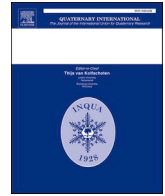




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## Problems with *Paranthropus*

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### ABSTRACT

Carbon isotopic analysis has been challenging our ideas about hominin diet for nearly 30 years. The first study in 1994 revealed that *Paranthropus robustus* from South Africa consumed principally C<sub>3</sub> foods (e.g., tree fruits and leaves) but also about 25% C<sub>4</sub>/CAM resources (e.g., tropical grasses and sedges). This result was largely consistent with morphological and dental microwear evidence suggesting *P. robustus* had a diet which included hard objects like nuts and seeds. Decades later, however, *P. boisei* from eastern Africa was shown to have eaten nearly 80% C<sub>4</sub>/CAM plants like the contemporaneous grass-eating primate *Theropithecus*. Moreover, dental microwear revealed no evidence of hard object consumption in *P. boisei*, suggesting a diet of tough foods such as grass or sedge leaf and stem. So *Paranthropus* presents us with two central problems: 1) Why do dietary proxies suggest different diets for the two robust australopithecids despite their morphological congruity; and 2) How could *P. boisei* have consumed tough foods with teeth that seem unsuited to the task. Here we review these questions and more with a particular focus on new isotopic data from the Omo and insights that can be gleaned from mammals outside the haplorhine primates. We argue that extant Primates do not capture the ecomorphological diversity of *P. boisei* and other extinct primates and should not narrowly circumscribe the behaviors we ascribe to extinct taxa. We also discuss possible digestive strategies for *P. boisei* in light of its morphology, dietary proxy data, food mechanical properties, and comparative data on mammalian digestive kinetics.

### 1. Introduction

Our understanding of early hominin diets has undergone significant, if not massive, revision since the first carbon isotope study of *Paranthropus robustus* was published almost 30 years ago (Lee-Thorp et al., 1994). By 1994 carbon isotope analysis of bone collagen was well established as a method for investigating the diets of Holocene peoples (e.g., Vogel & Van Der Merwe, 1977; Tauber, 1981; Schoeninger et al., 1983; Ambrose and DeNiro, 1986; Sealy & van der Merwe, 1988), particularly regarding the spread of C<sub>4</sub> crops and marine resources. However, bone collagen is rarely well-preserved after 10,000 years, and thus studies of early hominins awaited methodological developments showing that enamel not only survived into deep time, but was sufficiently resistant to diagenetic processes that it preserved biogenic carbon isotopic patterns in fossil herbivores (Lee-Thorp & van der Merwe,

1987; Lee-Thorp & van der Merwe, 1991). Once this was established, *Paranthropus* was the first target for stable isotope study at least partly because its highly derived masticatory apparatus led some to argue it was a specialized herbivore of one sort or another (Robinson, 1954; Jolly, 1970a; Pilbeam and Gould, 1974; Du Brul, 1977; Grine, 1981; Kay, 1985; Susman, 1988; Vrba, 1988) and carbon isotopes held the potential for revealing whether or not it consumed <sup>13</sup>C-enriched animal tissues.

Stable carbon isotope analysis continued to challenge our ideas about hominin diets in subsequent decades (Sponheimer and Lee-Thorp, 1999; Lee-Thorp et al., 2000, 2012; van der Merwe et al., 2003, 2008; Sponheimer et al., 2005a; 2006, 2013; White et al., 2009; Cerling et al., 2011a, 2013a; Henry et al., 2012; Wynn et al., 2013, 2020; Levin et al., 2015; Lüdecke et al., 2018). *Australopithecus*, for instance, was shown to have higher  $\delta^{13}\text{C}$  values than savanna chimpanzees, which was

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unexpected given early dental microwear studies showing that *A. africanus* and frugivorous chimpanzees (*Pan troglodytes*) evinced molar occlusal surfaces with similar amounts of pitting (Grine, 1986; Grine and Kay, 1988). This suggested that when in woodland/savanna habitats, *Australopithecus* used the landscape more like baboons (*Papio* spp.) than savanna chimpanzees (*Pan troglodytes*), as the latter tend to focus nearly exclusively on the C<sub>3</sub> resources therein (e.g., tree fruits and leaves; Schoeninger et al., 1999; Sponheimer et al., 2006; Codron et al., 2007). Moreover, carbon isotopes revealed enormous  $\delta^{13}\text{C}$  variability within and between hominin individuals (van der Merwe et al., 2003; Sponheimer et al., 2005a; 2006; Lee-Thorp et al., 2010; Wynn et al., 2013), suggesting remarkable dietary flexibility at both short (e.g., seasonal, yearly) and long (e.g., decadal, millennial) timescales. Only as we neared 4 Ma did we find potential hominins (*Ardipithecus ramidus* and *A. anamensis*) that approximated the low variability and C<sub>3</sub>-dominated diets observed in savanna chimpanzees (White et al., 2009; Cerling et al., 2013a; Loudon et al., 2016).

For many, however, the greatest surprise proffered by carbon isotopic analysis was the finding that *P. boisei* had a diet of over 75% C<sub>4</sub>/CAM resources (e.g., C<sub>4</sub> tropical grasses/sedges, CAM *Euphorbia* and *Aloe*; van der Merwe et al., 2008; Cerling et al., 2011a, 2013a). This presented a two-fold problem. First, this result was markedly different from what had been observed in *P. robustus*, which consumed only about 30% C<sub>4</sub>/CAM vegetation on average (Lee-Thorp et al., 1994; Sponheimer et al., 2005a). This disparity in C<sub>4</sub>/CAM consumption is of the same magnitude seen in coeval *Papio robinsoni* and *Theropithecus oswaldi* in South Africa (Codron et al., 2005). But while *Papio* and *Theropithecus* are highly distinct craniodentally, so that such a dietary difference would be expected, the *Paranthropus* species have been labelled robust australopiths due to their shared craniodental robusticity, although *P. boisei* is characterized by an even greater degree of masticatory hypertrophy (Tobias, 1967; Rak, 1983; Teaford et al., 2002; Smith et al., 2015). Second, *Paranthropus boisei*, aka “Nutcracker man,” was often regarded as a hard object feeder (stress-limited foods like nuts, seeds, and corms) (Tobias, 1967; Rak, 1983; Peters, 1987; Teaford et al., 2002; Smith et al., 2015), but its  $\delta^{13}\text{C}$  values looked like contemporaneous *Theropithecus* and other herbivores that ate primarily, though not exclusively, tough (displacement-limited) grasses (Dunbar, 1983; Lee-Thorp et al., 1989a; Codron et al., 2005; Cerling et al., 2011a, 2013a, 2013b; Fashing et al., 2014; Shapiro et al., 2016; van der Merwe et al., 2008). Moreover, its molar microwear fabrics are low complexity and lightly pitted and hence more resemble those of leaf consuming *Theropithecus* than they do those of modern primates known to consume hard foods (Ungar et al., 2008; Grine et al., 2012; Scott et al., 2012).

