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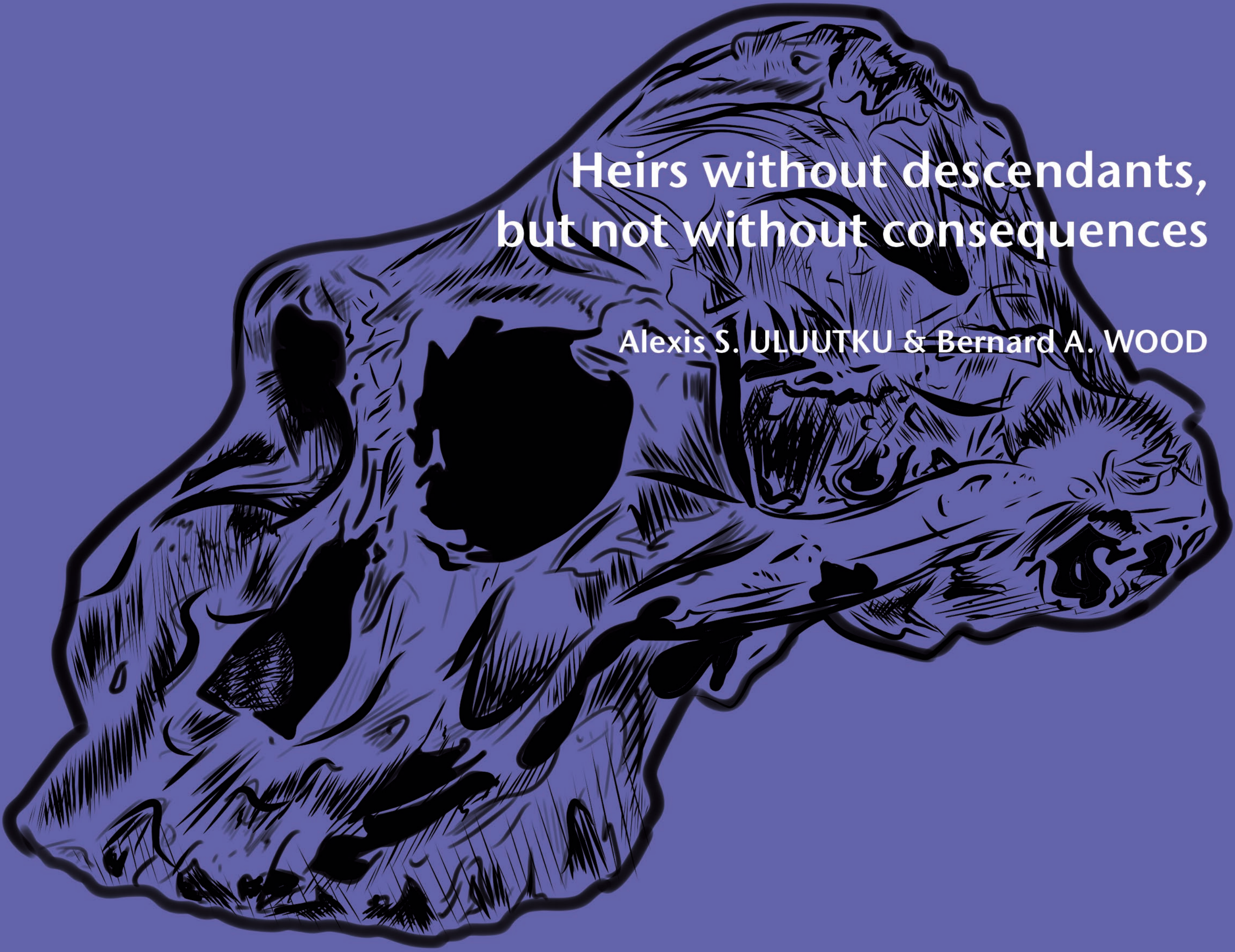

Heirs without descendants, but not without consequences

Alexis S. ULUUTKU & Bernard A. WOOD

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Heirs without descendants, but not without consequences

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ABSTRACT

In 1967, Camille Arambourg and Yves Coppens reported the discovery of an edentulous adult mandible from the Lower Omo Valley in Ethiopia. A year later they made it the type specimen of *Paraustralopithecus aethiopicus* (Arambourg & Coppens, 1968), claiming its morphology differed from other early hominins, including *Paranthropus boisei* (Robinson, 1960). Most researchers now include the type specimen and the hypodigm in the genus *Paranthropus* Broom, 1938 as either a separate species, or as part of an inclusive interpretation of *P. boisei* (i.e., *P. boisei sensu lato*). After briefly reviewing what is known about *P. boisei* and *P. aethiopicus* we suggest how interactions between those taxa and early *Homo* may have influenced the latter's evolutionary history. Although *Paranthropus* likely left no descendants, it may have made a critical contribution to our own evolutionary history.

