiology of Early Hominids.
699 *Science*. **326**, 75–86 (2009).
- 700 53. Henry, A. G. *et al.* The diet of *Australopithecus sediba*. *Nature* **487**, 90–93 (2012).
- 701 54. Lucas, P. W., Constantino, P. J. & Wood, B. A. Inferences regarding the diet of extinct
702 hominins: Structural and functional trends in dental and mandibular morphology within
703 the hominin clade. *J. Anat.* **212**, 486–500 (2008).
- 704 55. Ungar, P. S. & Grine, F. E. Incisor Size and Wear in *Australopithecus africanus* and
705 *Paranthropus robustus*. *J. Hum. Evol.* **20**, 313–340 (1991).
- 706 56. Lwanga, J. S., Butynski, T. M. & Struhsaker, T. Tree population dynamics in Kibale
707 National Park, Uganda 1975–1998. *Afr. J. Ecol.* **38**, 238–247 (2000).
- 708 57. Stewart, F. a & Piel, A. K. Termite fishing by wild chimpanzees: new data from Ugalla,
709 western Tanzania. *Primates*. **55**, 35–40 (2014).
- 710 58. Piel, A. K., Lenoel, A., Johnson, C. & Stewart, F. A. Deterring poaching in western
711 Tanzania: The presence of wildlife researchers. *Glob. Ecol. Conserv.* **3**, 188–199 (2015).
- 712 59. Carlson, B. A., Rothman, J. M. & Mitani, J. C. Diurnal Variation in Nutrients and
713 Chimpanzee Foraging Behavior. *Am. J. Primatol.* **75**, 342–349 (2013).
- 714 60. Houle, A., Chapman, C. & Vickery, W. Tree Climbing Strategies for Primate Ecological
715 Studies. *Int. J. Primatol.* **25**, 237–260 (2004).
- 716 61. Lucas, P. W. *et al.* Measuring the Toughness of Primate Foods and its Ecological Value.
717 *Int. J. Primatol.* **33**, 598–610 (2011).

- 718 62. Vogel, E. R. *et al.* Food mechanical properties, feeding ecology, and the mandibular
719 morphology of wild orangutans. *J. Hum. Evol.* **2014**, 110-124 (2014).
- 720 63. Ang, K. Y., Lucas, P. W. & Tan, H. T. W. Novel way of measuring the fracture toughness of
721 leaves and other thin films using a single inclined razor blade. *New Phytol.* **177**, 830–837
722 (2008).
- 723 64. van Casteren, A., Venkataraman, V., Ennos, A. R. & Lucas, P. W. Novel developments in
724 field mechanics. *J. Hum. Evol.* **98**, 5–17 (2016).
- 725 65. Ennos, A. R. *Solid Biomechanics*. (Princeton University Press, 2012).
- 726 66. Kouakou, C. Y., Boesch, C. & Kuehl, H. Estimating chimpanzee population size with nest
727 counts: Validating methods in Tai National Park. *Am. J. Primatol.* **71**, 447–457 (2009).
- 728 67. Mundry, R. & Oelze, V. M. Who is who matters—The effects of pseudoreplication in
729 stable isotope analyses. *Am. J. Primatol.* **78**, 1017–1030 (2016).
- 730 68. Oelze, V. M. Reconstructing temporal variation in great ape and other primate diets: A
731 methodological framework for isotope analyses in hair. *Am. J. Primatol.* **78**, 1004–1016
732 (2016).
- 733 69. Carlson, B. A. & Kingston, J. D. Chimpanzee isotopic ecology: A closed canopy C3
734 template for hominin dietary reconstruction. *J. Hum. Evol.* **76**, 107–115 (2014).
- 735 70. Carlson, B. A. & Crowley, B. E. Variation in carbon isotope values among chimpanzee
736 foods at Ngogo, Kibale National Park and Bwindi Impenetrable National Park, Uganda.
737 *Am. J. Primatol.* **78**, 1031–1040 (2016).

738 71. O'Connell, T. C., Hedges, R. E. M., Healey, M. A. & Simpson, A. H. R. W. Isotopic
739 Comparison of Hair, Nail and Bone: Modern Analyses. *J. Archaeol. Sci.* **28**, 1247–1255
740 (2001).