So nearly 30 years and more than 200 isotopic analyses later, we are still struggling with the diet of *Paranthropus*. In the 1990s, evidence from morphology, dental microwear, and even carbon isotopes could be interpreted in similar ways, though there were debates as to the degree of its animal food consumption (e.g., Wolpoff, 1973; Sillen, 1992; Lee-Thorp et al., 1994; Mann, 1981). Now, fresh data have called into question old notions of ecological congruity within the genus and have arguably pitted dietary inferences from morphology against those derived from other proxies. We will revisit this controversy and more herein. We will begin by making a brief foray into the topic of diet-enamel isotopic fractionation as this has received attention of late in the hominin-related isotope literature and beyond (Malone et al., 2021; Quinn, 2019; Tejada-Lara et al., 2018). We will follow with a brief history of research on the diet of *P. boisei* and consider the implications of newly available carbon isotope data from the Omo. Lastly, we will reflect on ways that taxa beyond the haplorrhine primates might enrich our understanding of *Paranthropus* diets.

We understand that the focus on *Paranthropus*, and especially *P. boisei*, herein might seem unnecessarily limiting given the myriad ways that diet has been implicated in the origin and extinction of hominin taxa (e.g., Dart, 1925; Foley, 1987; Vrba, 1988; Aiello and Wheeler, 1995; Potts, 1998). Nevertheless, we believe it is readily

justified. After all, there can be little doubt that it is the taxon whose diet has occasioned the most consternation of late (e.g., Rabenold and Pearson, 2011; Macho, 2014; Scott et al., 2014; Yeakel et al., 2014; Smith et al., 2015; Paine et al., 2018). But more importantly, *P. boisei* is the quintessence of the hyper-masticatory trend in australopiths, so unraveling its diet might provide clues to the drivers of dietary evolution in the australopiths broadly. Lastly, it is probably not an overstatement that if we cannot uncover the diet of the hominin with the most distinctive craniodental morphology and a bulk carbon isotope composition that is only compatible with a handful of foods, we have little chance of deciphering the dietary ecology of more generalized hominins whose carbon isotope compositions could have been derived in innumerable ways. Consequently, focusing on *Paranthropus* allows us to take one meaningful step towards a much larger project.

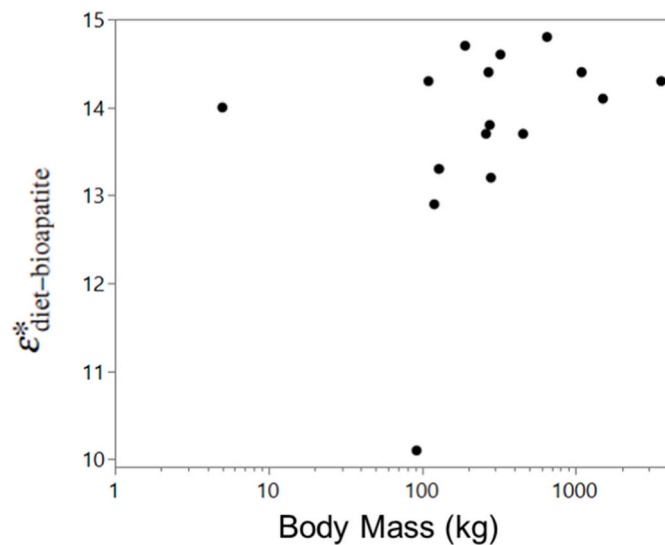
## 2. From food to tooth: a footnote on fractionation

All isotopic studies of hominin diet are predicated on our having reasonable knowledge of the relationship between dietary and enamel carbon isotope compositions (called fractionation or discrimination). Recent studies have called into question some of the assumed fractionations for early hominins and other taxa (e.g., Tejada-Lara et al., 2018; Quinn, 2019; Malone et al., 2021), so it is worth taking a few minutes to address these concerns here. We have long known that fractionation tends to be smaller for diminutive mammals like rodents (about 10‰; DeNiro and Epstein, 1978; Ambrose and DeNiro, 1986; Tieszen and Fagre, 1993) than larger mammals like suids or wildebeest (between about 12 and 14‰; Krueger & Sullivan, 1984; Lee-Thorp et al., 1989b; Balasse et al., 1999; Cerling and Harris, 1999; Passey et al., 2005; Cerling et al., 2021). This difference is largely, but not entirely, the product of differential methane production during digestive processes (see Cerling et al., 2021), as the methane produced is highly depleted in  $^{13}\text{C}$  (Schulze et al., 1997), resulting in  $^{13}\text{C}$ -enrichment of the inorganic carbon in the blood, and consequently, enamel.

Recently, Tejada-Lara et al. (2018) argued that fractionation differences with body size can be approximated with the equation  $\epsilon^* = 2.4 + 0.034 \text{ BM}$ , where  $\epsilon^*$  is apparent fractionation and BM is body mass (kg). We think, however, that there is good reason for caution in applying this to isotopic ecology studies of hominins and contemporaneous fauna. For one, Tejada-Lara et al. (2018) contains marsupial and xenarthran mammals (e.g., koalas and sloths) that are physiologically distinct from the Epitheria we find at early hominin sites. For another, available data on fractionation suggest that above 4 kg there is little evidence that fractionation and body mass are related. As can be seen in Fig. 1, when fractionation for Epitheria is plotted against body mass the relationship is uninspiring. We would argue that fractionation is more closely linked to methane production and differential digestion than to body size per se (see Cerling et al., 2021).

Another recent study calculated fractionation (11.8‰) for chimpanzees at Kibale National Park, Uganda, and suggested this implies greater C<sub>4</sub> consumption in hominins than was appreciated (Malone et al., 2021). We agree that a fractionation of 14‰ (from Cerling and Harris, 1999) is almost certainly inappropriate for most hominins. Indeed, a <14‰ diet-enamel fractionation is consistent with existing data on chimpanzees (Carter, 2001; Smith et al., 2010), baboons, and humans (Lee-Thorp et al., 1989a; Lee-Thorp, 1989; Kellner and Schoeninger, 2007). However, it is crucial to note that few hominin isotopic studies employ a 14‰ fractionation. Most studies have either assumed a 12‰ fractionation based upon Lee-Thorp et al. (1989b) (all earlier studies), made no explicit assumptions about fractionation (e.g., Wynn et al., 2013), or used 13‰ (e.g., Loudon et al., 2016).