KEY WORDS
Hominins,
Paranthropus,
early *Homo*,
taxonomy,
paleoecology,
competition,
evolution.

RÉSUMÉ

Héritiers sans descendance, mais pas sans conséquences.

En 1967, Camille Arambourg et Yves Coppens présentent la découverte d'une mandibule d'adulte édentée dans la basse vallée de l'Omo en Éthiopie. Un an plus tard, ils en font le spécimen type de *Paraustralopithecus aethiopicus* (Arambourg & Coppens, 1968), affirmant que sa morphologie différait de celle d'autres hominines primitifs, dont *Paranthropus boisei* (Robinson, 1960). La plupart des chercheurs incluent désormais le spécimen type et l'hypodigme dans le genre *Paranthropus* Broom, 1938, soit en tant qu'espèce distincte (i.e., *P. aethiopicus*), soit dans le cadre d'une interprétation inclusive de *P. boisei* (i.e., *P. boisei sensu lato*). Après avoir brièvement passé en revue nos connaissances sur *P. boisei* et *P. aethiopicus*, nous suggérons comment les interactions entre ces taxons et les premiers *Homo* ont pu influencer l'histoire évolutive de ces derniers. Bien que *Paranthropus* n'ait probablement pas laissé de descendants, il pourrait avoir apporté une contribution essentielle à notre propre histoire évolutive.

MOTS CLÉS
Hominins,
Paranthropus,
premiers *Homo*,
taxonomie,
paléoécologie,
compétition,
évolution.

INTRODUCTION

The species to which Lucy belongs, *Australopithecus afarensis* Johanson, White & Coppens, 1978, is currently the best candidate to be the common ancestor of later hominins, including the clade comprising *Homo* Linnaeus, 1758 and megadont/hyper-megadont hominins most researchers include in the genus *Paranthropus* Broom, 1938 (Suwa *et al.* 1996; Strait *et al.* 1997). The first fossil evidence of a hyper-megadont hominin (i.e., a hominin with absolutely and relatively large post-canine tooth crowns) in eastern Africa came in 1955 with the recovery of two deciduous teeth from locality BK in Lower Bed II at Olduvai (also called Oldupai) Gorge in Tanzania (Leakey 1958a).

The significance of the exceptionally large size of the OH 3 deciduous maxillary molar (Leakey 1958b) became clearer in 1959 when Mary Leakey noticed fragments of a cranium on the surface at locality FLK in Bed I at Olduvai. After the fragments were painstakingly reassembled, it was apparent they belonged to a mostly well-preserved and undistorted hominin cranium, OH 5, with exceptionally large post-canine tooth crowns (Leakey 1959). The combination of open sutures and partially-erupted third molars, together with well-developed sagittal crests, and a large, wide, and tall face, all pointed to the OH 5 cranium being a sub-adult male of a hitherto unknown hominin species.

The new species was initially included in its own genus as *Zinjanthropus boisei* (Leakey, 1959), but it is now known as *Australopithecus boisei* (Tobias, 1967) or *Paranthropus boisei* (Robinson, 1960). Since the discovery of OH 5, cranial (e.g. OH 26, 30, 32, 38, 46 and 60) and postcranial (e.g. OH 8, 10, 36) fossils, and an associated skeleton (OH 80) from Olduvai, as well as fossils from Peninj, Chesowanja and Konso, have been added to the *P. boisei* hypodigm (Fig. 1).

OMO-TURKANA BASIN

The majority of the eastern African fossil evidence for *Paranthropus* – and the evidence we focus on here – comes from sites in the Omo-Turkana Basin. Among the first evidence recovered there was a mandible (Omo 18-1967-18) from Member C of the Shungura Formation (Arambourg & Coppens 1967). Its discoverers pointed to its unusually low and thick corpus, distinctive symphyseal profile and V-shaped dental arcade as reasons why the mandible could not readily be accommodated within *P. boisei*, so they made it the holotype of a novel species and genus, *Paraustralopithecus aethiopicus* (Arambourg & Coppens, 1968) (Fig. 2). The generic distinction was soon abandoned, and if researchers want to distinguish this material from *P. boisei*, they refer to it as *Paranthropus aethiopicus* (see below). The following year, fossil evidence resembling *P. boisei* began to be recovered from the east side of what was then called Lake Rudolf (now Lake Turkana), and along with evidence subsequently recovered from sites on the west side of the lake, this material makes up the bulk of the hypodigm of *P. boisei* (Wood & Constantino 2007; Wood & Leakey 2011).

