

## Dinner with Lucy: what does *Paranthropus boisei* bring to the table?

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# Dinner with Lucy: what does *Paranthropus boisei* bring to the table?

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## ABSTRACT

Recent findings have transformed our thinking about early hominin diets. Most notably, evidence from dental microwear, carbon isotopes, and dental chipping has challenged notions of hard object feeding in “Nutcracker Man”, *Paranthropus boisei* Leakey, 1959. Less attention has been paid to its likely ancestor, *Australopithecus afarensis* Johanson, White & Coppens, 1978. Yet, there are reasons to suspect that disruptive ideas about *P. boisei* diet are highly relevant for Lucy and her kin. These reasons include: 1) the dental microwear of *Au. afarensis* and *P. boisei* is virtually identical, and shows no evidence of variation linked to habitat change; 2) the carbon isotope ratios of *Au. afarensis* are similar to those of early *Paranthropus* Broom, 1938 in the Omo; and 3) *Au. afarensis* manifests an early stage of a masticatory trend that reaches its quintessence in *P. boisei*, making it reasonable to argue that these taxa experienced similar selective pressures regarding diet. In this paper, we discuss the dietary ecology of *Au. afarensis* in light of lessons gleaned from its highly derived and enigmatic descendant *P. boisei*.

## RÉSUMÉ

*Dîner avec Lucy : qu’apporte Paranthropus boisei à la table ?*

Les découvertes récentes ont conduit à une transformation de notre réflexion sur les régimes alimentaires des premiers hominines. Plus particulièrement, l’étude de l’usure dentaire microscopique, des isotopes du carbone, et des éclats dentaires ont remis en question l’idée que le régime alimentaire de « Nutcracker Man », *Paranthropus boisei* Leakey, 1959, soit principalement composé d’objets durs. Moins d’attention a été accordée à son ancêtre probable, *Australopithecus afarensis* Johanson, White & Coppens, 1978. Pourtant, il existe des raisons de soupçonner que la remise en question du régime alimentaire de *P. boisei* soit hautement pertinente pour Lucy et ses proches. Ces raisons incluent : 1) l’usure microscopique des dents d’*Au. afarensis* et *P. boisei* est pratiquement identique, et ne montre aucune variation qui serait liée au changement d’habitat; 2) les rapports isotopiques du carbone de *Au. afarensis* sont similaires à ceux des premiers *Paranthropus* Broom, 1938 dans l’Omo; et 3) *Au. afarensis* montre une étape précoce d’une tendance masticatoire qui atteint sa quintessence chez *P. boisei*, ce qui rend raisonnable l’hypothèse selon laquelle ces taxons aient subi des pressions sélectives similaires en ce qui concerne leur régime alimentaire. Dans cet article, nous discutons de l’écologie alimentaire d’*Au. afarensis* à la lumière des leçons tirées de son descendant hautement dérivé et énigmatique *P. boisei*.

## INTRODUCTION

Paleodiet has always been central in discussions of human evolution. Darwin (1871), Dart (1925), Robinson (1954), and others have argued to varying degrees that dietary change underlay hominin origins, the craniodental diversity of australopiths, and the encephalization and stone tool use that characterized early *Homo* Linnaeus, 1758. These dietary shifts are often tethered to broad environmental changes, as exemplified by Coppens’ elegant “East Side Story”. Coppens (1994) argued that the formation of the East African Rift isolated hominins from panins, causing the former to adapt to food resources in increasingly open and dry environments. In turn, subsequent climatic change precipitated the appearance of specialized herbivores – the robust australopiths – and generalist, tool-wielding, meat-eating *Homo*.

While the dawn of hominins and the emergence of *Homo* understandably garnered the most attention, arguably the most dramatic morphological innovation is found in the australopiths which evince craniodental variations linked to diet including the masticatory hypertrophy of the redoubtable “Nutcracker Man”. And while australopith diet has received a great deal of attention generally, *Australopithecus afarensis*

Johanson, White & Coppens, 1978 in particular (as exemplified by “Lucy” which will synecdochically represent the entire species hereafter) has received less than its due, despite being a logical starting point for discussions of hominin dietary adaptation. *Australopithecus afarensis* has larger cheek teeth, thicker molar enamel, and a more robust chewing apparatus than its predecessors, yet is generalized enough that it stands at the cusp of the extremely derived morphology of the robust australopiths on the one hand, and the more gracile *Homo* on the other. *Australopithecus afarensis* is also conceivably an ancestor of both lineages (Johanson & White 1979; Kimbel *et al.* 1984; Post *et al.* 2023) which potentially appear soon after Lucy and her kind disappear from the fossil record.

While a considerable fossil record for *Au. afarensis* has existed since the 1970s, there was not an abundance of dietary data beyond modest investigations of dental microwear that received relatively little attention because they either focused on incisal wear (Ryan & Johanson 1989) and/or were qualitative, low magnification studies (Puech & Albertini 1983, 1984; Puech *et al.* 1983, 1986; Puech 1992). Thus, while debates about australopith diets were lively in the 1970s and 80s (Jolly 1970; Wolpoff 1973; Grine 1981, 1986; Walker 1981; Peters & Maguire 1981; Sept 1986; Grine & Kay 1988),

less attention was given to Lucy, despite it being the oldest recognized australopith at the time, even though *Au. afarensis* stood, and continues to stand, front and center in discussions of hominin locomotion (Harmon 2013; Prang 2015; Prabhat *et al.* 2021), habitat (Reed 2008; Su & Harrison 2008; Fillion *et al.* 2022), and phylogeny (Kimbel *et al.* 2004; Lockwood 2013; Post *et al.* 2023). In this paper, we provide a brief and tendential discussion of research on the diet of *Au. afarensis*, discuss challenges to this research that arose beginning in 2006, and make the case that an analysis of *Au. afarensis* diet through a *P. boisei* Leakey, 1959 lens is important, even if, paradoxically, it could prove to be a stumbling block for understanding Lucy's dietary proclivities.

## WHY BOISEI?

Why should *P. boisei* inform our understanding of *Au. afarensis* diet? Firstly, *Au. afarensis* exhibits masticatory features that foreshadow those seen in its likely descendant, *P. boisei* (Rak *et al.* 2007). In fact, based on craniodental morphology it could be reasonably argued that the diets of *Au. afarensis* and *P. boisei* were not very different, and that *P. boisei*'s more extreme adaptations simply made it better at eating that diet than its predecessor. We see similar evidence in fossil suids. For instance, *Metridiochoerus* Hopwood, 1926 in northern Kenya was a nearly pure  $C_4$  consumer when its M3s were *c.* 50 mm in length, and as its descendants' M3s increased to 80 mm (presumably better adapted to  $C_4$  grass diets), there was no increase in  $C_4$  consumption (Harris & Cerling 2002). This has also been observed in eastern African elephants, which adopted primarily  $C_4$  diets about eight million years ago (mya), with major changes in hypsodonty and lamellar number emerging three million years later (Lister 2013). Thus, while *Au. afarensis* and *P. boisei* have divergent masticatory systems, this does not necessarily translate to qualitative differences in diet.

More importantly, the occlusal dental microwear of the two taxa is indistinguishable (Ungar *et al.* 2008; Grine *et al.* 2012). This is markedly different from the situation in southern Africa, where *Au. africanus* and *P. robustus* have overlapping yet distinct microwear fabrics, with the latter showing greater pitting than the former (Grine 1981, 1986; Grine & Kay 1988; Scott *et al.* 2005; Peterson 2017; Peterson *et al.* 2018). A broad similarity in diet of *Au. afarensis* and *P. boisei* was not anticipated on morphological grounds and also ran counter to habitat-based expectations. Whereas *Au. afarensis* is believed to have inhabited highly varied environments from riparian forests to grasslands (Boaz 1988; Reed 2008; Su & Harrison 2008; Su 2024), all *P. boisei* specimens are much younger and recovered from areas where grasses were prevalent (Shipman & Harris 1988; Reed 1997; Cerling *et al.* 2011b; Stewart 2014; Uno *et al.* 2016). There is also no reasonable way to attribute the low pitting and lack of differentiation in eastern African *Paranthropus* Broom, 1938 and *Australopithecus* R.A.Dart, 1925 to environmental differences. Fossil antilopine bovids at eastern African sites have more complex and pitted surfaces

than their South African equivalents, so there is no environmental impediment to producing highly complex and pitted enamel surfaces in eastern African landscapes (Ungar *et al.* 2016; cf. Strait *et al.* 2013). One interpretation of the virtually identical microwear of *Au. afarensis* and *P. boisei* is that, like the suids and elephants mentioned above, the ancestral and descendant taxa ate similar things, but the descendant taxa were better adapted to do so.

That said, carbon isotope analysis could be used to argue against a dietary similarity, as initial results of *Au. afarensis* and *P. boisei* were highly divergent (van der Merwe *et al.* 2008; Wynn *et al.* 2013; Cerling *et al.* 2011a). However, interpreting these data is complicated for several reasons. For one, while unlikely, it is plausible that two species with similar dietary proclivities could have different carbon isotope compositions. Such counterintuitive isotopic differences usually happen with grazing herbivores inhabiting areas with differing proportions of  $C_3$  and  $C_4$  grasses. A good example of this can be observed in South African wildebeest (*Connochaetes* spp.). Outside of winter rainfall zones, wildebeest have nearly pure  $C_4$  diets, but in the Western Cape they have  $C_3$ -dominated diets even while still mowing grass (Sponheimer *et al.* 2003; Stowe & Sealy 2016). This scenario can probably be discounted for most *Au. afarensis* and *P. boisei* specimens analyzed to date as they are typically found alongside grazing herbivores that consumed  $C_4$ , not  $C_3$ , grasses (Wynn *et al.* 2013, 2016; Cerling *et al.* 2011a). There is, however, one potential wrinkle in this interpretation that revolves around sedges;  $C_3$  sedges can be locally abundant even where  $C_4$  grasses predominate as in Kruger National Park, South Africa, today (Stock *et al.* 2004; Sponheimer *et al.* 2005; see below). Higher growing season temperatures are linked to greater percentages of  $C_4$  grasses and sedges (Teeri *et al.* 1980; Ehleringer *et al.* 1997; Stock *et al.* 2004), but the link is weaker in sedges and local effects (e.g. soil type and nutrients, hydrology) more greatly influence sedge  $C_3/C_4$  distributions (e.g. Kotze & O'Connor 2000). Thus, if *Au. afarensis* ate significant amounts of sedges, it would not only be plausible but likely that many individuals would have very  $C_3$  isotopic compositions.