But this also raises the question, “Is there a proper fractionation that we should apply to all hominins?” We would argue that the answer is, “Probably not,” and that the notion of a proper species-specific fractionation is a fantasy, albeit often a useful one. Animals living in the same room on the same experimental diet can have apparent diet-tissue



**Fig. 1.** The relationship between  $\epsilon^*$  diet-bioapatite and body mass (kg) for Epitheria over 4 kg (data from Cerling and Harris, 1999; Passey et al., 2005; Tejada-Lara et al., 2018 and references therein). The six lowest  $\epsilon^*$  diet-bioapatite values are for camelids, suids, equids, and ursids—none of the lowest values are for Ruminantia.

fractionations that differ by at least 0.5‰ (Passey et al., 2005). Furthermore, we know that factors like dietary fiber, secondary compound, and digestive microflora differences impact methanogenesis (Jensen and Jørgensen, 1994; Min et al., 2020), so even one individual might have different diet-enamel fractionations over time if its diet or physiological state changes significantly. Moreover, it is possible, or even probable, that fractionation differed between early hominin taxa (Schoeninger, 2014). For instance, if *P. boisei* had microflora and digestive physiology that maximized digestion of refractory dietary components it was probably more methanogenic than either early *Homo* or contemporary chimpanzees and would have had a higher diet-enamel fractionation. Fortunately, however, the observed fractionation differences between large-bodied mammals are sufficiently small that they will engender few interpretive difficulties (see Fig. 1). For example, nothing significantly changes our understanding of *P. boisei* if their diets were 85%, 75%, or even 65%  $C_4$  vegetation. We are faced with the same basic problem—the importance of  $^{13}C$ -enriched resources—either way.

### 3. A brief history of dietary studies

#### 3.1. A tough nut to crack

Despite the “Nutcracker Man” moniker bestowed upon OH 5, the hard-object feeding inference – for australopiths in general and *Paranthropus* in particular – was initially less central to discussions of diet. Leakey (1959) initially thought OH 5 was significantly carnivorous, which fit well with the idea that the stone tools at Olduvai were of *Zinjanthropus*’ making. Dart also mused that South African australopiths were skilled and enthusiastic hunters (Dart, 1957). Robinson (1954) and Du Brul (1977) speculated that the important axis of dietary adaptation among australopiths was one of omnivory and herbivory rather than an increasing reliance on durophagy.

While linkage of australopith craniodental morphology and hard-object feeding existed early on, it only became de rigueur more recently. Evidence cited in support of this idea included 1) the massive and thickly-enamelled postcanine dentition, 2) anteriorly positioned and hypertrophied zygoma, 3) sagittal crests, and 4) massive mandibular corpora with high rami in *Paranthropus* (Rak, 1983; Grine and Kay, 1988; Strait et al., 2013; Smith et al., 2015). But this anatomical evidence had obviously been present for a long time prior, and the notion

on durophagy did not reach fruition until the “Man the Hunter” paradigm began to collapse, in no small measure due to Jolly’s (1970a) gelada analogy. Jolly argued that hominins and *Theropithecus* shared craniodental, manipulatory, and environmental similarities that suggested a dependence on monocots, although in the form of seed rather than grass leaf consumption. He argued this would have initially occurred in dambos where trees are few but high-quality grasses and sedges abound year round. The (implicitly hard) seed-eating adaptation received further support from dental microwear, as some *P. robustus* specimens display highly pitted and complex surfaces that we see in modern primates, such as *Cercocebus atys*, that eat hard foods (Grine and Kay, 1988; Scott et al., 2005, 2012; Daegling et al., 2011).

Recent studies, however, slowed the momentum of the hard object train, and some might argue brought it to a crashing halt. Stable carbon isotope analysis of two *P. boisei* specimens from Tanzania (OH 5 and the Peninj mandible) suggested a diet of nearly 80%  $C_4$ /CAM foods (van der Merwe et al., 2008) that was very different from what had been observed in South African *P. robustus* (Lee-Thorp et al., 1994). This was not only markedly different from expectations for typical primate hard object feeders, but was surprisingly similar to that of broadly contemporaneous grazing warthogs (*Phacochoerus modestus*) (van der Merwe, 2013). Furthermore, all living herbivores with  $\delta^{13}C$  values like those of *P. boisei* specialize on grass (primarily leaf and culm). Indeed, even carnivores that consume principally grazing herbivores (e.g., Serengeti lions) rarely have such high  $\delta^{13}C$  values, although they do get there from time to time (Codron et al., 2007, 2016; Lee-Thorp et al., 2007; Yeakel et al., 2009). So from the perspective of modern mammals, having such high  $\delta^{13}C$  values without grass being a major portion of the diet would be singular. While evidence from carbon isotopes, function morphology, and comparative ecology makes significant animal food consumption in *P. boisei* unlikely, we acknowledge that other isotopic systems and elemental ratios could potentially speak to animal food consumption in *P. boisei*. However, these proxies are not fully developed, beset by diagenesis concerns, or uninterpretable at present (e.g., Martin et al., 2020; Leichliter et al., 2021).

A similar problem arose from studies of *P. boisei*’s occlusal microwear. Remarkably for a reputed “nutcracker,” its microwear lacks complexity, which is very unlike contemporary hard object feeders such as *Cercocebus atys* and *Sapajus apella*, but very similar to folivorous primates like *Alouatta palliata* and *Semnopithecus entellus* (Ungar et al., 2008; Grine et al., 2012; Scott et al., 2012). Most notably, its complexity is virtually identical to that of extant *Theropithecus*, for which the leaves of graminoids are the most eaten foods (Teaford, 1993; Scott et al., 2012; Fashing et al., 2014; Shapiro et al., 2016), and indeed, this would be the default expectation for any primate with evidence of such high  $C_4$ /CAM consumption. It is true that the *P. boisei* has less anisotropy or directionality than *Theropithecus* or other folivores (Ungar et al., 2008; Scott et al., 2012), but that would be expected on morphological grounds given that its flat postcanine dentition would constrain jaw movement less than teeth with well-developed shearing crests. The buccal microwear of *P. boisei* also most resembles that of primate folivores (Martínez et al., 2016), although the interpretation of this is more difficult as its etiology is poorly resolved at present.

This also comports well with evidence from tooth chipping, as the exceptionally low chipping frequency in *P. boisei* (2%) is more similar to that found in colobine folivores (~5%) than primates known to eat hard and/or underground foods like *Cercocebus atys* (60%) and *Papio ursinus* (52%) (Constantino and Konow, 2021; Ungar and Berger, 2018; Fannin et al., 2020; Towle et al., 2021). It also works well from the perspective of resource availability—grasses were abundant everywhere we find *P. boisei* as evidenced by the surfeit of co-occurring grazing ungulates and  $C_4$  consuming *Theropithecus* (Reed, 1997; Alemseged, 2003; Bobe and Eck, 2001). Indeed, *P. boisei* is most closely associated with *Theropithecus oswaldi* and the grazing suid *Metridiochoerus andrewsi* in the Shungura and Koobi Fora formations (Bobe and Behrensmeyer, 2004; Alemseged and Bobe, 2009; Bobe et al., 2022). In short, carbon isotope,



dental microwear, tooth chipping analyses, and comparative mammalian ecology are all consistent with, and in some cases, argue strongly for high levels of tough graminoid consumption by *P. boisei* (we will address hard or stress-limited C<sub>4</sub> foods below).

The only real problem with the consumption of such displacement-limited graminoids for eastern African *Paranthropus* is the argument that its morphology is inconsistent with such a diet. But is it? Arguments have been made from the facial architecture and dentognathic morphology of hominins like *P. boisei* that they were designed for withstanding high magnitude loads associated with hard object feeding, but others have argued that a large number of loads experienced during the consumption of tough foods is consistent with their facial and mandibular morphology (Hylander, 1988; Scott et al., 2014; Daegling and Grine, 2017; Marcé-Nogué et al., 2020). Thus, from the perspective of bone biology, there is nothing to argue that a tough diet is impossible, or in fact, even improbable. Indeed, it is notable that facial and mandibular morphology of *Paranthropus* more closely approximates that of folivorous colobines than hard-object specialists (Daegling et al., 2011).