Nearly two decades after the discovery of the holotype of *P. aethiopicus*, a distinctive *c.*2.5 Ma-old cranium (KNM-WT 17000) with large post-canine tooth roots and large ectocranial crests, was recovered from West Turkana (Walker *et al.* 1986). Because the presumed male KNM-WT 17000 cranium differed from presumed male *P. boisei* crania in having a more prognathic face, larger incisors and canines, and an elongated and flat cranial base, researchers naturally considered whether this new evidence should also be assigned to *P. aethiopicus*. Two years later, Suwa (1988) suggested the less derived post-canine tooth crown morphology of the pre-2.3 Ma sample of eastern African *Paranthropus* warranted the recognition of a separate species, and Wood *et al.* (1994) found that several features of the mandible and the mandibular dentition of *Paranthropus* also changed around 2.3 Ma. Both studies supported the interpretation that the "early" and the "late" stages of the hyper-megadont archaic lineage in eastern Africa should be recognized as different species, with the earlier taxon taking the available species name *Paranthropus aethiopicus* (Wood & Chamberlain 1987). What looks from the preserved alveolar morphology to be a hyper-megadont archaic hominin maxilla recovered from Malema in Malawi (Kullmer *et al.* 1999), and a right maxillary fragment and a proximal tibia from the *c.* 2.66 Ma Upper Ndolanya Beds at Laetoli, may also belong to *P. aethiopicus* (Harrison 2011).

Researchers who do not consider the differences between the pre-2.3 Ma and post-2.3 Ma eastern African *Paranthropus* fossils merit specific recognition combine the two samples within *Paranthropus boisei sensu lato.* Although views differ about the alpha taxonomy of *Paranthropus* in eastern Africa, and whether *P. boisei sensu lato* and *Paranthopus robustus* are sister taxa, there is unanimity that "it is very unlikely that *any Paranthropus* taxon was the direct ancestor of modern humans" (Wood & Schroer 2017: 105). *Paranthropus* had no descendants, but in both eastern and southern Africa it was almost certainly sympatric with early hominins that are more credible candidates for being ancestral to modern humans.

PARANTHROPUS BOISEI SENSU LATO AND EARLY *HOMO* IN THE OMO-TURKANA BASIN

When the fossil evidence from the Shungura Formation is combined with evidence from localities on the east and west side of Lake Turkana, the first appearance of *P. boisei sensu lato* in the Omo-Turkana Basin is in Shungura Member C (e.g. L62-17 and L55-33) (Bobe & Wood 2021) dating to *c.* 2.7 Ma. Its last appearance is fossil evidence from sediments at Ileret on the east side of the lake that are dated to *c.* 1.4 Ma (McDougall *et al.* 2012). The earliest fossil evidence for *Homo* sp. in the Omo-Turkana Basin is from the Shungura Formation (Suwa *et al.* 1996) and the Nachukui Formation (Prat *et al.* 2005), both of which date to *c.* 2.4 Ma. The most recent evidence, which consists of fossils assigned to *Homo ergaster* Groves & Mazák, 1975 from the Nachukui Formation, is just over 1.4 Ma (McDougall *et al.* 2012). Thus, within the Omo-Turkana Basin there is approximately at least one million years of temporal overlap between *Paranthropus* and *Homo*.

PARANTHROPUS AS COMPETITOR

It has been suggested that hominins were too specialized and/or too reliant on culture, to be governed by the ecological principles that apply to non-hominin mammals (Wolpoff 1968; Potts 1998). The first attempt to apply ecological principles to the alpha taxonomy of the hominin fossil record used Ernst Mayr's principle of competitive exclusion (Mayr 1950). Researchers suggested that intense competition would prevent the survival of more than one species of bipedal hominin. This application of the principle of competitive exclusion that came to be known as the "single-species concept" (Wolpoff 1971).

It is now almost universally accepted that synchronic variation within the samples of hominins from sites in eastern Africa during the Pleistocene is too great to be accommodated within a single species (Leakey & Walker 1976). Instead, as many as six hominin species – *Paranthropus aethiopicus*, *Paranthropus boisei*, *Homo habilis* Leakey, Tobias & Napier, 1964, *Homo rudolfensis* (Alekseyev, 1986), *Homo ergaster*, and *Homo erectus* (Dubois, 1893) – could have been sympatric during the Pleistocene in the Omo-Turkana Basin and elsewhere in eastern Africa (Spoor *et al.* 2007; Sept 2015; Wood & Boyle 2016), with overlap in the dietary resources consumed by each taxon (Cerling *et al.* 2013; Patterson *et al.* 2019). This taxic diversity, along with the high resolution of isochronous volcanic tuff layers throughout the Omo-Turkana Basin (Brown 1982), mean this region provides an opportunity to study whether, and if so how, sympatric early hominin species may have interacted through time. A recent attempt to quantitatively test for "functional sympatry" in the hominin fossil record of the Omo-Turkana Basin (Uluutku 2024) by applying Hutchinson's rule to the hominin fossil record, found circumstantial evidence for direct competition between *Paranthropus* and early *Homo* through time.