The plot thickens given recent results from the Omo. There, it was shown that *Australopithecus* (likely *Au. afarensis*) was not very different isotopically from *P. aethiopicus* (*P. boisei*'s predecessor), despite well-established morphological differences (Wynn *et al.* 2020). Essentially out of nowhere, and despite no evidence of morphological change, *P. aethiopicus* shifts to a  $C_4$ -dominated diet (N.B., this is intraspecific and not a shift to *P. boisei*). So we are forced to ask ourselves, did *Paranthropus* in the Omo undergo some large dietary change virtually overnight at 2.37 mya, or was there some fundamental change in the isotopic composition of the foods it had always been eating? Either is certainly possible, though both would seem unlikely from first principles. However, changes in climate, hydrology, soil texture, and/or nutrient availability could conceivably lead to large changes in the relative proportions of  $C_3/C_4$  sedges (Li *et al.* 1999; Kotze & O'Connor 2000; Stock *et al.* 2004), and since these are not typically major foods for most mammals, such a change might not be immediately



obvious when looking at results for the other fauna (Negash *et al.* 2020). Following this conjecture, the high  $\delta^{13}\text{C}$  values (median =  $-0.7\text{‰}$ ) of two 2.8 mya *Paranthropus* specimens from Nyayanga in southwestern Kenya could reflect local edaphic and hydrological conditions driving differences in  $\text{C}_3/\text{C}_4$  sedge abundance (Plummer *et al.* 2023), although alternatives are certainly possible.

In summary, if *Au. afarensis* is the ancestor of *P. boisei*, some dietary continuity might be expected. Also, despite morphological differences, *Au. afarensis*, like *P. boisei*, has been interpreted as a likely consumer of “nuts, seeds, and hard fruits” (Wood & Richmond 2000). The dental microwear of *Au. afarensis* and *P. boisei* is highly similar and very different from *P. robustus* from South Africa. And while some *Paranthropus* and *Australopithecus* are very different isotopically, early *P. aethiopicus* and *Australopithecus* from Omo are very similar. Thus, revisiting the diet of *Au. afarensis*, with a particular focus on potential continuity with *P. boisei*, seems warranted.

One might speculate that the differences in size, shape, and structure of teeth between *Au. afarensis* and *P. boisei* could present another example of Van Valen’s (1973) “Red Queen” hypothesis, possibly via competition with other herbivores or even due to intraspecific competition. Neither species has shearing crests like gorillas or crenulations like orangutans (*sensu* Vogel *et al.* 2008) for fracturing tough vegetation, but *P. boisei* does have larger occlusal tables, increasing the area of the chewing platform to process more food per chew. Bite pressures between *Au. afarensis* and *P. boisei* were probably similar (Demes & Creel 1988; Eng *et al.* 2013) despite the marked differences in occlusal area. Just as Kay & Ungar (1997) suggested that living hominoids have longer crests than their Early Miocene predecessors with a similar range of diets, judging from their microwear, perhaps *Au. afarensis* and *P. boisei* have flatter teeth than modern ecological equivalents.

## LUCY’S LACUNA

In the 1980s, both *Au. africanus* and *P. robustus* were lavished with attention given new developments in dental microwear which confirmed strong dietary differences between taxa as was suggested by morphology (Grine 1981, 1986; Grine & Kay 1988). After this, it was widely accepted that *Australopithecus* ate fleshy fruits and leaves while *Paranthropus* munched on small hard objects. Even in the 1990s, when stable carbon isotope and trace element analyses were initially applied (Sillen 1992; Lee-Thorp *et al.* 1994), the focus was on South African australopiths because Bob Brain saw the potential of such chemical techniques and granted access to the fossils.

Excepting a few studies focused on microwear of the anterior dentition (Puech *et al.* 1983, 1986; Puech & Albertini 1984; Ryan & Johanson 1989), explicit dialog about *Au. afarensis* diet had been fairly dormant. Lucy arrived on the scene too late to be incorporated in Robinson’s (1954) dietary hypothesis or to be explicitly dealt with in Jolly’s (1970) seed-eater hypothesis. However, it was generally acknowledged that its robust mandible and dentition, and thicker enamel compared

to extant apes, represented the “initial functional steps that would eventually culminate in the far more derived, specialized masticatory apparatus of later hominid species, particularly *A. boisei* [*P. boisei*]” (White *et al.* 2000). Thus, it was seen as a step towards the “Nutcracker Man”, but not so far down the road that it could not have also been ancestral to *Homo*.

At the time, extrapolating South African australopith dietary inferences more or less directly to their eastern African congeners seemed unproblematic. For one, despite clear craniodental differences, *Au. afarensis* and *Au. africanus* were generally regarded as variations on a theme – gracile australopiths – with some arguing that the difference between the two was insufficient to warrant species-level designations (e.g. Tobias 1980). Thus, most were comfortable with the notion that *Au. afarensis* had an *Au. africanus*-like diet, although given its less derived morphology, possibly with more emphasis on foods favored by chimpanzees (certainly many people [e.g. Hunt 1998] favored the idea of the LCA being quite chimpanzee-like at the time). In turn, because dental microwear was confirming notions of hard-object feeding for *P. robustus*, the even more craniodentally robust *P. boisei* seemed to be an obvious hard-object specialist (although Walker’s [1981] microwear study had to be overlooked in making that case). In short, it seemed reasonable that all *Australopithecus* species shared a similar adaptive zone, as did all *Paranthropus* species. After all, blue wildebeest (*Connochaetes taurinus* (Burchell, 1823)) and black wildebeest (*Connochaetes gnou* (Zimmermann, 1780)) have highly similar, although not identical, diets (Codron & Brink 2007) as do both species of *Pan* Oken, 1816 (Hohmann *et al.* 2010).

## ANNI CONFUSIONIS

The first real challenge to the assumption of parallel dietary adaptations in eastern and South African australopiths was a study on dental microwear published in 2006 which had several notable findings (Grine *et al.* 2006). First, the occlusal microwear of *Au. afarensis* was quite similar to that of *Gorilla beringei* (typified by few pits), and clearly different from that of hard object feeders like tufted capuchins (*Sapajus apella* (Linnaeus, 1758)) and grey-cheeked mangabeys (*Lophocebus albigena* (Gray, 1850)) which tend to have highly-pitted molars. So, contrary to expectations, there was no evidence of *Au. afarensis* representing an early step along an australopith dietary trajectory towards hard, brittle food consumption. Second, the microwear of *Au. afarensis* revealed no evidence of dietary differentiation across time or habitats, contrary to expectations for a generalist primate. In retrospect, this publication was a major challenge to received wisdom that was arguably swept under the rug, for more congenial, if now less likely, notions.

One interpretation of the occlusal microwear data was that *Au. afarensis* did eat hard foods as morphology suggested, but that these were possibly fallback foods that were eaten infrequently so microwear evidence was absent (Grine *et al.* 2006). While a plausible explanation, and one that was consistent

with conventional wisdom about australopith masticatory biomechanics at the time, it was not especially parsimonious given the study's ample sample of 19 molars. In addition, this explanation effectively negates the possibility of falsifying hard-object feeding hypotheses with occlusal microwear. Another response that arose, albeit initially for *Au. africanus*, was that dental microwear was unable to discern certain types of hard object consumption (e.g. wrong food size, wrong teeth, wrong habitat; Strait *et al.* 2009; Lucas *et al.* 2013). However, this idea was countered by evidence from modern hard object feeders like sooty mangabeys (*Cercocebus atys* (Audebert, 1797)) that have highly-pitted microwear fabrics on both premolars and molars (Daegling *et al.* 2011) and by other mammals at hominin sites that preserve pitted teeth (Ungar *et al.* 2016). Subsequently, a study of tooth chipping showed low chip frequencies in *Au. afarensis* that appeared inconsistent with durophagy (Constantino & Konow 2021). Most crucially, both the fallback supposition and arguments that microwear does not consistently track durophagy are attempts to explain away unexpected results with negative evidence. In and of itself, this does not mean that these explanations are incorrect, but we feel it is instructive that the field seemed to prefer, at least for a while, explanations with so little empirical support. We submit that this initial study should have occasioned a deeper rethink of *Au. afarensis* than it did in practice.

Then, in 2008, the dam broke. A study of *P. boisei* occlusal microwear revealed no evidence of hard object consumption – “Nutcracker Man” looked like folivorous geladas (*Theropithecus gelada* (Rüppell, 1835)) or gorillas (*Gorilla gorilla* (Savage, 1847)) based on the complexity of its molar microwear, and nothing like well-known consumers of hard and brittle foods (Ungar *et al.* 2008). In addition, a study on the carbon isotopic compositions of *P. boisei* from Tanzania revealed a high  $C_4$  signal of the sort found in warthogs (*Phacochoerus africanus* (Gmelin, 1788)) and zebra (*Equus quagga* Boddaert, 1785) (van der Merwe *et al.* 2008). No extant hominoids have such high  $\delta^{13}C$  values, save for modern human populations that are almost completely dependent on  $C_4$  grasses like maize (Tykot 2002). The combination of dental microwear and carbon isotope data began to paint a picture of a hominin with a wholly unexpected dietary ecology, strongly hinting that the field's expectations needed to be reassessed.

## ADDRESSING THE $C_4$ CONUNDRUM

Since 2008, much attention has been paid to the diet of *P. boisei*, and little explicitly to the diet of *Au. afarensis* (Martínez *et al.* 2016; Wynn *et al.* 2013 being exceptions). In studies on *P. boisei*, much of the effort has been on hypotheses to explain its apparent high  $C_4$  resource consumption. Such an extreme  $C_4$  isotopic composition has few potential causes: dedicated consumption of  $C_4$  monocots like grasses and sedges, eating animals that eat those foods, such as wildebeest and zebra, or consumption of less abundant and typically less-palatable crassulacean acid metabolism (CAM) plants that can isotopically mimic  $C_4$  consumption.

Although some have advanced ideas about animal food consumption in hominins with *Paranthropus*-like adaptations (Cachel 1975; Szalay 1975), most scholars agree that a high  $C_4$  signal via animal food consumption is unlikely. For one, if the animal foods were arthropods, this would have required the consumption of hundreds of thousands of harvester-type termites or ants per night (other termites and ants would not impart the needed isotopic signal; see Sponheimer *et al.* 2005; Lesnik 2014; Phillips *et al.* 2021), and there is no evidence of adaptations for insect consumption in *P. boisei*. And to obtain *P. boisei*'s  $C_4$  signal from the consumption of mammals is a feat that even lions have difficulty achieving today (Codron *et al.* 2007, 2016; Lee-Thorp *et al.* 2007; Yeakel *et al.* 2009), making any invocation of hominin “zebravory” suspect at best. Moreover, the very evidence used to inveigh against a heavy monocot diet for *P. boisei*, namely its flat teeth, also makes *P. boisei* an unlikely consumer of tough animal tissues. It is easy to see why a monocot origin for the  $C_4$  signal is favored by many given that: 1) all mammalian herbivores with a similar isotopic composition eat grass; 2) grass is far more abundant on landscapes than grazing mammals and arthropods; and 3) monocots are less inclined to run away than most animal foods.

Another wrinkle seldom entertained is the possibility that *Paranthropus*, or even australopiths in general, were tool-users (Susman 1988, 1998; Wood 1997; Plummer *et al.* 2023). Susman (1988, 1998) argued for tool use in robust australopiths, noting that species-level hominin-tool associations were inferred rather than established at different localities. *Paranthropus* was coeval with *Homo* in both South and eastern Africa, but postcranial evidence of manual elements indicating tool-making capacity (SKX 5016, SKX 5020) can be linked to *P. robustus* based on a probabilistic criterion (i.e., lots of *Paranthropus* fossils and very few of *Homo*). Susman was skeptical that earlier *Australopithecus* hands had morphological features indicating tool-making capabilities.