741

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755

756 **Author Contributions**

757 Project conceived and planned by AvC and KK. In field management, logistics and support by
758 CB, HJK, KEL, AKP, FAS. Food mechanical data was collected and analysed by AvC. Isotopic

759 samples were collected by SA, AKK and MK. Isotopic samples were analysed by VO. Manuscript
760 prepared by AvC, KK and VO, drafting and editing conducted by CB, HJK, AKK, KEL, AKP, FAS, VO,
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762

763 **Competing interests**

764 The authors declare no competing financial or non-financial interests.

765

766 **Figure 1.**

767 The overt differences in habitat structure where the two distinct chimpanzee communities of
768 this study inhabit. Ngogo (a) is a tropical and subtropical moist broadleaf forest where tree
769 species transition between montane and lowland forest. Issa Valley (b) is a tropical and
770 subtropical savannahs, grasslands, and shrub lands biome dominated by central Zambezi
771 Miombo woodlands. Photo credit to AvC.

772

773 **Figure 2.**

774 Bivariate plot showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in (a) Ngogo plants categories³³ (b) Issa plant
775 categories and (c) chimpanzee hair. Analytical errors are smaller than the depicted data points.
776 Despite similar isotopic signals in the plant isotopic signals at both sites results from hair show
777 significant separation in both the $\delta^{13}\text{C}$ values and the $\delta^{15}\text{N}$ values ($\delta^{13}\text{C}$ values: $\chi^2 = 61.45$, $df =$
778 1 , $p < 0.0001$ and the $\delta^{15}\text{N}$ values $\chi^2 = 80.67$, $df = 1$, $p < 0.0001$). This indicates that the
779 chimpanzee communities at these two sites utilize foods from distinct habitat types.

780

781 **Figure 3.**

782 The toughness (a) and modulus (b) of broad food categories indicates variance between Ngogo
783 and Issa, particularly in the exocarps of fruits. Y-axis is a logarithmic scale. Means represented
784 by dashed line and medians represented by solid lines, boxes represent 10th and 90th quartile.
785 Asterisks represent the results of a Mann-Whitney U tests between plant tissues categories for
786 both toughness (Exocarp, $W = 2633.5$, $p < 0.001$; Mesocarp, $W = 9934$, $p < 0.001$; Leaf laminar,

787 $W = 2265, p = 0.007$; Leaf midrib, $W = 2267, p = 0.1703$) and modulus (Exocarp, $W = 442.5, p <$
788 0.001 ; Mesocarp, $W = 97705, p < 0.001$; Leaf laminar, $W = 1157, p = 0.005$).

789

790 **Figure 4.**

791 The savannah exocarps of Issa are often tougher (a) and stiffer (b) than those of the gallery
792 forest patches and the tropical forest. Y-axis is a logarithmic scale. Means represented by
793 dashed line and medians represented by solid lines, boxes represent 10th and 90th quartile.

794 Asterisks represent the results of Kruskal Wallis tests for both toughness ($\chi^2 = 79.3, p < 0.001$)
795 and elastic modulus ($\chi^2 = 78.8, p < 0.001$).

796

797 **Table 1.** Descriptive statistics for plants and chimpanzee isotope values from Issa and Ngogo

798

	All Plants		Fruit		Leaves		C4 grass		Hair		Δ plant-hair	
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\Delta^{15}\text{N}$	$\Delta^{13}\text{C}$
Issa												
mean	3	-27.6	4.2	-27.8	1.3	-28.5	3.4	-15	4.1	-22.5	1.0	5.1
stdev (1σ)	2.8	3.3	2.9	2.8	1.5	1.7	-	-	0.4	0.2		
Ngogo												
mean	4.7	-27.1	4.6	-26.8	5.1	-29.2	1.5	-11	7.2	-23.8	2.6	3.3
stdev (1σ)	1.3	3.6	1	1	1.5	2.8	-	-	0.3	0.2		

799

800

801 **Table 2.** Results from Ngogo displaying averages and standard deviations of R and E for tissues
 802 of different plant species tested.