Previous interpretations of eastern African *Paranthropus* (hereafter *Paranthropus*) stated that *Paranthropus* was driven to extinction because it was the victim of competition for finite resources. Researchers argued that its competitor, the genus *Homo*, was more resourceful and showed more behavioral flexibility (Klein 1988; Potts 1998; Fuentes *et al.* 2010; Quinn & Lepre 2021). That interpretation suggests competition for resources pushed *Paranthropus* into an increasingly narrow set of livable niches, a process that resulted in its eventual extinction (Quinn & Lepre 2021, 2022; O'Brien *et al.* 2023). In this scenario, *Paranthropus* would have had little or no influence on later hominin evolutionary history, but recently different competition-centered explanations have been considered and tested (Uluutku 2024). In the following sections, we introduce a different form of ecological competition, and show how alternative competitive scenarios might have affected the dietary and broader evolutionary history of *Paranthropus* and early *Homo* within the Omo-Turkana Basin during the Pleistocene.

ABIOTIC INFLUENCES

Most previous efforts to explain the appearance and disappearance of *Paranthropus* have focused on abiotic climatic factors (Cerling *et al.* 1977; Potts 1998; Quinn & Lepre 2021; Patterson *et al.* 2022). While these approaches offer a broad understanding of how the paleoclimate may have influenced any changes in the paleoecology of *Paranthropus* and *Homo*, they provide an inevitably incomplete picture, and they exclude consideration of whether, and if so how, *Paranthropus* and *Homo* may have interacted in response to changes in the paleoenvironment.

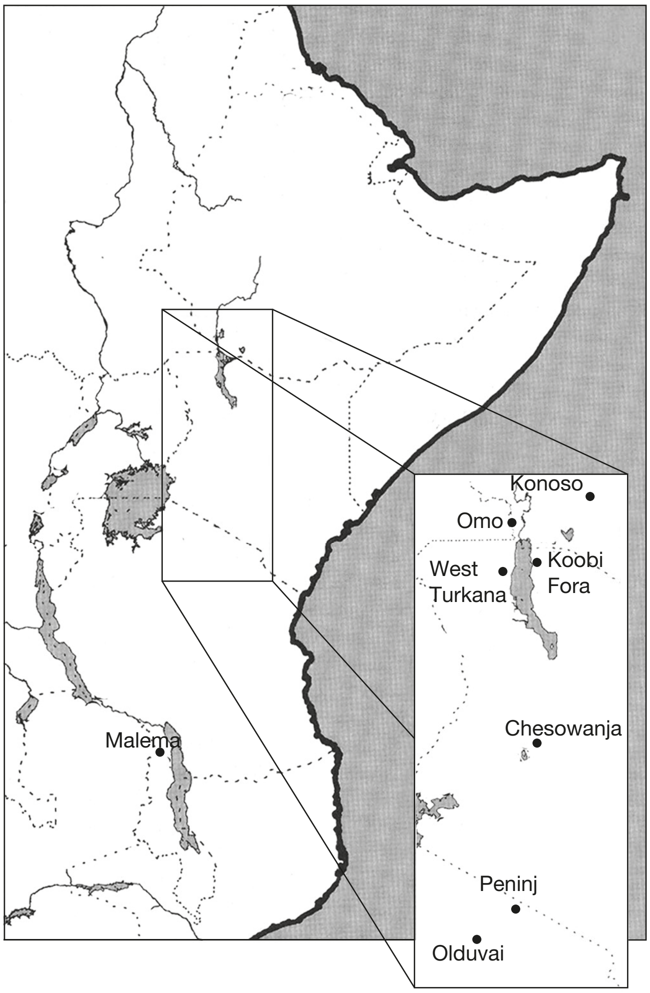

FIG. 1. — Map showing the sites in eastern Africa that have produced evidence of *Paranthropus boisei sensu lato.*

There have been several attempts to show how external abiotic factors may have influenced the evolution of eastern African hominin taxa during the Plio-Pleistocene. The first proposed that increasing aridity after 2.8 Ma resulted in selective pressures on hominins living in eastern Africa at this time (deMenocal 1995). This both updated the savannah hypothesis, and linked reconstructions of global and regional climate during the Pleistocene with hominin macroevolution. More recent contributions on this theme have suggested any links with changes in regional climates may be more complex (Bobe & Behrensmeyer 2004; Patterson *et al.* 2019).