The resistance to *Paranthropus* as tool-maker or tool-user is to some degree a hangover from the presumption that *Homo* should be the only hominin with tool technologies. A second reason why tool use in “robust” australopiths is deemed implausible – if not ignored altogether – is the inference that a modest brain size, postcanine megadontia, and facial hypertrophy indicate a species too dim to consider strategies of extraoral food preparation. Szalay's (1975) hyaena analogy falls apart if *Paranthropus* was, in fact, a scavenger but let the rocks do some work before ingestion. Cutting with the stone tool technologies of the Plio-Pleistocene probably did not greatly reduce the masticatory work required to process grasses or sedges, although it is worth noting that studies of artifact use wear at Kanjera South, Kenya suggested that cutting of grass/sedge culm and underground storage organs (USOs) was equally if not more important than processing animal foods (Lemorini *et al.* 2014). However, pounding of USOs (and possibly culm) may well have increased energetic intake (Zink & Lieberman 2016), and if *Paranthropus* was opportunistic in exploiting other resources (e.g. termites, USOs), tools would have been instrumental for accessing them.

The identification of the Lomekwian tool tradition (Harmand *et al.* 2015) and evidence of butchery at Dikika over three mya (McPherron *et al.* 2010) further undermines the principle that tool manufacture was the exclusive domain of *Homo*. There is no necessary conflict between tool use in *Paranthropus* and the hypertrophy of the masticatory apparatus. That lithic technology solves some foraging and ingestive problems is more reasonable than the idea it solves all of them. Gracilization of the skeleton does not have to be proportional to material culture innovation. Neanderthal robusticity is obviously not a product of some kind of technological regression.

Thus, from a comparative standpoint, the simplest solution to the *P. boisei* problem is C<sub>4</sub> grass and/or sedge consumption. Consumption of CAM plants is also possible. Some primates like baboons and some lemurs can eat a fair bit of CAM vegetation, and while this is obvious in their isotopic compositions (Codron *et al.* 2005), in no cases do they look like *P. boisei*, even in habitats where CAM vegetation is dominant such as the Spiny Forest of Madagascar (Crowley *et al.* 2011). The only possible exception is the extinct lemur, *Hadropithecus* Lorenz, 1899, which can approach *P. boisei*'s  $\delta^{13}\text{C}$  values, and which arguably consumed CAM plants rather than grasses, although it did so in CAM-dominated landscapes quite dissimilar to those associated with mainland early hominins (Godfrey *et al.* 2016). Thus, we cannot definitively rule out the possibility that *P. boisei* was a CAM specialist. After all, eponymous Olduvai Gorge is named after the CAM plant oldupai (now *Dracaena hanningtonii* Baker), the wild sisal plant, which is consumed by baboons sparingly (Barton *et al.* 1993; 1% feeding time in Laikipia, Kenya, CAM *Euphorbia* represent about 5% of feeding time there). Yet, as many potential CAM foods are poisonous or purgatives, and are usually not abundant in likely hominin habitats (certainly not compared to C<sub>4</sub> grasses), the consumption of CAM alone is unlikely to explain the high apparent C<sub>4</sub> signal in *P. boisei*, though some combination of C<sub>4</sub> monocots and CAM is plausible (see Peters & Vogel 2005).

It is worth noting that the main reason for considering CAM plants as a *P. boisei* dietary resource is the seeming implausibility of C<sub>4</sub> grass consumption. The relatively flat occlusal surfaces of *P. boisei* post-canine teeth seem poor tools for the comminution of displacement-limited foods like tough grasses (Kay *et al.* 1978; Kay 1985). However, most of the available CAM vegetation is leafy material for which the teeth of *P. boisei* were purportedly equally unsuited. Thus, to argue that *P. boisei* obtained its C<sub>4</sub> signal via CAM vegetation, one would face the same mechanical conundrum a CAM explanation was trying to avoid in the first place. Thus, C<sub>4</sub> monocot consumption makes sense since all extant mammalian herbivores with *P. boisei*'s carbon isotope composition eat them, they were very abundant in the environments of *P. boisei* most of the time (Reed 1997; Cerling *et al.* 2011b; Uno *et al.* 2016), and because the potential alternatives offer similar mechanical challenges.

## PESKY TEETH

### (OR A SOLUTION WITHOUT A PROBLEM?)

Many of the problems we are currently experiencing in the world of early hominin paleodietary studies can be distilled down to the fact that the behavioral and morphological signals do not perfectly align (e.g. Ungar *et al.* 2008; Smith *et al.* 2015; Sponheimer *et al.* 2023; Teaford *et al.* 2023). *Paranthropus boisei* especially, but to a certain extent all australopiths, are characterized by a hypertrophied chewing apparatus with megadont cheek teeth and thick enamel (Wood & Richmond 2000; White *et al.* 2000; Daegling & Grine 2017). While these have been interpreted conventionally as indicating a durophagous diet (Wood & Richmond 2000; White *et al.* 2000), they are also consistent with a diet dominated by tough foods like leaves (Hylander 1988; Pearson & Rabenold 2011; Daegling *et al.* 2011; Daegling & Grine 2017). Indeed, when comparing the skulls of sooty mangabeys, red colobus, and *P. boisei* in lateral profile, the similarity of *P. boisei* with the leaf-eating colobus as opposed to the hard-object feeding mangabey is striking. From this perspective, the need to explain away indications of C<sub>4</sub> monocot consumption disappears.

But what about those flat teeth? Australopith cheek teeth, especially *P. boisei*, are indeed relatively flat and do not have the high shearing crests typically observed in folivorous primates (Kay 1985). At face value, this would make it unlikely that any australopith ate large quantities of monocot (or dicot) leaf, although the seeds or USOs of such plants would be fair game (Hatley & Kappelman 1980; Conklin-Brittain *et al.* 2002; Laden & Wrangham 2005; Dominy *et al.* 2008; Lee-Thorp 2011; Macho 2014). The principal difficulties of proposing reproductive parts or storage organs to explicate the apparent C<sub>4</sub> dominance in *P. boisei* are that: 1) they would likely result in pitted occlusal microwear which has not been observed (Daegling & Grine 1999; *Theropithecus* I. Geoffroy Saint-Hilaire, 1843 eats grass seeds and USOs without pitted molar microwear but the bulk of its diet is grass leaves which apparently dominate its microwear [Shapiro *et al.* 2016]); 2) they are unlikely given the lack of tooth chipping in *P. boisei* (Constantino & Konow 2021); and 3) such high  $\delta^{13}\text{C}$  values would be difficult to achieve in practice by eating such fare. Grass seed is not always available, and even mole rats, which specialize on USOs in areas with C<sub>4</sub> grasses, do not typically have such high  $\delta^{13}\text{C}$  values (Robb *et al.* 2012, 2016). Thus, while consumption of these foods by *P. boisei*, and australopiths generally, is not only possible but even probable, the likelihood that they alone could engender the high C<sub>4</sub> signature seen in *P. boisei* seems remote. Moreover, there has been a tendency to underestimate the indigestible fraction of wild tubers and other USOs (Schoeninger *et al.* 2001; Paine *et al.* 2019), such that the energetic return (without fire), given gut fill constraints, would probably be insufficient without massive supplementation of high-energy, low-fiber, foods which are rarely C<sub>4</sub> resources. The chief virtue of the USO argument is that it retains conventional thinking about *P. boisei*'s masticatory morphology and durophagous diet – one simply replaces seeds and nuts with hard items such as corms



(Dominy *et al.* 2008; Macho 2014). Still, Smith *et al.* (2015) question whether or not corms could have driven the masticatory hypertrophy observed in *Paranthropus* given that their elastic moduli are orders of magnitude lower than those of seed and nut shells. While we acknowledge that USOs could account for *P. boisei*'s high  $\delta^{13}\text{C}$  values, although impediments to this interpretation are substantial, our focus here is alternatives to prevailing notions of australopith durophagy given challenges from multiple lines of evidence.

The central problem is that while it would not be impossible for *P. boisei* to obtain its observed carbon isotope composition without eating monocot leaf or pith, it would be extraordinarily difficult to do so. And given the likely superabundance of  $\text{C}_4$  leaf/pith in australopith habitats, it is very easy to invoke their consumption as a solution to the  $\text{C}_4$  problem. But would that have been plausible? Mammals like the panda (*Ailuropoda melanoleuca* (David, 1869)) are suggestive in this regard. The giant panda eats primarily bamboo and its masticatory apparatus shows many convergences with *Paranthropus* including a flattened face, flaring zygomatic arches, expanded temporalis muscles, robust mandibles, and, by ursid standards, flat, megadont molars and premolars (Du Brul 1977). Such convergence could bespeak similar diets, or at least diets that pose similar mechanical demands. Pandas do crush hard bamboo, but there can be no denying that their predominant masticatory challenge is the consumption of enormous quantities of fibrous vegetation which they digest very poorly (Dierenfeld *et al.* 1982; Senshu *et al.* 2007; Sims *et al.* 2007; Finley *et al.* 2011). Their teeth are poorly suited for the reduction of tough foods (Davis 1964), so they chew each mouthful desultorily while eating constantly – they favor bulk consumption over digestive efficiency. Other consumers of bamboo (and other monocots), such as the bamboo lemurs of the genus *Hapalemur*, have a diametrically opposed digestive strategy. They use classic folivore cheek teeth to efficiently break down foods which they digest impressively over an extended period (Overdorff & Rasmussen 1995; Campbell *et al.* 2004).

*Paranthropus boisei* diet is, from a Sherlock Holmesian perspective, a five-pipe problem. Its teeth would not be remarkable if it were a durophage, but while durophagy cannot be excluded, hard foods were probably not a dominant component of its diet. Its microwear would be unexceptional if it were an amiable muncher of leaves, but its occlusal relief is atypical for folivores. Its isotopic composition is typical for grazing savanna mammals, but once again, occlusal morphology militates against such an interpretation. There is no living mammal that demonstrates its combination of morphology, microwear, and carbon isotopic composition.

## ET TU, LUCY: A HYPOTHESIS

So what does this discussion of *P. boisei* mean for *Au. afarensis*? Clearly these taxa pose common interpretive problems. Ostensibly, in both cases, morphological and behavioral approaches of paleodietary retrodiction give different signals, and some

of those behavioral signals (especially occlusal microwear) are most consistent with a diet of tough foods (or at the very least not hard ones). Conventionally speaking, however, the problems are less severe for *Au. afarensis*: it appears less specialized (and it is certainly less morphologically-derived) than *P. boisei*, and its megadontia, thick enamel, and robust masticatory package might prove beneficial for withstanding the repetitive loading associated with most tough diets. The carbon isotopic data for *Au. afarensis* are also consistent with a diet of displacement-limited foods such as leaves or pith, as is the remarkably high variation in its  $\delta^{13}\text{C}$  values (Wynn *et al.* 2013). In more forested areas, tree leaves, terrestrial herbaceous vegetation, and  $\text{C}_3$  monocots would be abundant leading to the predominantly  $\text{C}_3$  signal of most individuals. In contrast, in more open and/or wetland environments,  $\text{C}_4$  grasses and sedges would be regularly encountered, consistent with the  $\delta^{13}\text{C}$  values of others. Indeed, the  $\delta^{13}\text{C}$  values of *Au. afarensis* are what one would expect for hominins eating leaf/pith in their known habitats regardless of their photosynthetic pathway (Boaz 1988; Reed 2008).