Hyperthick enamel has also been posited as evidence of durophagy in *Paranthropus* and other primates (Vogel et al., 2008; Lucas et al., 2008; Constantino et al., 2010). However, Rabenold & Pearson (2011) found that enamel thickness was correlated with the quantity of silica phytoliths in primate diets, and hence may be principally a mechanism for resisting abrasion—and the steep wear gradient in *Paranthropus* molars may also indicate an abrasive diet (Grine, 1981; Cerling et al., 2013a). Moreover, if thick enamel was an adaptation for resisting fracture during the consumption of hard foods, enamel microstructure would also be expected to be so optimized. Strong prism decussation might be expected in enamel optimized to resist fracture due to heavy loads as it limits crack propagation (Shimizu et al., 2005; Bajaj and Arola, 2009; but see Macho, 2015), but it is notably lacking in *P. boisei* (Beynon and Wood, 1986; Ramirez Rozzi, 1998). So, once again, there is nothing about the enamel thickness of *P. boisei* that would make tough food consumption impossible.

It is fairly clear that most of the masticatory package of *Paranthropus* is consistent with a diet dominated by tough graminoids. Nonetheless, it is unquestionably true that the flat teeth of *P. boisei* more resemble the teeth of frugivores than those of folivores (Jolly, 1970a; Kay, 1985; Venkataraman et al., 2014). Thus, it is the lack of shearing capability in *Paranthropus*' teeth that presents the only solid argument against the consumption of tough graminoids. We suggest, however, that while the flat teeth of *P. boisei* are not optimal for a diet of tough foods, they might well be better suited for the consumption of such fare than the teeth of its more thinly enameled predecessors. Changes to tooth cusp architecture are genetically complex and require millions of years to effectuate, while numerous lines of evidence suggest that changes in enamel thickness can occur quite quickly (Ungar and Hlusko, 2016). Thus, increased tooth enamel thickness may have been the path of least evolutionary resistance if the ancestors of *Paranthropus* began eating tougher foods—especially as those immediate ancestors already had flatter and more thickly enameled teeth than extant African hominoids. At the very least, this would have made the teeth more resistant to the additional wear necessitated by the larger number of chewing cycles required for a tougher diet. So, while the flat teeth of *P. boisei* may not have been optimal for a tough diet, they may still reflect selection for such diets given their phylogenetic constraints (Daegling and Grine, 2017). And indeed, the steep wear gradient between M1 and M3 on specimens such as OH 5 and the Peninj mandible makes it clear that these teeth are suboptimal. It is well known that excessive tooth wear can impact digestive efficiency and reproductive success (e.g., King et al., 2005) – though clearly these teeth were sufficient for the species to survive about a million years.

### 3.2. Fallback foods to the rescue?

One attempt to harmonize the hard object interpretation from morphology, and contrary evidence from microwear, and to a lesser extent carbon isotopes, is the fallback food hypothesis. The idea is that the morphological interpretations are correct, but that hard object feeding was uncommon or irregular, but adaptively important (Grine et al., 2006; Ungar et al., 2008; Strait et al., 2009, 2013; Smith et al., 2015). In this interpretation, hard fallback foods were consumed during short periods of resource stress, and thus occlusal microwear, which only records a short period of dietary behavior before death (Grine, 1986), might miss these relatively fleeting, if important, dietary excursions. Indeed, this phenomenon has often been noted in the primatological literature. For example, Yamashita (1998) argued that the dental morphology of lemur species better indicates the hardest foods eaten than those consumed most frequently, and Lambert et al. (2004) found that despite large differences in the enamel thickness of *Lophocebus albigena* and *Cercopithecus ascanius*, their diets only differed in hardness during times of fruit scarcity. So, on the face of it, hard fallback foods could explain the apparent discrepancy between morphology and dental microwear. We would argue, however, that in the light of the carbon isotope and tooth chipping data this explanation explains very little—at least for *P. boisei*.

Why? Well let's imagine that *P. boisei* consumed the hard C<sub>3</sub> foods favored by *Cercocebus atys* (*Sacoglottis gabonensis* nuts) and *Sapajus apella* (e.g., *Metrodora stipularis* seeds). We still must explain how this taxon ate about 80% C<sub>4</sub>/CAM foods—and most C<sub>4</sub>/CAM foods are tough. If we take as axiomatic that the flat teeth of *Paranthropus* are poor tools for the mastication of leafy material (Kay, 1985; Strait et al., 2013; but see below), then the C<sub>4</sub>/CAM consumption in *P. boisei* almost has to be some combination of the seeds and underground parts of grasses or sedges—and these foods would have to dominate the *P. boisei* diet given its carbon isotopic composition. The idea that *P. boisei* consumed USOs of C<sub>4</sub> plants like grasses and sedges is also hard to accord with dental microwear, as consumers of USOs tend to have highly pitted enamel (Daegling and Grine, 1999; Scott et al., 2012; but see Shapiro et al., 2016). Such a diet would also be unlike that of any living mammal today, with the closest being USO-specialist mole rats, but even they have trouble reaching the high  $\delta^{13}\text{C}$  values of *P. boisei* (Yeakel et al., 2007; Robb et al., 2012, 2016; Patterson et al., 2016). Moreover, these hard USOs would have to have been selectively important without leaving telltale traces by way of tooth chipping (Constantino and Konow, 2021). This is difficult to imagine, especially as a principal selling point for tooth chipping analysis is that it can reveal infrequent behavior since it is not overwritten like microwear (Constantino et al., 2010).

So a fallback explanation for the hypertrophied masticatory apparatus of *P. boisei* does not work very well: after all, sooty mangabeys crack *Sacoglottis* nuts daily, and their unremarkable papionin faces can produce the needed forces (and withstand the attendant stresses) without apparent difficulty (McGraw et al., 2011). If *P. boisei* were consuming hard C<sub>3</sub> plant parts as fallback foods they still needed to eat tough C<sub>4</sub>/CAM foods to obtain their warthog-like  $\delta^{13}\text{C}$  values—so the morphological problem persists. Or if they ate enough hard C<sub>4</sub> sedge corms to derive their  $\delta^{13}\text{C}$  values these would have constituted the bulk of *P. boisei*'s diet making a fallback argument problematic. It is worth noting that another way to salvage the hard object interpretation from morphology is to argue that hard object feeding does not lead to complex and pitted microwear (Lucas et al., 2013). This does not comport with decades of comparative ecological work in primates, artiodactyls, carnivores, and more, so we will not discuss it further herein (Ungar, 2015; Calandra & Merceron, 2016). However, we think it is important to note that even if this were true, most of the other objections above would still apply. Tough C<sub>4</sub>/CAM foods would have been consumed in abundance, which has been argued to be contrary to the morphological evidence, or abundant C<sub>4</sub>/CAM hard objects would have been consumed, which

would be difficult on ecological grounds and inconsistent with the lack of tooth chipping in *P. boisei*'s molars (Constantino and Konow, 2021).