The pulsed climate variability hypothesis (PCVH) attempted to combine evolutionary processes with ecological principles by melding the notions of punctuated equilibrium and allopatric and sympatric speciation, together with the aridity hypothesis (deMenocal 1995), the turnover pulse hypothesis (TPH) (Vrba

DECOUVERTE D'UN AUSTRALOPITHECIEN NOUVEAU DANS LES GISEMENTS DE L'OMO (ETHIOPIE)

C. ARAMBOURG et Y. COPPENS

ABSTRACT

On the first season of a new systematic excavation of the site Omo in Southern Ethiopia, the authors — part of an international team of French, Kenyan, American and Ethiopian workers — made two important discoveries which are placed on record in this note. They have found a chronological succession of at least three periods represented at Omo, which they regard as three stages of the Lower Pleistocene. In the middle zone, they have recovered a hominid mandible without tooth crowns, but with roots in position. In this, their second scientific announcement of the discovery, they indicate the australopithecine affinities of the jaw; and they claim that it differs from all the other australopithecine fossils known, being somewhat more primitive. They propose to call the form represented *Paraustralopithecus aethiopicus*. (P.V.T.)

L'exploration en 1933 par l'un de nous (C.A.) des gisements pléistocènes de la vallée de l'Omo (Ethiopie), en révélant l'extraordinaire richesse paléontologique de ces gisements, avait, en même temps, permis de déterminer les grandes lignes de la stratigraphie de ces formations et d'en fixer l'âge au Pléistocène inférieur.

Au cours de la nouvelle expédition franco-kenyo-américaine et éthiopienne, dont la première campagne vient de se terminer, il nous a été possible d'apporter deux éléments de connaissance nouveaux.

A — tout d'abord, une série de précisions stratigraphiques qui, complétant les résultats de 1933, a permis d'établir, dans l'ensemble des gisements de l'Omo, une succession chronologique d'au moins trois périodes:

1°) — une série basale à *Elephas africanavus*;

2°) — une série moyenne à *El. hysudricus recki*, contenant la faune classique de l'Omo et qui constitue la masse la plus importante des dépôts;

3°) — une série supérieure dont la faune renferme, associés à des éléments survivants

Fig. 1 — Mandibule de *Paraustralopithecus aethiopicus*. **Face occlusale. G.N.**

Februarie 1968 58 *Suid-Afrikaanse Tydskrif vir Wetenskap*

Fig. 2. — The first page of Arambourg & Coppens (1968), showing the Omo 18-1967-18 mandible in occlusal view.

1985), the variability selection hypothesis (VSH) (Potts 1998), and the Red Queen hypothesis (Van Valen 1977). The PCVH suggested that a long-term drying trend in eastern Africa was punctuated by alternating short periods of extreme humidity and aridity, a combination that helped drive hominin speciation, encephalization, and dispersals out of Africa (Maslin & Trauth 2009). However, the PCVH, like the VSH, does not provide the tools to resolve the several orders of magnitude difference in temporal scale between the dated tuffs in eastern Africa and the lifespan of a hominin, nor does it address how individual hominins were interacting with, and responding to, their environments during their lifetimes.

Many environmental hypotheses are framed as mutually exclusive, but it is likely that the response of hominins to any change in their environment was the result of complex interactions among several contributing factors. The response of hominins has also been framed in binary extremes: a species either goes extinct or adapts (Vrba 1985; Potts 1998). However, where extinct taxa are sampled is a function of geological contingency, and those samples should not be confused with the actual geographical and temporal ranges of those taxa, both of which will always be greater than the observed ranges. Even if a taxon disappears from the fossil record, it does not mean it necessarily becomes extinct across its geographical range, and observed first and last appearance dates are always going to underestimate the origination and extinction of a species (Wood & Smith 2022).

Biotic evidence of competition

Abiotic evidence alone cannot explain all the changes we observe in the hominin fossil record. For example, there were substantial changes in the stable isotope signal of fossil hominins in the Omo-Turkana Basin during the Pleistocene, despite there being no significant shifts in the geochemistry of the paleosols of East Turkana (Patterson *et al.* 2019). Although some non-hominin mammal taxa increased their C4 signal during this time, others showed a decrease in C4 signal (Patterson *et al.* 2019). In this section, we explore how different forms of interspecific competition might help explain the discrepancy between soil geochemistry and the stable isotope signals of the fossil hominins.

Of the many studies looking at possible causes of the disappearance of *Paranthropus* in eastern Africa, relatively few have considered biotic, competition-based, explanations (Wolpoff 1971; Winterhalder 1980; Klein 1988; Fuentes *et al.* 2010; Schroer & Wood 2015). Of the studies that do consider biotic explanations, most explore a narrow subset of competition-based explanations, such as competitive exclusion, which would predict symmetrical morphological responses (Fig. 3). The concepts of ecological niche incumbency and pre-sympatric niche divergence have only recently been considered in this context (Uluutku 2024).