Consequently, problems with our interpretation of dietary data for *Au. afarensis* are twofold. The first is that Lucy and her kin come off as less chimp-like than many envisioned, although this is perhaps less shocking now than it was in the past (e.g. Sayers & Lovejoy 2008; White *et al.* 2015). The second is that *P. boisei*, with its bizarre “Nutcracker Man” combination of morphology, microwear, and isotopic composition necessitated serious consideration of outré diets dominated by corms, rhizomes, seeds, and/or CAM plants. And if *P. boisei* had a diet comprising such unexpected things, it stands to reason that *Au. afarensis* had taken a step or three down that dietary path. So without *P. boisei*, modern discussions of *Au. afarensis* diet might have followed a different and simpler course.

Before the *anni confusionis*, a reasonable vision of *Au. afarensis* could be derived from extant hominoid ecology, comparative morphology, and behavioral data available for *Au. africanus*. One version of this might be labeled the chimpanzee-plus model, meaning that *Australopithecus* would have been similar to modern chimpanzees in savanna environments, except that Lucy would have exploited more foods available in the open portions of her habitat (Sponheimer *et al.* 2007). By analogy, this would be something like the situation that exists around the Tana River today, where the Tana River Mangabey (*Cercocebus galerritus* Peters, 1879) is a dietary generalist but is nevertheless endangered because its diverse diet is limited to what is found in the gallery forest (Wahungu 1998). Sympatric *Papio* Erxleben, 1777, playing the ecological doppelgänger of *Au. afarensis* in this scenario, has a diet that overlaps with the mangabeys seasonally, but when needed it can utilize resources from more open portions of the landscape (Wahungu 1998; Bentley-Condit & Power 2018). So *Papio* thrives, while *Cercocebus galerritus* limps toward oblivion. In such a scenario, if *Pan* and *Australopithecus* were sympatric in “savanna” type environments, we would expect *Australopithecus* to outcompete its chimpanzee cousins. Chimpanzees do not suffer from the extreme habitat limitations of Tana River mangabeys; however, in savanna environments, they greatly extend their home

ranges and have low densities despite having larger party sizes, most likely as an anti-predator strategy (Moore 1996; Pruett & Bertolani 2009; Giuliano *et al.* 2022). This long-distance ranging is at least partly because savanna chimpanzees have diets quite similar to those of forest chimpanzees (fruit and tree leaves; Hohmann *et al.* 2010), and this means most of their habitat is of limited use to them dietarily – particularly the ubiquitous C<sub>4</sub> grasses (Schoeninger *et al.* 1999; Sponheimer *et al.* 2006). *Australopithecus*, with its ability to utilize the C<sub>4</sub> vegetation that dominates these environments, would not have had to range so far afield for food. Thus, it would be difficult to envision *Pan* in any abundance in areas once occupied by *Australopithecus*. This scenario works admirably with available dietary data for *Au. africanus*.

But what scenario can be envisioned to explain current paleodietary data for *Au. afarensis*, as well as its possible descendant *P. boisei*? If we imagine environmental change, competition, or both leading the ancestors of *Au. afarensis* to use more open portions of the landscape, woodlands, or perhaps river courses, fruits would have generally been less abundant in these areas (Copeland 2009). Monocots, in contrast, would have been ubiquitous. These hominins might have broken down monocots with hard stems to extract pith, for which their relatively flat teeth and a powerful masticatory apparatus were well-suited. The pith or other vegetative material would have been chewed to access readily extractable nutrients and the quid would have been expectorated (at least for especially refractory foods). Masticatory cycles might have increased if more food was consumed, but the soft tissue digestive apparatus would have been less taxed because smaller quantities of fibrous material would have been swallowed. This scenario would be consistent with what we see in *Au. afarensis* hard tissue anatomy and microwear, and the expected result might be a predominantly C<sub>3</sub> isotopic signature. However, in areas with large stands of *Cyperus* L. or other C<sub>4</sub> sedges, C<sub>4</sub> foods would become more important. In some ways, this is not so different from what is seen in chimpanzees, orangutans (*Pongo* spp.), and modern humans who also spit out highly indigestible dietary components after extracting readily digestible components (cell solubles) (Tutin *et al.* 1997; Remis & Dierenfeld 2004; Dominy *et al.* 2008; van der Merwe *et al.* 2008; Vogel *et al.* 2008; Yamagiwa & Basabose 2006).

Under the scenario above, further climate and environmental change could explain the eventual rise of *P. boisei* with its more derived masticatory apparatus (perhaps we can call it *Australopithecus-plus*?). As environments opened, and perhaps along lake shore environments with extensive stands of sedges and/or grasses, the same basic diet would result in an increasingly C<sub>4</sub> isotopic composition with only a marginal impact on occlusal microwear. The mechanical requirements might not change much, but the dental battery might continue to become optimized, as in the elephant and suid examples above. In fact, Ungar & Hlusko (2016) argued that for a hominoid, the easiest evolutionary path to becoming a tough and fibrous food specialist is to increase occlusal surface size and lay down thicker enamel. This might also be useful if a

more open environment led to more grit-laden plant food thus increasing tooth wear. Once again, the teeth would be well-suited for breaking down hard stems, and their thickly enameled flat teeth might impose few barriers for a taxon that does not seek to break down more refractory foods. In a way, this is analogous to the situation with pandas, except that pandas expel long undigested chunks of vegetation via the fecal route. It is also noteworthy that *P. boisei* has a calcium isotope ratio that is very different from other early African hominins (Martin *et al.* 2020), but very similar to those observed in *Gigantopithecus blacki* von Koenigswald, 1935 and pandas (Hu *et al.* 2022). While interpretation of calcium isotope data remains challenging, this clustering of two taxa that eat (or ate) bamboo to greater or lesser extents (giant pandas and *Gigantopithecus* von Koenigswald, 1935; Daegling & Grine 1994) and a hominin for which dietary proxy data is suggestive of tough food consumption is remarkable, especially in light of masticatory convergences in all three taxa (White 1975).

## CONCLUSIONS

As our colleague Dr Bernard Wood once opined, “If we can’t figure out what a morphological hyperspecialist like *P. boisei* ate, we have no hope of figuring out what any of the more generalized hominins ate”. Just so. We have argued that *P. boisei* is the key to unlocking our understanding of australopith diet in a general sense (e.g. Sponheimer *et al.* 2013, 2023). The reasons for this are many. When stepping back, it is easy to see the highly-derived dentognathic morphology of *P. boisei* as the quintessence of a trend towards dietary specialization that begins with the earliest australopiths. By this logic, *P. boisei* would be doing more of the same, or the same but better than its predecessors. This has further empirical support in the significant relationship between larger cheek teeth and apparent C<sub>4</sub> consumption in the australopiths – more C<sub>4</sub> correlating with a larger dental battery (Sponheimer *et al.* 2013). A further inducement to focus on *P. boisei* was that questions about its diet should be readily approached because its masticatory morphology is so extreme, and because its isotopic composition and dental microwear are only compatible with a limited set of potential foods. Given its likely descendant status with *Au. afarensis*, the case was even stronger that the diet of *P. boisei* should prove revelatory.

And perhaps it has been. While there is no simple solution to the problem posed by the multifarious dietary data, one scenario that is broadly consistent with current datasets is that a purported *Au. afarensis*-*P. boisei* lineage began consuming fibrous vegetation more frequently, but with a possible focus on material that would be wadded and expectorated. While this diet would require intense and regular chewing, it might not require the occlusal relief that is usually a hallmark of tough food consumption among extant primates (Kay *et al.* 1978; Kay 1985). As discussed previously, the dentition of these australopiths, while suboptimal for a diet of displacement-limited foods, might have been the evolutionary path of least



resistance given the relatively flat teeth of their forebears, the ease of increasing enamel thickness, and the relative difficulty of making changes to crown morphology (Ungar & Hlusko 2016). This scenario had the additional advantage of being better able to explain the quick change towards apparent  $C_4$  consumption witnessed in the Omo hominins with a much smaller  $C_4$  change in other fauna: perhaps hominins tracked vegetation at or near the water interface where changes in hydrology, soil texture, or nutrient availability led to large changes in  $C_4$  abundance, whereas most other mammals tracked subtler changes in gross  $C_4$  grass availability in opening environments (Negash *et al.* 2020). Perhaps the closest analogy to this today is with the marsh and swamp-loving sitatunga (*Tragelaphus spekii* Speke, 1863). They typically have diets of greater than 50% monocots, and yet can have  $\delta^{13}C$  values indicating pure  $C_3$  consumption in forests, but in more open environments, can have  $\delta^{13}C$  values in the *P. boisei* range (Cerling *et al.* 2003; Sponheimer *et al.* 2003). Notably, there is abundant evidence of water-loving plants and animals at most *A. afarensis* and *Paranthropus* sites in eastern Africa (Stewart 2014).

An irony in this, however, is that it might have been easier to generate such hypotheses if we knew nothing about *P. boisei*. For instance, Picq (1990) argued that the anterior tooth wear and anatomy of *Au. afarensis* were consistent with a diet requiring more chewing than that of a chimpanzee, and which would have included more savanna resources and leafy vegetation/abrasive foods. The main difference between this interpretation and the hypothesis presented here is that Picq (1990) saw USOs as important foods for Lucy and her ilk, which now appears less likely given occlusal microwear and dental fracture data. It was the seeming improbability of *P. boisei*, with its much flatter teeth, and a diet dominated by tough vegetation that suggested something strange was afoot: for instance, high consumption of tubers or nuts without leaving traces in dental microwear or tooth fracture frequencies. So what did *P. boisei* bring to the table? Trouble, but possibly the good kind.

Indeed, it could be argued that *P. boisei* was the straw that broke the durophage's back, and prompted some to cast off the vestiges of nutcracker "orthodoxy" when it comes to deciding what is special about australopiths in the realm of diet. Of course, for many, this will be a step too far, but it is consistent with Kay's (1981) dentognathic survey of Miocene hominoids which established that thick enamel and robust mandibles (large corpora) are plesiomorphic, such that these characters do not explain the emergence of australopiths. This also means that durophagy as the initial or enduring dietary strategy of australopiths is difficult to justify: indeed, *P. robustus* might be the only committed hard-object specialist among them, and as such an outlier rather than a paradigmatic example of the radiation. Furthermore, we only have dietary proxy data for *P. robustus* from a highly restricted area of the South African highveld, so we cannot be certain that durophagy was its constant companion or something forced upon it in an idiosyncratic local habitat hosting plants of comparatively poor nutritional quality

(Paine *et al.* 2019). Regardless, what is novel, late in the australopith radiation, is postcanine megadontia and a correlated change in adductor mass to maintain sufficient bite pressures (Demes & Creel 1988; Eng *et al.* 2013).