### 3.3. Update from the Omo

Before we dive deeper into the likely nature of *P. boisei*'s diet, it is important to acknowledge new wrinkles introduced by recently available carbon isotope data from the Omo (86 hominins and hundreds of associated non-hominins) (Wynn et al., 2020; Negash et al., 2020). The Omo *Australopithecus* specimens are similar to coeval *A. afarensis* from Hadar and *Kenyanthropus platyops* from Turkana in that they are isotopically variable—ranging from C<sub>4</sub>/CAM dominated diets to near pure C<sub>3</sub> ones, yet they are more C<sub>3</sub> on average (−9.5‰ vs. −7.4 and −6.2‰). The greater consumption of C<sub>3</sub> vegetation makes sense in light of isotopic, taxonomic, and ecomorphological studies pointing to closed and wet environments during Shungura Member B (Reed, 1997; Bobe and Eck, 2001; Alemseged, 2003; Cerling et al., 2011b; Barr, 2015; Negash et al., 2020). *Homo* from the Omo, in contrast, is unexpectedly C<sub>4</sub>/CAM dominant (−2.7‰). Most *Homo* specimens from Turkana and South Africa indicate much less consumption of <sup>13</sup>C-enriched foods (Lee-Thorp et al., 2000; Cerling et al., 2013a). This is especially perplexing as the Omo specimens inhabited areas with fewer C<sub>4</sub> resources (Bobe, 2006; Cerling et al., 2011b). There is not enough evidence from morphology, microwear, or other sources to make sense of this at present, and the Omo hominins had more surprises in store. The earliest *Paranthropus* specimens, presumably *P. aethiopicus*, preserve little evidence of C<sub>4</sub>/CAM consumption, unlike contemporaneous *P. aethiopicus* from Turkana, which are already over 50% C<sub>4</sub> consumers (Wynn et al., 2020; Cerling et al., 2013a). Even more unexpectedly, there is a major change in the <sup>13</sup>C values of late *P. aethiopicus* from the Omo—after about 2.37 Ma the taxon's carbon isotope composition indicates C<sub>4</sub>-dominated diets like *P. boisei* in the Omo and Turkana (Fig. 2). During Members C & D *Paranthropus* is most associated with *Parapapio* (primarily a C<sub>3</sub>-consumer), but thereafter its closest association switches to *Theropithecus oswaldi* (primarily a C<sub>4</sub>-consumer), so some increase in the proportion of C<sub>4</sub> foods eaten might be anticipated from a habitat perspective (Bobe and Behrensmeyer, 2004).

However, there is no evidence elsewhere of such strong isotopic shifts within a hominin genus over time. Smaller changes exist, such as those within Kenyan early *Homo*, but they are much smaller and may

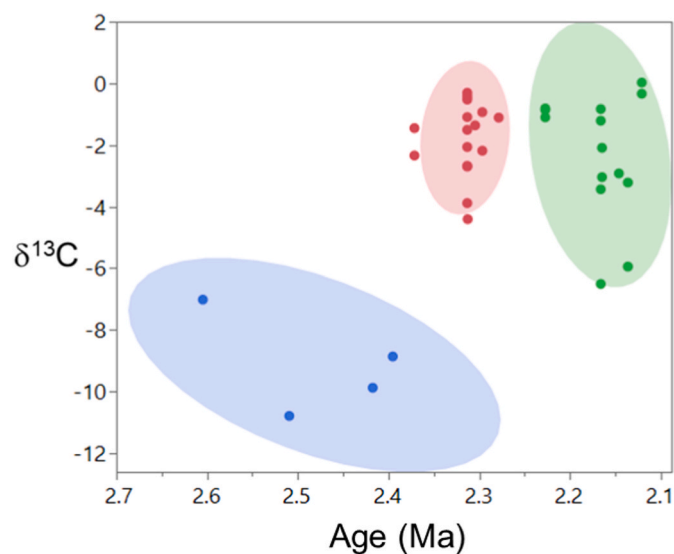


Fig. 2. Carbon isotope composition of early *P. aethiopicus* (blue), late *P. aethiopicus* (red), and *P. boisei* from the Omo. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

occur across multiple species (*H. rudolfensis*, *H. habilis*, *H. erectus*) with divergent dietary proclivities (Patterson et al., 2019). There are also changes in the <sup>13</sup>C values of associated fauna, some of which are occurring over the same period, but these tend to be much smaller (Negash et al., 2020). Indeed, there is a much greater change in the Hominidae than in other families (Fig. 3), and it is not associated with either taxonomic or morphological change that might signal a transition in hominin dietary adaptations.

To put this in perspective, this switch from C<sub>3</sub> to C<sub>4</sub> consumption is so massive that it is larger than that seen in grazing Equidae (~6.5‰) when C<sub>4</sub> grasses first became important components of African ecosystems after 10 Ma (Uno et al., 2011). And in the case of Miocene African equids, there need not have been any meaningful change in their diets given that C<sub>4</sub> grasses may have supplanted C<sub>3</sub> grasses due to decreasing global CO<sub>2</sub> concentrations (Feakins et al., 2013; Uno et al., 2016). As no changes of this scale are found in other families from the Omo (Negash et al., 2020), it is unlikely that the change in *Paranthropus* simply reflects changes in the photosynthetic pathways of available grasses. It is, nevertheless, plausible that a loss in the abundance of wetland- or river-associated C<sub>3</sub> grasses like *Phragmites*, which could occur due to local tectonic activity rather than climate change, could have led to increased C<sub>4</sub> graminoid consumption if *Paranthropus* had a greater predilection for moist environs than most grazing herbivores. Shifts in the relative proportions of C<sub>3</sub> and C<sub>4</sub> sedges could also be invoked to explain this change. Controls of sedge isotopic compositions are different from those of grasses. In both eastern Africa and southern Africa the vast majority of savanna grass biomass uses C<sub>4</sub> photosynthesis (e.g., Codron et al., 2005b; Uno et al., 2016), whereas sedges can be mostly C<sub>3</sub> in southern Africa (Stock et al., 2004; Sponheimer et al., 2005a) but predominantly C<sub>4</sub> in eastern Africa (Hesla et al., 1982). The primary driver of this difference is probably the higher temperatures in eastern Africa, as temperature increases have been linked to greater percentages of C<sub>4</sub> sedges across multiple continents (Teeri et al., 1980; Ueno and Takeda, 1992; Stock et al., 2004). But subtle changes in climate, tectonics, soil nutrients, hydrology, or some combination thereof, could plausibly lead to a large change in the abundance of C<sub>4</sub> sedges (e.g., Kotze & O'Connor, 2000). There were transformations in the Omo depositional environment at this time and a burgeoning dominance of Reduncini, especially *Menelekia* (Clark Howell et al., 1987; Bobe and Eck, 2001), so the possibility of changing hydrology and a concomitant transition in the abundance and type of wetland resources cannot be dismissed.