Pre-sympatric niche divergence (e.g. Quintero & Landis 2020) is an asymmetrical form of competition in which ecological niche incumbency effectively prevents another species from colonizing the incumbent organism's preferred niche (Algar *et al.* 2013). This results in niche divergence between the two species *before* they were ever in effective sympatry, hence the qualifying prefix "pre-sympatric." Since *Paranthropus* is the more likely – and in some cases it is specified as the assumed incumbent (Joordens *et al.* 2019) – it is possible that ecological niche incumbency may have occurred between *Paranthropus* and early *Homo* in eastern Africa, with *Paranthropus* the incumbent, and early *Homo* the potential colonizer. We should not expect pre-sympatric niche divergence to cause extinction of the attempted colonizer because the latter can fall back on other parts of its fundamental niche, or revert to its original niche (Quintero & Landis 2020). Both of these possibilities are consistent with the long-term survival of the genus *Homo* and its presence in a variety of paleoenvironments during the Pleistocene (Quintero & Landis 2020; O'Brien *et al.* 2023).

The evidence of morphological stasis in *P. boisei* (Wood *et al.* 1994) is also more consistent with pre-sympatric niche divergence than with post-sympatric niche divergence, traditional character displacement, or competitive exclusion. Uluutku (2024) used 3D geometric morphometrics on all suitable adult molars of *Paranthropus* and early *Homo* specimens housed at the National Museums of Kenya to test for evidence of character displacement and pre-sympatric niche divergence (PSND) in these lineages through time. Uluutku's results show more support for PSND than traditional character displacement (Fig. 5). This conclusion is consistent with *Paranthropus* being a stronger competitor than early *Homo* in the Omo-Turkana Basin for an extended period of time, and

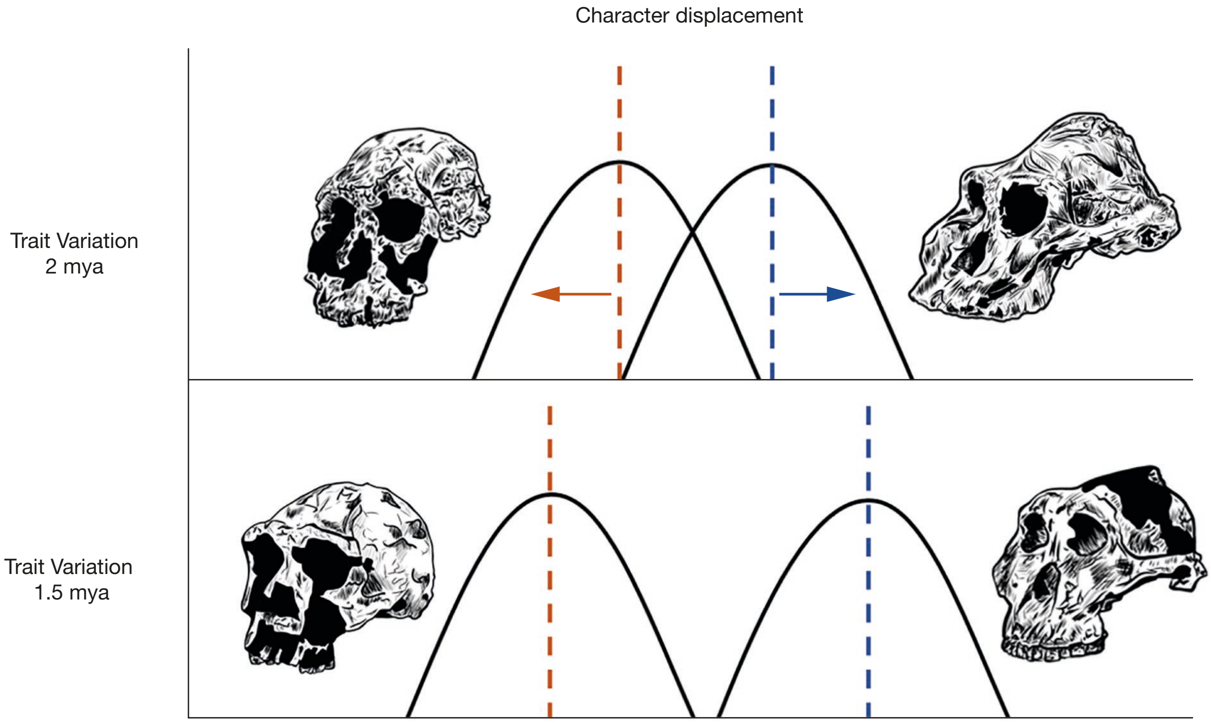

Fig. 3. — The expected (hypothetical) trajectories of mean morphological trait values through time if species are undergoing character displacement. The trait means should repel each other when in sympatry. This figure does not reflect true dates alongside the referenced specimens depicted, it is simply a reference of expected outcomes under this particular hypothesis.