Robinson's (1954) take, prior to OH 5's discovery, was that *Paranthropus* was a "herbivore" in contrast to the omnivorous *Au. africanus*. Only later, with the field's elevation of *Ramapithecus* and the accumulation of eastern African *Paranthropus* did the idea of durophagous adaptation fully calcify into the explanans of early hominin feeding ecology. The newer ecological data for *P. boisei* make it defensible, or even necessary, to imagine other dietary possibilities for Lucy's kin.

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## REFERENCES

- BARTON R. A., WHITEN A., BYRNE R. W. & ENGLISH M. 1993. — Chemical composition of baboon plant foods: implications for the interpretation of intra- and interspecific differences in diet. *Folia Primatol* 61: 1-20. <https://doi.org/10.1159/000156722>
- BENTLEY-CONDIT V. K. & POWER M. L. 2018. — The nutritional content of Tana River yellow baboon (*Papio cynocephalus*) foods in a partially forested habitat. *PLoS One* 13: e0207186. <https://doi.org/10.1371/journal.pone.0207186>
- BOAZ N. T. 1988. — Status of *Australopithecus afarensis*. *American Journal of Physical Anthropology* 31: 85-113.
- CACHEL S. 1975. — A new view of speciation in *Australopithecus*, in TUTTLE R. H. (ed.), *Paleoanthropology: Morphology and Paleoecology*. De Gruyter, The Hague: 183-202. <https://doi.org/10.1515/9783110810691.183>
- CAMPBELL J. L., WILLIAMS C. V. & EISEMANN J. H. 2004. — Use of total dietary fiber across four lemur species (*Propithecus verreauxi coquereli*, *Haplemur griseus griseus*, *Varecia variegata*, and *Eulemur fulvus*): does fiber type affect digestive efficiency? *American Journal of Primatology* 64: 323-335. <https://doi.org/10.1002/ajp.20081>
- CERLING T. E., HARRIS J. M. & PASSEY B. H. 2003. — Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy* 84 (2): 456-470. [https://doi.org/10.1644/1545-1542\(2003\)084%3C0456:DOEABB%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084%3C0456:DOEABB%3E2.0.CO;2)
- CERLING T. E., MBUA E., KIRERA F. M., MANTHI F. K., GRINE F. E., LEAKEY M. G., SPONHEIMER M. & UNO K. T. 2011a. — Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences of the United States of America* 108: 9337-9341. <https://doi.org/10.1073/pnas.1104627108>
- CERLING T. E., WYNN J. G., ANDANJE S. A., BIRD M. I., KORIR D. K., LEVIN N. E., MACE W., MACHARIA A. N., QUADE J. & REMIEN C. H. 2011b. — Woody cover and hominin environments in the past 6 million years. *Nature* 476: 51-56. <https://doi.org/10.1038/nature10306>
- CODRON D. & BRINK J. S. 2007. — Trophic ecology of two savanna grazers, blue wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*. *European Journal of Wildlife Research* 53: 90-99. <https://doi.org/10.1007/s10344-006-0070-2>

- CODRON D., CODRON J., LEE-THORP J. A., SPONHEIMER M. & DE RUITER D. 2005. — Animal diets in the Waterberg based on stable isotopic composition of faeces. *South African Journal of Wildlife Research* 35: 43-52. <https://doi.org/10.5167/uzh-25362>
- CODRON D., CODRON J., LEE-THORP J. A., SPONHEIMER M., DE RUITER D. & BRINK J. S. 2007. — Stable isotope characterization of mammalian predator-prey relationships in a South African savanna. *European Journal of Wildlife Research* 53: 161-170. <https://doi.org/10.1007/s10344-006-0075-x>
- CODRON D., CODRON J., SPONHEIMER M. & CLAUS M. 2016. — Within-population isotopic niche variability in savanna mammals: disparity between carnivores and herbivores. *Frontiers in Ecology and Evolution* 4: 15. <https://doi.org/10.3389/fevo.2016.00015>
- CONKLIN-BRITTAIN N. L., WRANGHAM R. W. & SMITH C. C. 2002. — A two-stage model of increased dietary quality in early hominid evolution: the role of fiber, in UNGAR P. S. & TEAFORD M. F. (eds), *Human Diet: Its Origin and Evolution*. Bergin & Garvey, Westport: 61-76.
- CONSTANTINO P. J. & KONOW K. A. 2021. — Dental chipping supports lack of hard-object feeding in *Paranthropus boisei*. *Journal of Human Evolution* 156: 103015. <https://doi.org/10.1016/j.jhevol.2021.103015>
- COPPELAND S. R. 2009. — Potential hominin plant foods in northern Tanzania: semi-arid savannas versus savanna chimpanzee sites. *Journal of Human Evolution* 57 (4): 365-378. <https://doi.org/10.1016/j.jhevol.2009.06.007>
- COPPENS Y. 1994. — East side story: the origin of humankind. *Scientific American* 270: 88-95. <https://doi.org/10.1038/scientificamerican0594-88>
- CROWLEY B. E., GODFREY L. R. & IRWIN M. T. 2011. — A glance to the past: subfossils, stable isotopes, seed dispersal, and lemur species loss in Southern Madagascar. *American Journal of Primatology* 73 (1): 25-37. <https://doi.org/10.1002/ajp.20817>
- DAEGLING D. J. & GRINE F. E. 1994. — Bamboo feeding, dental microwear, and diet of the Pleistocene ape *Gigantopithecus blacki*. *South African Journal of Science* 90: 527-532.
- DAEGLING D. J. & GRINE F. E. 1999. — Terrestrial foraging and dental microwear in *Papio ursinus*. *Primates* 40: 559-572. <https://doi.org/10.1007/BF02574831>
- DAEGLING D. J. & GRINE F. E. 2017. — Feeding behavior and diet in *Paranthropus boisei*: the limits of functional inference from the mandible, in MAROM A. & HOVERS E. (eds), *Human Paleontology and Prehistory: Contributions in Honor of Yoel Rak, Vertebrate Paleobiology and Paleoanthropology*. Springer International Publishing, Cham: 109-125. [https://doi.org/10.1007/978-3-319-46646-0\\_9](https://doi.org/10.1007/978-3-319-46646-0_9)
- DAEGLING D. J., MCGRAW W. S., UNGAR P. S., PAMPUSH J. D., VICK A. E. & BITTY E. A. 2011. — Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. *PLoS One* 6: e23095. <https://doi.org/10.1371/journal.pone.0023095>
- DART R. A. 1925. — *Australopithecus africanus* the man-ape of South Africa. *Nature* 115: 195-199. <https://doi.org/10.1038/115195a0>
- DARWIN C. 1871. — *The Descent of Man and Selection in Relation to Sex*. Second edition. John Murray, London.
- DAVIS D. D. 1964. — *The Giant Panda: A Morphological Study of Evolutionary Mechanisms*. Chicago Natural History Museum, Chicago. <https://doi.org/10.5962/bhl.title.5133>
- DEMES B. & CREEL N. 1988. — Bite force, diet, and cranial morphology of fossil hominids. *Journal of Human Evolution* 17 (7): 657-670. [https://doi.org/10.1016/0047-2484\(88\)90023-1](https://doi.org/10.1016/0047-2484(88)90023-1)
- DIERENFELD E. S., HINTZ H. F., ROBERTSON J. B., VAN SOEST P. J. & OFTEDAL O. T. 1982. — Utilization of bamboo by the giant panda. *The Journal of Nutrition* 112 (4): 636-641. <https://doi.org/10.1093/jn/112.4.636>
- DOMINY N. J., VOGEL E. R., YEAKEL J. D., CONSTANTINO P. & LUCAS P. W. 2008. — Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evolutionary Biology* 35: 159-175. <https://doi.org/10.1007/s11692-008-9026-7>
- DU BRUL E. L. 1977. — Early hominid feeding mechanisms. *American Journal of Physical Anthropology* 47 (2): 305-320. <https://doi.org/10.1002/ajpa.1330470211>
- ENG C. M., LIEBERMAN D. E., ZINK K. D. & PETERS M. A. 2013. — Bite force and occlusal stress production in hominin evolution. *American Journal of Physical Anthropology* 151 (4): 544-557. <https://doi.org/10.1002/ajpa.22296>
- FILLION E. N., HARRISON T. & KWEKASON A. 2022. — A nonanalogue Pliocene ungulate community at Laetoli with implications for the paleoecology of *Australopithecus afarensis*. *Journal of Human Evolution* 167: 103182. <https://doi.org/10.1016/j.jhevol.2022.103182>
- FINLEY T. G., SIKES R. S., PARSONS J. L., RUDE B. J., BISSELL H. A. & OUELLETTE J. R. 2011. — Energy digestibility of giant pandas on bamboo-only and on supplemented diets. *Zoo Biology* 30 (2): 121-133. <https://doi.org/10.1002/zoo.20340>
- GIULIANO C., STEWART F. A. & PIEL A. K. 2022. — Chimpanzee (*Pan troglodytes schweinfurthii*) grouping patterns in an open and dry savanna landscape, Issa Valley, western Tanzania. *Journal of Human Evolution* 163: 103137. <https://doi.org/10.1016/j.jhevol.2021.103137>
- GODFREY L. R., CROWLEY B. E., MULDOON K. M., KELLEY E. A., KING S. J., BEST A. W. & BERTHAUME M. A. 2016. — What did *Hadropithecus* eat, and why should paleoanthropologists care? *American Journal of Primatology* 78 (10): 1098-1112. <https://doi.org/10.1002/ajp.22506>
- GRINE F. E. 1981. — Trophic differences between “gracile” and “robust” australopithecines: a scanning electron microscope analysis of occlusal events. *South African Journal of Science* 77: 203-230. [https://hdl.handle.net/10520/AJA00382353\\_1525](https://hdl.handle.net/10520/AJA00382353_1525)
- GRINE F. E. 1986. — Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *Journal of Human Evolution* 15 (8): 783-822. [https://doi.org/10.1016/S0047-2484\(86\)80010-0](https://doi.org/10.1016/S0047-2484(86)80010-0)
- GRINE F. E. & KAY R. F. 1988. — Early hominid diets from quantitative image analysis of dental microwear. *Nature* 333: 765-768. <https://doi.org/10.1038/333765a0>
- GRINE F. E., UNGAR P. S., TEAFORD M. F. & EL-ZAATARI S. 2006. — Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *Journal of Human Evolution* 51: 297-319. <https://doi.org/10.1016/j.jhevol.2006.04.004>
- GRINE F. E., SPONHEIMER M., UNGAR P. S., LEE-THORP J. & TEAFORD M. F. 2012. — Dental microwear and stable isotopes inform the paleoecology of extinct hominins. *American Journal of Physical Anthropology* 148 (2): 285-317. <https://doi.org/10.1002/ajpa.22086>
- HARMAND S., LEWIS J. E., FEIBEL C. S., LEPRE C. J., PRAT S., LENOBLE A., BOËS X., QUINN R. L., BRENET M., ARROYO A., TAYLOR N., CLÉMENT S., DAVER G., BRUGAL J.-P., LEAKEY L., MORTLOCK R. A., WRIGHT J. D., LOKORODI S., KIRWA C., KENT D. V. & ROCHE H. 2015. — 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521: 310-315. <https://doi.org/10.1038/nature14464>
- HARMON E. H. 2013. — Age and sex differences in the locomotor skeleton of *Australopithecus*, in REED K. E., FLEAGLE J. G. & LEAKEY R. E. (eds), *The Paleobiology of Australopithecus*. Springer Netherlands, Dordrecht: 263-272. [https://doi.org/10.1007/978-94-007-5919-0\\_18](https://doi.org/10.1007/978-94-007-5919-0_18)
- HARRIS J. M. & CERLING T. E. 2002. — Dietary adaptations of extant and Neogene African suids. *Journal of Zoology* 256 (1): 45-54.
- HATLEY T. & KAPPELMAN J. 1980. — Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of belowground food resources. *Human Ecology* 8: 371-387. <https://doi.org/10.1007/BF01561000>