Species	$R(\text{J m}^{-2})$	n	sd	$E_i(\text{MPa})$	sd	$E_\infty(\text{MPa})$	sd	n	E_∞/E_i
Exocarp									
<i>Ficus bracylypis</i>	206.7	15	59.0	-	-	-	-	-	-
<i>Ficus capensis</i>	580.4	5	131.2	-	-	-	-	-	-
<i>Ficus dawei</i>	289.8	10	122.5	0.4	0.4	0.3	0.4	7	0.7
<i>Ficus mercuso</i>	246.6	35	90.3	1.2	0.6	0.8	0.4	20	0.8
<i>Ficus pericifolia</i>	-	-	-	1.9	1.0	1.2	0.3	4	0.7
<i>Pseudospondis microcarpa</i>	611.7	5	117.5	-	-	-	-	-	-
<i>Pterygota mildbraedii</i>	1056.6	5	142.6	3.6	0.6	2.7	0.4	5	0.8
<i>Uvariopsis congenensis</i>	196.3	8	49.0	0.1	0.1	-	-	6	-
<i>Zanha golungensis</i>	875.7	10	281.8	2.1	1.4	1.6	1.2	5	0.7
Mesoderm									
<i>Aphania senegalensis</i>	31.4	20	10.8	0.4	0.2	0.3	0.2	15	0.7
<i>Ficus bracylypis</i>	164.3	20	88.1	0.6	0.5	0.4	0.4	19	0.6
<i>Ficus capensis</i>	712.8	4	59.0	-	-	-	-	-	-
<i>Ficus dawei</i>	311.4	20	333.6	0.6	0.9	0.4	0.7	15	0.6
<i>Ficus mercuso</i>	120.6	49	69.5	0.5	0.6	0.4	0.5	50	0.7
<i>Ficus pericifolia</i>	129.0	20	43.0	0.4	0.1	0.3	0.1	20	0.7
<i>Morus mesozygia</i>	664.1	15	291.8	0.6	0.5	0.4	0.3	35	0.7
<i>Pseudospondis microcarpa</i>	227.4	5	46.4	0.5	0.1	0.3	0.1	6	0.6
<i>Pterygota mildbraedii</i>	-	-	-	0.0	0.0	-	-	5	-
<i>Zanha golungensis</i>	-	-	-	0.2	0.1	0.1	0.1	10	0.7
Flowers									
<i>Antiaris toxicaria</i>	141.5	8	80.0	0.5	0.6	0.3	0.4	4	0.6
<i>Pterygota mildbraedii</i>	296.2	20	131.2	2.6	2.0	1.5	0.5	10	0.7
Pith									
<i>Afromumum</i>	780.2	12	137.7	4.4	1.6	1.8	0.5	12	0.4
Leaf laminar									
<i>Antiaris toxicaria</i>	359.1	5	45.3	4.5	2.3	4.1	2.3	6	0.9
<i>Celtis africana</i>	119.3	23	49.7	-	-	-	-	-	-
<i>Celtis mildbraedii</i>	123.2	10	43.8	47.8	22.7	43.0	21.5	9	0.9
<i>Ficus exasperata</i>	572.4	15	278.3	27.7	12.1	24.0	11.0	15	0.9
<i>Ficus varifolia</i>	284.1	28	178.1	8.6	6.3	7.5	5.9	20	0.9
<i>Pterygota mildbraedii</i>	306.1	20	257.1	20.5	9.9	19.9	9.6	23	1.0
Leaf Midrib									
<i>Celtis africana</i>	840.6	24	504.8	-	-	-	-	-	-
<i>Celtis mildbraedii</i>	648.0	20	165.9	-	-	-	-	-	-
<i>Ficus exasperata</i>	4167.2	8	935.0	-	-	-	-	-	-
<i>Ficus varifolia</i>	1507.2	24	882.1	-	-	-	-	-	-
<i>Pterygota mildbraedii</i>	3715.3	25	2352.9	-	-	-	-	-	-

803 **Table 3** - Results from Issa displaying averages and standard deviations of R and E for tissues of
 804 different plant species tested.