This major isotopic shift within *P. aethiopicus*, with a lack of accompanying evidence for concomitant morphological change in its posterior dentition, may also make it less tenable to argue that the

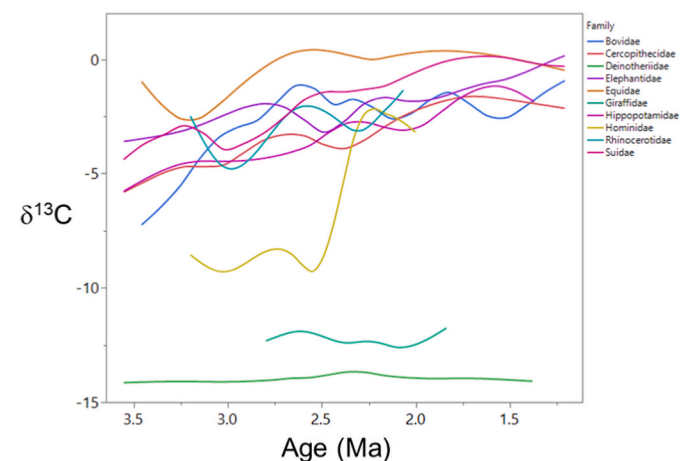


Fig. 3. Smoothed fits of Family <sup>13</sup>C values from the Omo (Negash et al., 2020; Wynn et al., 2020). Note the large jump at about 2.4 Ma within the Hominidae and the much smaller change, lack of change, or even opposite direction of change in other families at that time.

material properties of foods consumed changed during this transition. This argument would be stronger if we had evidence of cranial or mandibular morphology across the 2.37 Ma boundary, but the paucity of such evidence for *P. aethiopicus* outside of Omo 18-1967-18 and KNM-WT 17000 (the “Black Skull”) (Constantino et al., 2010) makes it impossible to evaluate. Dental microwear would also be ideal for testing the hypothesis for changes in food mechanical properties but is untenable at present given the extensive post-depositional damage in the Omo hominins analyzed thus far (Ungar et al., 2008). Fortunately, tooth chipping data are available for *P. aethiopicus* and they suggest a lack of hard foods in its diet as was found in *P. boisei* (Constantino and Konow, 2021). So evidence for mechanical change within eastern African *Paranthropus* is currently non-existent. We cannot, however, rule out the possibility of exaptation at present, in which early *Paranthropus* or an earlier ancestor was a hard object feeder, and the attendant masticatory morphology was ultimately co-opted for the consumption of tough foods. In this scenario, subsequent change to C<sub>4</sub>/CAM foods could have begun with those of similar mechanical properties to C<sub>3</sub> hard objects such as grass seed, rhizomes, or sedge USOs (Jolly, 1970a; Dominy et al., 2008; Paine et al., 2018). However, the story of a co-opted masticatory apparatus is unconvincing for multiple reasons. For one, these foods are either in relatively low abundance seasonally (e.g., grass seeds) or difficult to square with data from dental microwear and tooth chipping (e.g., rhizomes, corms; Daegling and Grine, 1999; Constantino and Konow, 2021). Moreover, dental microwear and tooth chipping studies of *A. afarensis*, the likely lineal ancestor of *Paranthropus*, revealed no hard object signal (Grine et al., 2006, 2012; Constantino and Konow, 2021). It is also notable that from the perspective of modern herbivores, having such high  $\delta^{13}\text{C}$  values without the above ground portion of grass being a major component of the diet would be singular.

All told, there are many reasons to doubt that *P. aethiopicus* and *P. boisei* ate hard foods, or that they inherited the rudiments of their masticatory package from a hard object feeding ancestor. There are fewer reasons to doubt the consumption of tough foods, and current evidence is consistent with the notion that increasing consumption of tough foods drove the evolution of the australopith masticatory package. Therefore, it behooves us to ask if there are ways that *Paranthropus* could have consumed tough grass or sedge material that are congruent with its morphology. One way to proceed is to look for lessons from beyond the haplorhine primates that form the comparative basis for most studies of hominin diets.

#### 4. Lessons from the phylogenetic hinterlands

Attempts to reconstruct the ecology of fossil taxa are perforce grounded in the comparative method. If we find, for instance, that the degree of shearing crest development in catarrhine primates can be used to discriminate between folivores and frugivores, and that there are sound functional reasons for this discriminating power, we are happy to use this trait to ascribe dietary behavior to fossil catarrhines (Anthony and Kay, 1993). Nevertheless, it is a mistake to think that there can be only one solution to a particular adaptive problem. As noted by Anthony and Kay (1993), the discovery of a primate that solved the problem of folivory through digestive tract modification rather than increased molar shear would not falsify our ideas of this morphology-diet relationship. It might, however, force us to acknowledge that contemporary primates might provide an incomplete snapshot of the order’s historical adaptive diversity. This is the curse of presentism. It is reasonable to assume that most ancient species will solve adaptive problems in ways like those of their closest surviving kin, but if we are faced with multiple lines of evidence that suggest that our understanding of a form-function relationship is wanting for a given taxon, we should be willing to look for alternate solutions to the adaptive problem in question. And a productive way to do this would be to broaden the taxonomic scope to glean hints from nature’s cornucopia, even if from phylogenetically distant sources. So with regard to *P. boisei*, which we know has a combination of

carbon isotope composition, microwear, tooth chipping, morphology, and more that are in toto unmatched in contemporary primates, we should be willing to look beyond the primates to try to make sense of its perplexity. And, indeed, researchers have looked to bears (Hatley and Kappelman, 1980; Du Brul, 1977), pigs (Hatley and Kappelman, 1980), tapirs (DeSantis et al., 2020), carnivores (Thompson, 1975; Szalay, 1975; Schaller and Lowther, 1969), and sea otters (Constantino et al., 2011) to address questions about the dietary adaptations of early hominins.

Sea otters (*Enhydra lutris*) have garnered interest in this regard because, outside of the primates, their bunodont molars are among the most similar to those we find in australopiths (Walker, 1981). An additional inducement to their study is that they are consumers of hard foods including mollusks, crabs, and sea urchins, which may be mechanically analogous to the hard nuts and seeds that some believe underlie the evolution of dentognathic hypertrophy in robust australopiths. It is notable, however, that their enamel is much thinner than that of *Paranthropus* and more prone to fracture (Constantino et al., 2011), suggesting that robust australopith molars were optimized for higher loads, or potentially, for resistance to abrasion that is the concomitant of diets requiring repetitive loading (Rabenold and Pearson, 2011). The dental adaptations of other marine mammals may also prove illustrative in other ways. Manatees (*Trichechus* spp.) have bilophodont teeth comparable to those of savanna baboons which they use to process a diet of seagrass (Marsh et al., 1999; Allen et al., 2018). Their teeth lack the shearing potential associated with folivory in terrestrial mammals, but in compensation, they have a system of horizontal tooth replacement with the addition of supernumerary molars that prolongs the life of their dental batteries (Domning, 1982). Seagrass also has less fiber and is more friable than terrestrial grass (Lanyon and Sanson, 2006a). With such facilitation the manatee’s occlusal morphology is clearly fit for the purpose of seagrass comminution.