- HOHMANN G., POTTS K., N'GUESSAN A., FOWLER A., MUNDY R., GANZHORN J. U. & ORTMANN S. 2010. — Plant foods consumed by Pan: exploring the variation of nutritional ecology across Africa. *American Journal of Physical Anthropology* 141 (3): 476-485. <https://doi.org/10.1002/ajpa.21168>
- HU Y., JIANG Q., LIU F., GUO L., ZHANG Z. & ZHAO L. 2022. — Calcium isotope ecology of early *Gigantopithecus blacki* (~2 Ma) in South China. *Earth and Planetary Science Letters* 584: 117522. <https://doi.org/10.1016/j.epsl.2022.117522>
- HUNT K. D. 1998. — Ecological morphology of *Australopithecus afarensis*: traveling terrestrially, eating arboreally, in STRASSER E., FLEAGLE J. G., ROSENBERGER A. L. & MCHENRY H. M. (eds), *Primate Locomotion*. Springer, Boston, MA: 397-418. [https://doi.org/10.1007/978-1-4899-0092-0\\_20](https://doi.org/10.1007/978-1-4899-0092-0_20)
- HYLANDER W. L. 1988. — Implications of in vivo experiments for interpreting the functional significance of “robust” australopithecine jaws, in GRINE F. E. (ed.), *Evolutionary History of the Robust Australopithecines*. Aldine de Gruyter, New York, 30 p.
- JOHANSON D. C. & WHITE T. D. 1979. — A systematic assessment of early African hominids. *Science* 203 (4378): 321-330. <https://doi.org/10.1126/science.104384>
- JOLLY C. J. 1970. — The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5 (1): 5. <https://doi.org/10.2307/2798801>
- KAY R. F. 1981. — The nut-crackers – a new theory of the adaptations of the Ramapithecinae. *American Journal of Physical Anthropology* 55 (2): 141-151. <https://doi.org/10.1002/ajpa.1330550202>
- KAY R. F. 1985. — Dental evidence for the diet of *Australopithecus*. *Annual Review of Anthropology* 14: 315-341. <https://www.jstor.org/stable/2155599>
- KAY R. F. & UNGAR P. S. 1997. — Dental evidence for diet in some Miocene Catarrhines with comments on the effects of phylogeny on the interpretation of adaptation, in BEGUN D. R., WARD C. V. & ROSE M. D. (eds), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Springer US, Boston, MA: 131-151. [https://doi.org/10.1007/978-1-4899-0075-3\\_7](https://doi.org/10.1007/978-1-4899-0075-3_7)
- KAY R. F., SUSSMAN R. W. & TATTERSALL I. 1978. — Dietary and dental variations in the genus *Lemur*, with comments concerning dietary-dental correlations among Malagasy primates. *American Journal of Physical Anthropology* 49 (1): 119-127. <https://doi.org/10.1002/ajpa.1330490118>
- KIMBEL W. H., WHITE T. D. & JOHANSON D. C. 1984. — Cranial morphology of *Australopithecus afarensis*: a comparative study based on a composite reconstruction of the adult skull. *American Journal of Physical Anthropology* 64 (4): 337-388. <https://doi.org/10.1002/ajpa.1330640403>
- KIMBEL W. H., RAK Y. & JOHANSON D. C. 2004. — *The Skull of Australopithecus afarensis*. Oxford University Press. <https://doi.org/10.1093/oso/9780195157062.001.0001>
- KOTZE D. C. & O'CONNOR T. G. 2000. — Vegetation variation within and among palustrine wetlands along an altitudinal gradient in KwaZulu-Natal, South Africa. *Plant Ecology* 146: 77-96. <https://doi.org/10.1023/A:1009812300843>
- LADEN G. & WRANGHAM R. 2005. — The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopithecine origins. *Journal of Human Evolution* 49 (4): 482-498. <https://doi.org/10.1016/j.jhevol.2005.05.007>
- LEE-THORP J. 2011. — The demise of “Nutcracker Man”. *Proceedings of the National Academy of Sciences of the United States of America* 108: 9319-9320. <https://doi.org/10.1073/pnas.1105808108>
- LEE-THORP J. A., VAN DER MERWE N. J. & BRAIN C. K. 1994. — Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *Journal of Human Evolution* 27 (4): 361-372. <https://doi.org/10.1006/jhevol.1994.1050>
- LEE-THORP J. A., SPONHEIMER M. & LUYT J. 2007. — Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites. *Journal of Human Evolution* 53: 595-601.
- LESNIK J. J. 2014. — Termites in the hominin diet: a meta-analysis of termite genera, species and castes as a dietary supplement for South African robust australopithecines. *Journal of Human Evolution* 71: 94-104. <https://doi.org/10.1016/j.jhevol.2013.07.015>
- LI M.-R., WEDIN D. A. & TIESZEN L. L. 1999. — C<sub>3</sub> and C<sub>4</sub> photosynthesis in *Cyperus* (Cyperaceae) in temperate eastern North America. *Canadian Journal of Botany* 77 (2): 209-218. <https://doi.org/10.1139/b98-216>
- LISTER A. M. 2013. — The role of behaviour in adaptive morphological evolution of African proboscideans. *Nature* 500: 331-334. <https://doi.org/10.1038/nature12275>
- LOCKWOOD C. 2013. — Whence *Australopithecus africanus*? Comparing the skulls of South African and East African *Australopithecus*, in REED K. E., FLEAGLE J. G. & LEAKEY R. E. (eds), *The Paleobiology of Australopithecus*. Springer Netherlands, Dordrecht: 175-182. [https://doi.org/10.1007/978-94-007-5919-0\\_11](https://doi.org/10.1007/978-94-007-5919-0_11)
- LUCAS P. W., OMAR R., AL-FADHALAH K., ALMUSALLAM A. S., HENRY A. G., MICHAEL S., THAI L. A., WATZKE J., STRAIT D. S. & ATKINS A. G. 2013. — Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *Journal of the Royal Society Interface* 10 (80): 20120923. <https://doi.org/10.1098/rsif.2012.0923>
- MACHO G. A. 2014. — Baboon feeding ecology informs the dietary niche of *Paranthropus boisei*. *PLoS One* 9: e84942. <https://doi.org/10.1371/journal.pone.0084942>
- MARTIN J. E., TACAIL T., BRAGA J., CERLING T. E. & BALTER V. 2020. — Calcium isotopic ecology of Turkana Basin hominins. *Nature Communications* 11: 3587. <https://doi.org/10.1038/s41467-020-17427-7>
- MARTÍNEZ L. M., ESTEBARANZ-SÁNCHEZ F., GALBANY J. & PÉREZ-PÉREZ A. 2016. — Testing dietary hypotheses of East African hominines using buccal dental microwear data. *PLoS One* 11: e0165447. <https://doi.org/10.1371/journal.pone.0165447>
- MCPHERRON S. P., ALEMSEGED Z., MAREAN C. W., WYNN J. G., REED D., GERAADS D., BOBE R. & BÉARAT H. A. 2010. — Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466: 857-860. <https://doi.org/10.1038/nature09248>
- MOORE J. 1996. — Savanna chimpanzees, referential models and the last common ancestor, in MCGREW W. C., MARCHANT L. F. & NISHIDA T. (eds), *Great Ape Societies*. Cambridge University Press: 275-292. <https://doi.org/10.1017/cbo9780511752414.022>
- NEGASH E. W., ALEMSEGED Z., BOBE R., GRINE F., SPONHEIMER M. & WYNN J. G. 2020. — Dietary trends in herbivores from the Shungura Formation, southwestern Ethiopia. *Proceedings of the National Academy of Sciences of the United States of America* 117 (36): 21921-21927. <https://doi.org/10.1073/pnas.2006982117>
- OVERDORFF D. J. & RASMUSSEN M. A. 1995. — Determinants of Nighttime Activity in “Diurnal” Lemurid Primates, in ALTERMAN L., DOYLE G. A. & IZARD M. K. (eds), *Creatures of the Dark: The Nocturnal Prosimians*. Springer, Boston, MA: 61-74. [https://doi.org/10.1007/978-1-4757-2405-9\\_5](https://doi.org/10.1007/978-1-4757-2405-9_5)
- PAINE O. C. C., KOPPA A., HENRY A. G., LEICHLITER J. N., CODRON D., CODRON J., LAMBERT J. E. & SPONHEIMER M. 2019. — Seasonal and habitat effects on the nutritional properties of savanna vegetation: potential implications for early hominin dietary ecology. *Journal of Human Evolution* 133: 99-107. <https://doi.org/10.1016/j.jhevol.2019.01.003>
- PETERS C. R. & MAGUIRE B. 1981. — Wild plant foods of the Makapansgat area: a modern ecosystems analogue for *Australopithecus africanus* adaptations. *Journal of Human Evolution* 10 (7): 565-583. [https://doi.org/10.1016/S0047-2484\(81\)80048-6](https://doi.org/10.1016/S0047-2484(81)80048-6)
- PETERS C. R. & VOGEL J. C. 2005. — Africa's wild C<sub>4</sub> plant foods and possible early hominid diets. *Journal of Human Evolution* 48 (3): 219-236. <https://doi.org/10.1016/j.jhevol.2004.11.003>