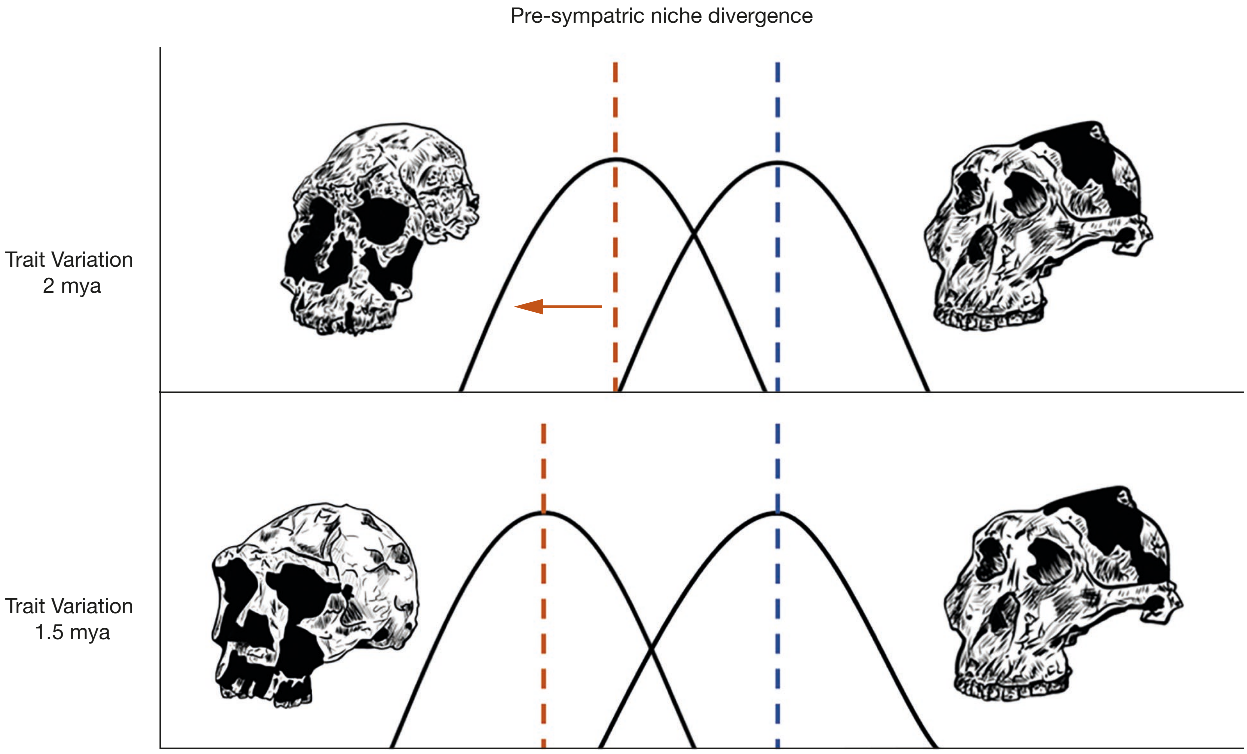

Fig. 4. — The expected (hypothetical) trajectories of mean morphological trait values through time if species are undergoing pre-sympatric niche divergence. The trait mean of the incumbent species, *Paranthropus boisei* (Robinson, 1960) in this diagram, should remain relatively constant through time while the other species' trait mean repels away from it. This figure does not reflect true dates alongside the referenced specimens depicted, it is simply a reference of expected outcomes under this particular hypothesis.