More remarkable is their fellow sirenian the dugong. Dugongs (*Dugong dugon*) also consume primarily seagrass (Marsh et al., 1999; André and Lawler, 2003; Lanyon and Sanson, 2006b) and their molars have exceptionally thin enamel that is worn away soon after birth, leaving them with flat dentine nubs. Moreover, the exposed dentine is much softer than that found in terrestrial herbivores (Lanyon and Sanson, 2006b), presumably leading to faster wear albeit in ever-growing teeth (hypselodonty). Dugongs also have horny pads that aid in transporting seagrass through the mouth and mechanical breakdown. No one would argue that either of these grass eaters can serve as referential analogs for early hominins or any other primate, yet they demonstrate that closely related taxa can solve similar dietary problems in vastly different ways. Their diets also remind us that grasses are not monolithic. Among savanna grasses, there are some that are astonishingly tough, while others are the consistency of lettuce or ripe fruit (Paine et al., 2018, 2019). Thus, when we talk about *P. boisei* as a potential consumer of grasses, we need not assume it would have required teeth fit to process the foods eaten by zebra or even geladas.

Du Brul (1977) noted that craniodental adaptations in pandas (*Ailuropoda melanoleuca*) are also well developed in *Paranthropus*. These include a flattened face, flaring zygomatic arches, massive temporalis muscles, and expanded and rounded (by carnivore standards) molars and premolars. This convergence invites speculation that the highly derived masticatory systems of *Paranthropus* and pandas are responses to similar mechanical demands. For pandas, this is the need to process large amounts of tough bamboo (C<sub>3</sub> grasses that can be hard depending on part and phenophase) (Yamashita et al., 2009). The teeth of pandas are very different from those we find in grass-eating ungulates or primates (Davis, 1964), which is to be expected given their phylogenetic inheritance from omnivorous ursid ancestors. But if we can allow that the panda is not dentally optimized for consumption of its staple food given its phylogenetic baggage, is it inconceivable that *P. boisei*, with its flat teeth, also had a predilection for graminoids?

In considering this question we need to go beyond hard tissue



morphology and food mechanical properties to understand how pandas really do what they do from the perspective of dietary adaptation. Pandas digest the bamboo astonishingly poorly—they digest only 20%–30% of what they ingest (Dierenfeld et al., 1982; Ssensu et al., 2007; Sims et al., 2007; Finley et al., 2011). Ruminant grazers and primate folivores including geladas, on the other hand, typically digest 60–80% of the dry matter they consume (Robbins, 1983; Dunbar and Bose, 1991; Iwamoto, 1993; Edwards and Ullrey, 1999; Remis and Dierenfeld, 2004). Given pandas' pathetic digestive performance, they have very different digestive strategies than most graminoid consumers. They pass bamboo through their digestive tracts very quickly, typically within 12 h, and in so doing make little attempt to digest the refractory components of their diets. Indeed, panda gut microflora shows little ability to break down plant cell walls (Ssensu et al., 2014), although they do appear to have some efficacy in breaking down secondary cyanide compounds in bamboo (Zhu et al., 2018). Thus, the panda's digestive strategy is to eat massive quantities of bamboo to access easily obtained cell solubles and pass the remaining fraction quickly and largely intact (Schaller et al., 1985).

If *P. boisei* ate food that its dental battery was ill-equipped to process, could it have followed a related, if less extreme, digestive strategy? Perhaps breaking down vegetation just enough to access suitable quantities of cell solubles while passing it through its digestive tract very quickly? This would have required the consumption of massive amounts of vegetation and would certainly be consistent with the thick enamel and high wear gradient on their molars. This might seem unlikely as short transit times are not typically observed in hominoids (Lambert, 1998), although there is no reason that selection could not favor changes in a hominoid's digestive kinetics. Chimpanzees and orangutans (*Pongo* spp.) handle foods with highly indigestible components in a different way—they chew it to obtain cell solubles and excrete the remaining residual wadge (Tutin et al., 1997; Remis and Dierenfeld, 2004; Dominy et al., 2008; Vogel et al., 2008; Yamagiwa and Basabose, 2009). Humans eating the rhizomes of the  $C_4$  sedge papyrus (*Cyperus papyrus*) do the same (van der Merwe et al., 2008). If a primate were to do this regularly it would present a considerable challenge to its masticatory apparatus and would be evoked the panda digestive strategy, only the refractory material would be leaving from the front rather than the back end. Once again, this might appear to be an unlikely strategy, but given the perplexing constellation of data we possess on the diet and masticatory adaptations of *P. boisei*, should we be expecting the unexpected? Others have asked about the possibility that *P. boisei* practiced coprophagy to maximize assimilation of complex carbohydrates with the added benefit of providing vitamins, minerals, and amino acids (see Soave and Brand, 1991). Coprophagy is practiced by hominoids in the wild, although it is mostly focused on the consumption of seeds ostensibly softened by passage through the digestive tract and never represents more than a small fraction of the diet (Harcourt and Stewart, 1978; Krief et al., 2004; Sakamaki, 2010). And while sitatunga (*Tragelaphus spekei*) and river hogs (*Potamochoerus porcus*) consume surprising quantities of large seeds from forest elephant (*Loxodonta cyclotis*) dung in streams (Magliocca et al., 2003), we think such behavior was unlikely to have been of adaptive significance for *P. boisei*, or that the “Nutcracker Man” moniker will need to be updated to something scatologically tinged.

A little closer to our phylogenetic home we find the curious case of *Hadropithecus stenognathus*. *Hadropithecus* shares masticatory features with *Paranthropus* including a short face, flaring zygoma, small anterior dentition coupled with molarized premolars and large molars, and thick mandibular corpora with high ascending rami (Jolly, 1970b; Godfrey et al., 2016). In contrast, *Hadropithecus* is notably different from robust australopiths in having much thinner enamel and occlusal morphology more like that of *Theropithecus*, and thus more like a classic tough food consumer. Given our earlier discussion of how most of *Paranthropus*' masticatory architecture is consistent with tough foods, and the fact that *Hadropithecus*' occlusal morphology is like that of folivores, one might imagine that *Hadropithecus* had a gelada-like dependence on grass.

Carbon isotope data for the taxon are largely consistent with this, but its  $\delta^{15}\text{N}$  values are higher than would be expected from grass consumers, leading to speculation that *Hadropithecus* was a specialist on CAM vegetation (Godfrey et al., 2016). As unique as this would be from the perspective of comparative mammalian ecology, there are several points in its favor beyond the fact that this is one of the few diets that works with its known isotopic composition. The most important of these is that Madagascar has spiny forests in which CAM plants from the Didiereoideae and Euphorbiaceae are important components (Winter, 1979; Waeber et al., 2015). The Didiereoideae are particularly important in this context as their leaves are protected by spines that closely related species from mainland Africa lack (Applequist and Wallace, 2003). This suggests significant predation was experienced by the Madagascan clade (Cooper and Owen-Smith, 1986), even if today they experience only light predation by *Lemur catta* and *Propithecus verreauxi* (Norscia and Palagi, 2011; LaFleur and Sautner, 2015). In fact, *Hadropithecus* is the only species we know that presumably had the capacity and stable isotope compositions to have predated upon these CAM plants regularly (Crowley and Godfrey, 2013).