Species	R(J m ⁻²)	n	sd	E _i (MPa)	sd	E _∞ (MPa)	sd	n	E _∞ /E _i
Exocarp									
<i>Ficus sp.</i>	174.8	6	60.7	-	-	-	-	-	-
<i>Ficus sp. 4</i>	227.2	5	121.0	-	-	-	-	-	-
<i>Ficus lutea</i>	391.0	10	191.2	-	-	-	-	-	-
<i>Keetia sp.</i>	384.7	11	182.1	1.2	0.3	-	-	5	-
<i>Garcinia huillensis</i>	823.4	13	252.6	2.7	1.5	1.5	0.8	10	0.6
<i>Grewia rugosifolia</i>	904.5	13	240.4	-	-	-	-	-	-
<i>Julbernardia globliflora</i>	10675.6	20	1802.4	465.7	159.0	-	-	25	-
<i>Julbernardia unijugata</i>	25525.6	2	-	203.6	54.3	-	-	5	-
<i>Parinari curatellifolia</i>	653.9	20	164.2	8.3	4.9	6.1	3.5	20	0.8
<i>Pterocarpus tinctorius</i>	791.8	11	308.4	3.0	1.3	2.0	1.1	10	0.7
<i>Saba comorensis</i>	1073.6	6	233.9	1.1	0.6	0.8	0.4	6	0.7
<i>Strychnos pungens</i>	6962.8	3	3130.1	31.5	13.1	19.4	12.8	4	0.6
<i>Strychnos sp.</i>	10178.6	15	3641.9	22.3	11.6	11.2	8.3	22	0.5
<i>Uapaca kirkiana</i>	748.8	11	347.2	6.2	2.2	5.7	2.4	5	0.9
<i>Ximenia caffra</i>	481.2	5	59.6	-	-	-	-	-	-
Mesoderm									
<i>Ficus sp.</i>	105.9	10	56.7	0.3	0.1	0.2	0.1	10	0.7
<i>Ficus sp.3</i>	49.1	6	25.8	0.2	-	-	-	-	-
<i>Ficus sp.4</i>	62.1	10	22.2	0.2	0.1	0.1	0.0	10	0.6
<i>Ficus lutea</i>	472.7	12	185.5	1.6	1.5	0.7	0.5	6	0.5
<i>Ficus varifolia</i>	153.8	17	58.8	0.2	0.3	-	-	15	-
<i>Garcinia huillensis</i>	109.3	12	54.5	0.5	0.2	0.2	0.1	10	0.5
<i>Parinari curatellifolia</i>	21.5	21	12.7	0.1	0.1	0.1	0.0	20	0.5
Unknow climber	13.1	6	2.9	0.2	0.1	0.1	0.1	5	0.7
<i>Ximenia caffra</i>	24.7	4	17.3	0.5	0.7	0.1	0.1	4	0.4
Endosperm									
<i>Julbernardia globliflora</i>	920.0	11	210.8	10.6	4.8	9.1	4.3	11	0.8
<i>Pterocarpus tinctorius</i>	308.5	9	95.3	4.4	3.5	3.1	2.8	10	0.6
Leaf laminar									
<i>Syzygium guineense</i>	180.5	10	96.3	3.8	1.8	3.6	1.8	3	0.9
<i>Julbernardia globliflora</i>	184.2	8	79.1	17.7	10.5	17.3	10.5	10	1.0
<i>Ficus exasperata</i>	242.0	5	46.4	8.9	3.3	5.7	2.6	5	0.7
<i>Pterocarpus tinctorius</i>	94.4	10	34.3	5.2	4.2	4.6	3.8	5	0.9
Leaf Midrib									
<i>Syzygium guineense</i>	497.2	10	204.5	-	-	-	-	-	-
<i>Pterocarpus tinctorius</i>	639.4	10	419.4	-	-	-	-	-	-
<i>Ficus exasperata</i>	807.8	5	328.8	-	-	-	-	-	-
<i>Julbernardia globliflora</i>	4338.6	8	4295.6	-	-	-	-	-	-
<i>Ficus sp.3</i>	4115.7	6	1336.9	-	-	-	-	-	-