- PETERSON A. S. 2017. — *Dental Microwear Textures of Paranthropus robustus from Kromdraai, Drimolen, and an Enlarged Sample from Swartkrans: Ecological and Intraspecific Variation*. University of Arkansas, Fayetteville.
- PETERSON A., ABELLA E. F., GRINE F. E., TEAFORD M. F. & UNGAR P. S. 2018. — Microwear textures of *Australopithecus africanus* and *Paranthropus robustus* molars in relation to paleoenvironment and diet. *Journal of Human Evolution* 119: 42-63. <https://doi.org/10.1016/j.jhevol.2018.02.004>
- PHILLIPS S., SCHEFFRAHN R. H., PIEL A., STEWART F., AGBOR A., BRAZZOLA G., TICKLE A., SOMMER V., DIEGUEZ P., WESSLING E. G., ARANDJELOVIC M., KÜHL H., BOESCH C. & OELZE V. M. 2021. — Limited evidence of C<sub>4</sub> plant consumption in mound building Macrotermes termites from savanna woodland chimpanzee sites. *PLoS One* 16: e0244685. <https://doi.org/10.1371/journal.pone.0244685>
- PICQ P. 1990. — The diet of *Australopithecus-Afarensis*: a tentative essay of reconstruction. *Comptes Rendus de l'Académie des Sciences Série IIc: Chimie* 311: 725-730.
- PLUMMER T. W., OLIVER J. S., FINSTONE E. M., DITCHFIELD P. W., BISHOP L. C., BLUMENTHAL S. A., LEMORINI C., CARICOLA I., BAILEY S. E., HERRIES A. I. R., PARKINSON J. A., WHITFIELD E., HERTEL F., KINYANJUI R. N., VINCENT T. H., LI Y., LOUYS J., FROST S. R., BRAUN D. R., REEVES J. S., EARLY E. D. G., ONYANGO B., LAMELA-LOPEZ R., FORREST F. L., HE H., LANE T. P., FROUIN M., NOMADE S., WILSON E. P., BARTILOLO S. K., ROTICH N. K. & POTTS R. 2023. — Expanded geographic distribution and dietary strategies of the earliest Oldowan hominins and *Paranthropus*. *Science* 379 (6632): 561-566. <https://doi.org/10.1126/science.abo7452>
- POST N. W., GILBERT C. C., PUGH K. D. & MONGLE C. S. 2023. — Implications of outgroup selection in the phylogenetic inference of hominoids and fossil hominins. *Journal of Human Evolution* 184: 103437. <https://doi.org/10.1016/j.jhevol.2023.103437>
- PRABHAT A. M., MILLER C. K., PRANG T. C., SPEAR J., WILLIAMS S. A. & DESILVA J. M. 2021. — Homoplasy in the evolution of modern human-like joint proportions in *Australopithecus afarensis*. *Elife* 10: e65897. <https://doi.org/10.7554/eLife.65897>
- PRANG T. C. 2015. — Calcaneal robusticity in Plio-Pleistocene hominins: implications for locomotor diversity and phylogeny. *Journal of Human Evolution* 80: 135-146. <https://doi.org/10.1016/j.jhevol.2014.09.001>
- PRUETZ J. & BERTOLANI P. 2009. — Chimpanzee (pan troglodytes verus) behavioral responses to stresses associated with living in a Savanna-mosaic environment: implications for hominin adaptations to open habitats. *PaleoAnthropology* 2009: 252-262. <https://doi.org/10.4207/PA.2009.ART33>
- PUECH P. F. 1992. — Microwear studies of early African hominid teeth. *Scanning Microscopy* 6: 1083-1087; discussion: 1087-1088.
- PUECH P. F. & ALBERTINI H. 1983. — Wearing of the teeth in *Australopithecus afarensis*: microscopic examination of the superior canine/lower first premolar complex. *Comptes rendus hebdomadaires des séances de l'Académie des sciences* III 296: 1083-1088.
- PUECH P.-F. & ALBERTINI H. 1984. — Dental microwear and mechanisms in early hominids from Laetoli and Hadar. *American Journal of Physical Anthropology* 65 (1): 87-91. <https://doi.org/10.1002/ajpa.1330650112>
- PUECH P.-F., ALBERTINI H. & SERRATRICE C. 1983. — Tooth microwear and dietary patterns in early hominids from Laetoli, Hadar and Olduvai. *Journal of Human Evolution* 12 (8): 721-729. [https://doi.org/10.1016/S0047-2484\(83\)80127-4](https://doi.org/10.1016/S0047-2484(83)80127-4)
- PUECH P., CIANFARANI F. & ALBERTINI H. 1986. — Dental microwear features as an indicator for plant food in early hominids: a preliminary study of enamel. *Human Evolution* 1: 507-515. <https://doi.org/10.1007/BF02437467>
- RABENOLD D. & PEARSON O. M. 2011. — Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. *PLoS One* 6: e28379. <https://doi.org/10.1371/journal.pone.0028379>
- RAK Y., GINZBURG A. & GEFFEN E. 2007. — Gorilla-like anatomy on *Australopithecus afarensis* mandibles suggests *Au. afarensis* link to robust australopithecines. *Proceedings of the National Academy of Sciences of the United States of America* 104 (16): 6568-6572. <https://doi.org/10.1073/pnas.0606454104>
- REED K. E. 1997. — Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* 32 (2-3): 289-322. <https://doi.org/10.1006/jhevol.1996.0106>
- REED K. E. 2008. — Paleocological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. *Journal of Human Evolution* 54 (6): 743-768. <https://doi.org/10.1016/j.jhevol.2007.08.013>
- REMIS M. J. & DIERENFELD E. S. 2004. — Digesta passage, digestibility and behavior in captive gorillas under two dietary regimens. *International Journal of Primatology* 25 (4): 825-845.
- ROBB G. N., WOODBORNE S. & BENNETT N. C. 2012. — Subterranean sympatry: an investigation into diet using stable isotope analysis. *PLoS One* 7: e48572. <https://doi.org/10.1371/journal.pone.0048572>
- ROBB G. N., HARRISON A., WOODBORNE S. & BENNETT N. C. 2016. — Diet composition of two common mole-rat populations in arid and mesic environments in South Africa as determined by stable isotope analysis. *Journal of Zoology* 300 (4): 257-264. <https://doi.org/10.1111/jzo.12378>
- ROBINSON J. T. 1954. — Prehominid dentition and hominid evolution. *Evolution* 8 (4): 324-334. <https://doi.org/10.2307/2405779>
- RYAN A. S. & JOHANSON D. C. 1989. — Anterior dental microwear in *Australopithecus afarensis*: comparisons with human and non-human primates. *Journal of Human Evolution* 18 (3): 235-268. [https://doi.org/10.1016/0047-2484\(89\)90051-1](https://doi.org/10.1016/0047-2484(89)90051-1)
- SAYERS K. & LOVEJOY C. O. 2008. — The chimpanzee has no clothes: a critical examination of *Pan troglodytes* in models of human evolution. *Current Anthropology* 49 (1): 87-114. <https://www.jstor.org/stable/10.1086/523675>
- SCHOENINGER M. J., BUNN H. T., MURRAY S. S. & MARLETT J. A. 2001. — Composition of tubers used by Hadza foragers of Tanzania. *Journal of Food Composition and Analysis* 14 (1): 15-25. <https://doi.org/10.1006/jfca.2000.0961>
- SCOTT R. S., UNGAR P. S., BERGSTROM T. S., BROWN C. A., GRINE F. E., TEAFORD M. F. & WALKER A. 2005. — Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436: 693-695. <https://doi.org/10.1038/nature03822>
- SENSHU T., OHYA A., IDE K., MIKOGAI J., MORITA M., NAKAO T., IMAZU K., JINGCAO L., XUANZHEN L., WENQI L. & LILI N. 2007. — Studies on the digestion in the Giant Panda, *Ailuropoda melanoleuca*, fed feedstuffs including bamboo. *Mammal Study* 32 (4): 139-149. [https://doi.org/10.3106/1348-6160\(2007\)32\[139:SOTDIT\]2.0.CO;2](https://doi.org/10.3106/1348-6160(2007)32[139:SOTDIT]2.0.CO;2)
- SEPT J. M. 1986. — Plant foods and early hominids at site FxJj 50, Koobi Fora, Kenya. *Journal of Human Evolution* 15 (8): 751-770. [https://doi.org/10.1016/S0047-2484\(86\)80008-2](https://doi.org/10.1016/S0047-2484(86)80008-2)
- SHAPIRO A. E., VENKATARAMAN V. V., NGUYEN N. & FASHING P. J. 2016. — Dietary ecology of fossil *Theropithecus*: inferences from dental microwear textures of extant geladas from ecologically diverse sites. *Journal of Human Evolution* 99: 1-9. <https://doi.org/10.1016/j.jhevol.2016.05.010>
- SHIPMAN P. & HARRIS J. M. 1988. — Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa, in GRINE F. E. (ed.), *Evolutionary history of the Robust Australopithecines*. Aldine de Gruyter, New York, 40 p.
- SILLEN A. 1992. — Strontium-calcium ratios (Sr/Ca) of *Australopithecus robustus* and associated fauna from Swartkrans. *Journal of Human Evolution* 23 (6): 495-516. [https://doi.org/10.1016/0047-2484\(92\)90049-F](https://doi.org/10.1016/0047-2484(92)90049-F)