Could *Paranthropus* have consumed CAM leaves too? There is reason to believe that CAM plants existed in the vicinity of early hominins. Indeed, the eponymous Olduvai Gorge derives its name from Oldupai (*Sansevieria ehrenbergii*), a succulent CAM plant. Modern baboons consume it sparingly (~1% of time spent feeding; Barton et al., 1993), and humans are more likely to use it as rope or antiseptic than they are for food (Khalumba et al., 2005). African savanna primates eat other CAM plants, especially *Euphorbia*, though they are typically a small fraction of their diets (Barton et al., 1993; Codron et al., 2006; Lent et al., 2010). The low levels of CAM plant consumption among most primates is unsurprising given that they are often toxic, unpalatable, and a small fraction of available plant biomass (Peters and Vogel, 2005; Johnson et al., 2006), although CAM plants can be abundant in a few places such as the Cape Floristic Region of South Africa (van der Merwe et al., 1990; Cowling et al., 2004). Outside of *Euphorbias*, some of the best CAM targets for hominins would be the corms of *Isoetes* in seasonal wetlands, and the flowers, nectar, and leaves of *Aloe* in drier habitats, although the latter are considered purgatives (van Wyk and Gricke, 2000; Peters and Vogel, 2005). So, in short, there is little reason to think that CAM plants would have been available in sufficient abundance or would have been palatable enough to have had a large and consistent impact on the carbon isotope composition of *P. boisei* or any other early hominin.

Lastly, despite the convergence evident in *Paranthropus* and *Hadropithecus*, and even the likelihood that both processed large quantities of displacement-limited vegetation, it is likely that their digestive strategies would have been very different given the dissimilarity in their occlusal morphology. The high shear in the molars of *Hadropithecus* would allow reduction of ingested food to finer particles than would the flat teeth of *Paranthropus* leading to faster and/or more complete digestion (Clauss and Hummel, 2005; Fritz et al., 2009; Matsuda et al., 2014). In fact, this appears to be one of the chief digestive differences between living *Papio* and *Theropithecus*. Both taxa can eat the same foods and display similar rates of microbial fermentation (Mau et al., 2011), but the teeth of *Theropithecus* enable it to break ingesta down to finer particles than can *Papio* (Dunbar and Bose, 1991). So the occlusal morphology of *Hadropithecus* would allow a digestive strategy similar to that of bamboo-eating *Hapalemur* which has a higher digestive efficiency and slower food passage rate than other Malagasy primates (Overdorff and Rasmussen, 1995; Campbell et al., 2004). A dietary strategy focused on quantity rather than digestive efficiency might have made more sense for *P. boisei* given its flat molars and would also be consistent with its hyperthick yet heavily worn enamel. The alternative, slowing the passage rate to allow more time for digesting much larger particles, is possible in principle for very large animals (e.g., sauropod dinosaurs) and those with low metabolic rates (e.g., herbivorous lizards), but would be energetically unrealistic in a hominoid (Karasov et al., 1986; Franz et al., 2009).

## 5. Conclusions

Conversations about the diet of *Paranthropus* have come a long way since the original carbon isotope study of Lee-Thorp et al. (1994). We have had to wrestle collectively with isotopic, dental microwear, and tooth chipping studies that have not always confirmed expectations. And while our understanding of robust australopith ecology remains nascent, one lesson is clear. The inference of behavior from morphology can be complicated. Few would surmise that goats in the Argan tree woodlands of Morocco spend over 70% of their time feeding in trees from the principles of biomechanics, but despite the functional implausibility of such behavior, and the goats' phylogenetic distance from arboreal taxa, they forge right ahead (El Aich et al., 2007). Form-function relationships will remain the bedrock of paleoecological inquiry, but the structuralist approach of Lauder (1981) and others in the late 20th century offers a sober response to unbridled functionalist logic: constraint is real and is discoverable in the investigation of development and phylogeny.

What this means with respect to *Paranthropus* is not entirely clear. However, a shift from trying to understand if robust australopiths could consume tough foods, to understanding how they might have done so, might be rewarding. Furthermore, while paleodietary proxy studies from isotopes and microwear may continue to shape our understanding of the ecology of ancient hominins, it is worth considering if they may help us develop a sounder basis for functional interpretation from hominin morphology. Perhaps not. But still, conventional fixed-wing aerodynamic theory suggested that bees should not be able to fly (Magnan, 1934). The reply to this counterfactual was not to be found in the domain of Harry Potter, but in continued observation and experimentation leading to the discovery of the physical principles that permitted a life aloft (e.g., Altshuler et al., 2005).

As for the diet of *Paranthropus*, continued investigation of the abundance, nutritional, and mechanical properties of plant foods should prove revealing about the diets of its eastern and southern African representatives. Is it possible, for instance, that a greater abundance of highly digestible C<sub>4</sub> foods in eastern Africa could underlie the higher  $\delta^{13}\text{C}$  values in *P. boisei* than in *P. robustus* (Paine et al., 2019)? And could the longer dry season and relatively poor dolomitic soils of the Sterkfontein Valley have required *P. robustus* to consume seeds, nuts, or USOs seasonally, while hard and/or gritty fallback resources were superfluous given the richer volcanic soils of eastern Africa, explaining the lack of complexity in *P. boisei*'s microwear (Scott et al., 2005; Ungar et al., 2008; Paine et al., 2019)? Furthermore, do we really understand the dietary differences of *P. robustus* and *P. boisei*? We have a paleodietary proxy record for *Paranthropus* in eastern Africa spanning more than a million years and over a thousand kilometers, and the variation observed therein is relatively limited—generally (though not always) less than the amount we see in *Theropithecus*. For *P. robustus*, in contrast, we have data from specimens that were found within 6 km of each other and which suggest greater dietary variability. Would a broader sample of *P. robustus* reveal that its dietary behavior was similar to that of *P. boisei* when in comparable ecosystems?

Finally, it is difficult to look at the totality of evidence for *P. boisei*'s diet and see just another primate. The present diversity within Primates does not comfortably encompass what we see in *P. boisei*, *H. stenognathus*, and a host of other taxa. Extant primates must inform, but should not narrowly circumscribe the behaviors we ascribe to extinct taxa. Lessons from beyond the primates may be especially important when considering the ways that food material properties, masticatory morphology, and digestive kinetics interact, as modern primates remain understudied in this regard.

## Author contributions

MS, DD, PU, RB and OP designed and performed the relevant research for this review paper. All authors wrote and reviewed the

manuscript.

## Data availability

This review uses previously published data. The data are freely available in the references cited and will be provided upon request to those who cannot access pay-for-access journals.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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