- SIMS J. A., PARSONS J. L., BISSELL H. A., SIKES R. S., OUELLETTE J. R. & RUDE B. J. 2007. — Determination of Bamboo-Diet Digestibility and Fecal Output by Giant Pandas. *Ursus* 18 (1): 38-45. [https://doi.org/10.2192/1537-6176\(2007\)18\[38:DOBD\]2.0.CO;2](https://doi.org/10.2192/1537-6176(2007)18[38:DOBD]2.0.CO;2)
- SMITH A. L., BENAZZI S., LEDOGAR J. A., TAMVADA K., PRYOR SMITH L. C., WEBER G. W., SPENCER M. A., LUCAS P. W., MICHAEL S., SHEKEBAN A., AL-FADHALAH K., ALMUSALLAM A. S., DECHOW P. C., GROSSE I. R., ROSS C. F., MADDEN R. H., RICHMOND B. G., WRIGHT B. W., WANG Q., BYRON C., SLICE D. E., WOOD S., DZIALO C., BERTHAUME M. A., VAN CASTEREN A. & STRAIT D. S. 2015. — The feeding biomechanics and dietary ecology of *Paranthropus boisei*. *The Anatomical Record* 298 (1): 145-167. <https://doi.org/10.1002/ar.23073>
- SPONHEIMER M., LEE-THORP J. A., DERUITER D. J., SMITH J. M., VAN DER MERWE N. J., REED K., GRANT C. C., AYLIFFE L. K., ROBINSON T. F., HEIDELBERGER C. & MARCUS W. 2003. — Diets of Southern African Bovidae: stable isotope evidence. *Journal of Mammalogy* 84 (2): 471-479. [https://doi.org/10.1644/1545-1542\(2003\)084%3C0471:DOSABS%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084%3C0471:DOSABS%3E2.0.CO;2)
- SPONHEIMER M., LEE-THORP J., DE RUITER D., CODRON D., CODRON J., BAUGH A. T. & THACKERAY F. 2005. — Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. *Journal of Human Evolution* 48 (3): 301-312. <https://doi.org/10.1016/j.jhevol.2004.11.008>
- SPONHEIMER M., LOUDON J. E., CODRON D., HOWELLS M. E., PRUETZ J. D., CODRON J., DE RUITER D. J. & LEE-THORP J. A. 2006. — Do “savanna” chimpanzees consume C<sub>4</sub> resources? *Journal of Human Evolution* 51 (2): 128-133. <https://doi.org/10.1016/j.jhevol.2006.02.002>
- SPONHEIMER M., LEE-THORP J. A. & DE RUITER D. J. 2007. — Icarus, isotopes, and australopith diets, in UNGAR P. S. (ed.), *Evolution of the human diet: the known, the unknown, and the unknowable*. Oxford Academic, New York: 132-149. <https://doi.org/10.1093/oso/9780195183474.001.0001>
- SPONHEIMER M., ALEMSEGED Z., CERLING T. E., GRINE F. E., KIMBEL W. H., LEAKEY M. G., LEE-THORP J. A., MANTHI F. K., REED K. E., WOOD B. A. & WYNN J. G. 2013. — Isotopic evidence of early hominin diets. *Proceedings of the National Academy of Sciences of the United States of America* 110 (26): 10513-10518. <https://doi.org/10.1073/pnas.1222579110>
- SPONHEIMER M., DAELING D. J., UNGAR P. S., BOBE R. & PAINE O. C. C. 2023. — Problems with *Paranthropus*. *Quaternary International* 650: 40-51. <https://doi.org/10.1016/j.quaint.2022.03.024>
- STEWART K. M. 2014. — Environmental change and hominin exploitation of C<sub>4</sub>-based resources in wetland/savanna mosaics. *Journal of Human Evolution* 77: 1-16. <https://doi.org/10.1016/j.jhevol.2014.10.003>
- STOCK W. D., CHUBA D. K. & VERBOOM G. A. 2004. — Distribution of South African C<sub>3</sub> and C<sub>4</sub> species of Cyperaceae in relation to climate and phylogeny. *Austral Ecology* 29 (3): 313-319. <https://doi.org/10.1111/j.1442-9993.2004.01368.x>
- STOWE M.-J. & SEALY J. 2016. — Terminal Pleistocene and Holocene dynamics of southern Africa's winter rainfall zone based on carbon and oxygen isotope analysis of bovid tooth enamel from Elands Bay Cave. *Quaternary International* 404 (Part B): 57-67. <https://doi.org/10.1016/j.quaint.2015.09.055>
- STRAIT D. S., CONSTANTINO P., LUCAS P. W., RICHMOND B. G., SPENCER M. A., DECHOW P. C., ROSS C. F., GROSSE I. R., WRIGHT B. W., WOOD B. A., WEBER G. W., WANG Q., BYRON C., SLICE D. E., CHALK J., SMITH A. L., SMITH L. C., WOOD S., BERTHAUME M., BENAZZI S., DZIALO C., TAMVADA K. & LEDOGAR J. A. 2013. — Viewpoints: diet and dietary adaptations in early hominins: the hard food perspective. *American Journal of Physical Anthropology* 151 (3): 339-355. <https://doi.org/10.1002/ajpa.22285>
- STRAIT D. S., WEBER G. W., NEUBAUER S., CHALK J., RICHMOND B. G., LUCAS P. W., SPENCER M. A., SCHREIN C., P. C., ROSS C. F., GROSSE I. R., WRIGHT B. W., CONSTANTINO P., WOOD B. A., LAWN B., HYLANDER W. L., WANG Q., BYRON C., SLICE D. E. & SMITH A. L. 2009. — The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proceedings of the National Academy of Sciences of the United States of America* 106 (7): 2124-2129. <https://doi.org/10.1073/pnas.0808730106>
- SU D. F. 2024. — Early hominin paleoenvironments and habitat heterogeneity. *Annual Review of Anthropology* 53: 21-35. <https://doi.org/10.1146/annurev-anthro-041222-102712>
- SU D. F. & HARRISON T. 2008. — Ecological implications of the relative rarity of fossil hominins at Laetoli. *Journal of Human Evolution* 55 (4): 672-681. <https://doi.org/10.1016/j.jhevol.2008.07.003>
- SUSMAN R. L. 1988. — Hand of *Paranthropus robustus* from Member 1, Swartkrans: fossil evidence for tool behavior. *Science* 240: 781-784. <https://doi.org/10.1126/science.3129783>
- SUSMAN R. L. 1998. — Hand function and tool behavior in early hominids. *Journal of Human Evolution* 35 (1): 23-46. <https://doi.org/10.1006/jhev.1998.0220>
- SZALAY F. S. 1975. — Hunting-scavenging protohominids: a model for hominid origins. *Man* 10 (3): 420-429. <https://doi.org/10.2307/2799811>
- TEAFORD M. F., UNGAR P. S. & GRINE F. E. 2023. — Changing perspectives on early hominin diets. *Proceedings of the National Academy of Sciences* 120 (7): e2201421120. <https://doi.org/10.1073/pnas.2201421120>
- TEERI J. A., STOWE L. G. & LIVINGSTONE D. A. 1980. — The distribution of C<sub>4</sub> species of the Cyperaceae in North America in relation to climate. *Oecologia* 47: 307-310. <https://doi.org/10.1007/BF00398522>
- TOBIAS P. V. 1980. — “*Australopithecus afarensis*” and *A. africanus*: critique and an alternative hypothesis.
- TUTIN C. E., HAM R. M., WHITE L. J. & HARRISON M. J. 1997. — The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42 (1): 1-24. [https://doi.org/10.1002/\(SICI\)1098-2345\(1997\)42:1%3C1::AID-AJP1%3E3.0.CO;2-0](https://doi.org/10.1002/(SICI)1098-2345(1997)42:1%3C1::AID-AJP1%3E3.0.CO;2-0)
- TYKOT R. H. 2002. — Contribution of stable isotope analysis to understanding dietary variation among the Maya. *Archaeological Chemistry: Materials, Methods, And Meaning* 831: 214-230.
- UNGAR P. S. & HLUSKO L. J. 2016. — Anthropology. The evolutionary path of least resistance. *Science* 353 (6294): 29-30. <https://doi.org/10.1126/science.aaf8398>
- UNGAR P. S., GRINE F. E. & TEAFORD M. F. 2008. — Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS One* 3: e2044. <https://doi.org/10.1371/journal.pone.0001951>
- UNGAR P. S., SCOTT J. R. & STEININGER C. M. 2016. — Dental microwear differences between eastern and southern African fossil bovids and hominins. *South African Journal of Science* 112 (3/4): 5. <https://doi.org/10.17159/sajs.2016/20150393>
- UNO K. T., POLISSAR P. J., JACKSON K. E. & DEMENOCAL P. B. 2016. — Neogene biomarker record of vegetation change in eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America* 113 (23): 6355-6363. <https://doi.org/10.1073/pnas.1521267113>
- VAN DER MERWE N. J., MASAO F. T. & BAMFORD M. K. 2008. — Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *South African Journal of Science* 104: 153-155.
- VAN VALEN L. 1973. — A new evolutionary law. *Evolutionary Theory* 1: 1-30.
- VOGEL E. R., VAN WOERDEN J. T., LUCAS P. W., UTAMI ATMOKO S. S., VAN SCHAIK C. P. & DOMINY N. J. 2008. — Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *Journal of Human Evolution* 55 (1): 60-74. <https://doi.org/10.1016/j.jhevol.2007.12.005>

- WAHUNGU G. 1998. — Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus*. *African Journal of Ecology* 36 (2): 159-173. <https://doi.org/10.1046/j.1365-2028.1998.00120.x>
- WALKER A. 1981. — Diet and teeth. Dietary hypotheses and human evolution. *Philosophical Transaction of the Royal Society B* 292 (1057): 57-64. <https://doi.org/10.1098/rstb.1981.0013>
- WHITE T. D. 1975. — Geomorphology to paleoecology: *Gigantopithecus* reappraised. *Journal of Human Evolution* 4 (3): 219-233. [https://doi.org/10.1016/0047-2484\(75\)90009-3](https://doi.org/10.1016/0047-2484(75)90009-3)
- WHITE T. D., SUWA G., SIMPSON S. & ASFAW B. 2000. — Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *American Journal of Physical Anthropology* 111 (1): 45-68. [https://doi.org/10.1002/\(SICI\)1096-8644\(200001\)111:1%3C45::AID-AJPA4%3E3.0.CO;2-I](https://doi.org/10.1002/(SICI)1096-8644(200001)111:1%3C45::AID-AJPA4%3E3.0.CO;2-I)
- WHITE T. D., LOVEJOY C. O., ASFAW B., CARLSON J. P. & SUWA G. 2015. — Neither chimpanzee nor human, *Ardipithecus* reveals the surprising ancestry of both. *Proceedings of the National Academy of Sciences of the United States of America* 112 (16): 4877-4884. <https://doi.org/10.1073/pnas.1403659111>
- WOLPOFF M. H. 1973. — Posterior tooth size, body size, and diet in South African gracile *Australopithecines*. *American Journal of Physical Anthropology* 39 (3): 375-393. <https://doi.org/10.1002/ajpa.1330390306>
- WOOD B. 1997. — Palaeoanthropology. The oldest whodunnit in the world. *Nature* 385: 292-293. <https://doi.org/10.1038/385292a0>
- WOOD B. & RICHMOND B. G. 2000. — Human evolution: taxonomy and paleobiology. *The Journal of Anatomy* 197 (Pt 1): 19-60. <https://doi.org/1046/j.1469-7580.2000.19710019.x>
- WYNN J. G., SPONHEIMER M., KIMBEL W. H., ALEMSEGED Z., REED K., BEDASO Z. K. & WILSON J. N. 2013. — Diet of *Australopithecus afarensis* from the Pliocene Hadar Formation, Ethiopia. *Proceedings of the National Academy of Sciences of the United States of America* 110 (26): 10495-10500. <https://doi.org/10.1073/pnas.1222559110>
- WYNN J. G., REED K. E., SPONHEIMER M., KIMBEL W. H., ALEMSEGED Z., BEDASO Z. K. & CAMPISANO C. J. 2016. — Dietary flexibility of *Australopithecus afarensis* in the face of paleoecological change during the middle Pliocene: faunal evidence from Hadar, Ethiopia. *Journal of Human Evolution* 99: 93-106. <https://doi.org/10.1016/j.jhevol.2016.08.002>
- WYNN J. G., ALEMSEGED Z., BOBE R., GRINE F. E., NEGASH E. W. & SPONHEIMER M. 2020. — Isotopic evidence for the timing of the dietary shift toward C<sub>4</sub> foods in eastern African *Paranthropus*. *Proceedings of the National Academy of Sciences of the United States of America* 117 (36): 21978-21984. <https://doi.org/10.1073/pnas.2006221117>
- YAMAGIWA J. & BASABOSE A. K. 2006. — Effects of fruit scarcity on foraging strategies of sympatric gorillas and chimpanzees, in HOHMANN G., ROBBINS M. M. & BOESCH C., *Feeding Ecology in Apes and Other Primates*. Cambridge University Press: 73-96.
- YEAKEL J. D., PATTERSON B. D., FOX-DOBBS K., OKUMURA M. M., CERLING T. E., MOORE J. W., KOCH P. L. & DOMINY N. J. 2009. — Cooperation and individuality among man-eating lions. *Proceedings of the National Academy of Sciences of the United States of America* 106 (45): 19040-19043. <https://doi.org/10.1073/pnas.0905309106>
- ZINK K. D. & LIEBERMAN D. E. 2016. — Impact of meat and Lower Palaeolithic food processing techniques on chewing in humans. *Nature* 531: 500-503. <https://doi.org/10.1038/nature16990>

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