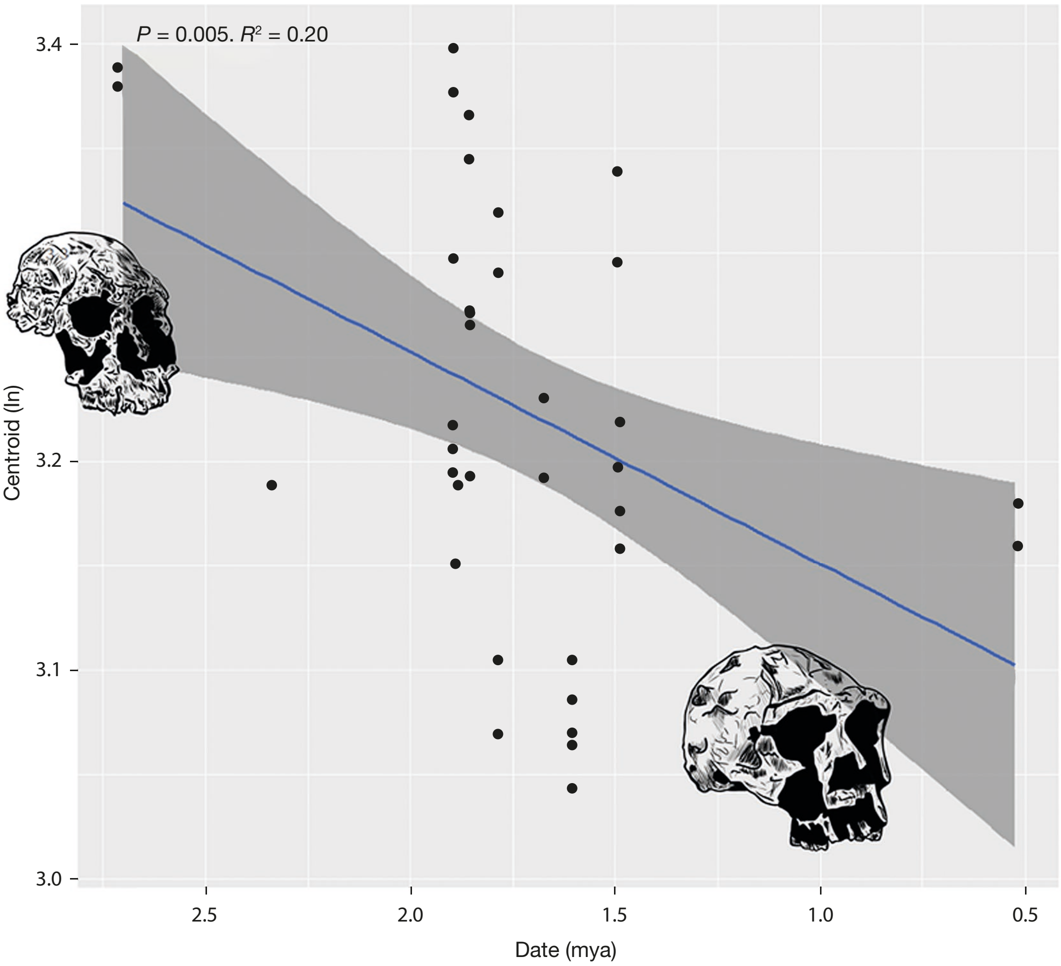

Fig. 5. — The change in size (centroid (ln)) through time in early *Homo* specimens included in the **closed circle landmark** scheme of Uluutku (2024). There is a significant change in size through time in early *Homo* (p = 0.005) when using the **closed circle landmark** scheme but not in *Paranthropus* (p = 0.299) (see Figure 6 below). This is more consistent with the pre-sympatric niche divergence hypothesis than with competitive exclusion.

its disappearance may have been for reasons unassociated with the presence of *Homo*. Clearly, there is more to be learned about how *Paranthropus* and early *Homo* interacted after their hypothesized divergence from a recent common ancestor.

Researchers have considered ecological explanations, but most have done so within a Manichean paradigm that categorizes taxa as either a "specialist" or a "generalist" (Wood & Strait 2004; Marcé-Nogué *et al.* 2020; Constantino & Konow 2021; O'Brien *et al.* 2023). However, a species' niche is a complex, n-dimensional concept, within which each of the n-dimensions could be assessed as being more, or less, specialized compared to other sympatric organisms. Rarely do the axes coincide to give a straightforward picture of "specialist" or "generalist" (Davies & Krebs 1993). This is especially evident when comparing closely-related species in deep time, where the presumed ancestral condition can be used as a comparison. If we use eastern African australopiths found before 4 Ma (Sponheimer *et al.* 2013) as a proxy for the assumed *Paranthropus*/*Homo* ancestral condition, then there is evidence of a dietary shift in both *Paranthropus* and *Homo*. Hominins before 4 Ma were consuming a broad range of C3 resources, comparable to the leafy vegetation consumed by chimpanzees (Oelze *et al.* 2014), but the dominant C4 signal seen in *Paranthropus* in eastern Africa suggests the latter occupied an unusual, if not unique, isotopic dietary niche within the hominin clade (Cerling *et al.* 2011; Martin *et al.* 2020). As for early *Homo*, its carbon stable isotope signal initially resembles that of the pre-4 Ma eastern African australopiths, but it changes *c.*1.6 Ma to a dominant C4 signal. Researchers suggest that the synchronic archaeological evidence is consistent with the hypothesis that the high C4 signal in post-*c.*1.6 Ma *Homo* reflects the consumption of animals that were eating C4 grasses (Patterson et al. 2019). Although *P. boisei* is referred to as a "C4 specialist" (Potts 1998; Van der Merwe *et al.* 2008; Cerling *et al.* 2011; Cerling *et al.* 2013; Quinn & Lepre 2021; O'Brien *et al.* 2023), the observed carbon stable isotope values suggest that the range of C4 foods it was consuming was as large as the range of C3/C4 mixed foods consumed by pre-*c.*1.6 Ma *Homo* (Patterson *et al.* 2019).

Despite the arguments that early *Homo* and *Paranthropus* were occupying more specialized versions of the niche of their possible precursors, both genera have at one time or another (Wood & Strait 2004; Lüdecke *et al.* 2018) been labelled as generalists. The suggestion that *P. boisei*'s hyper-megadont

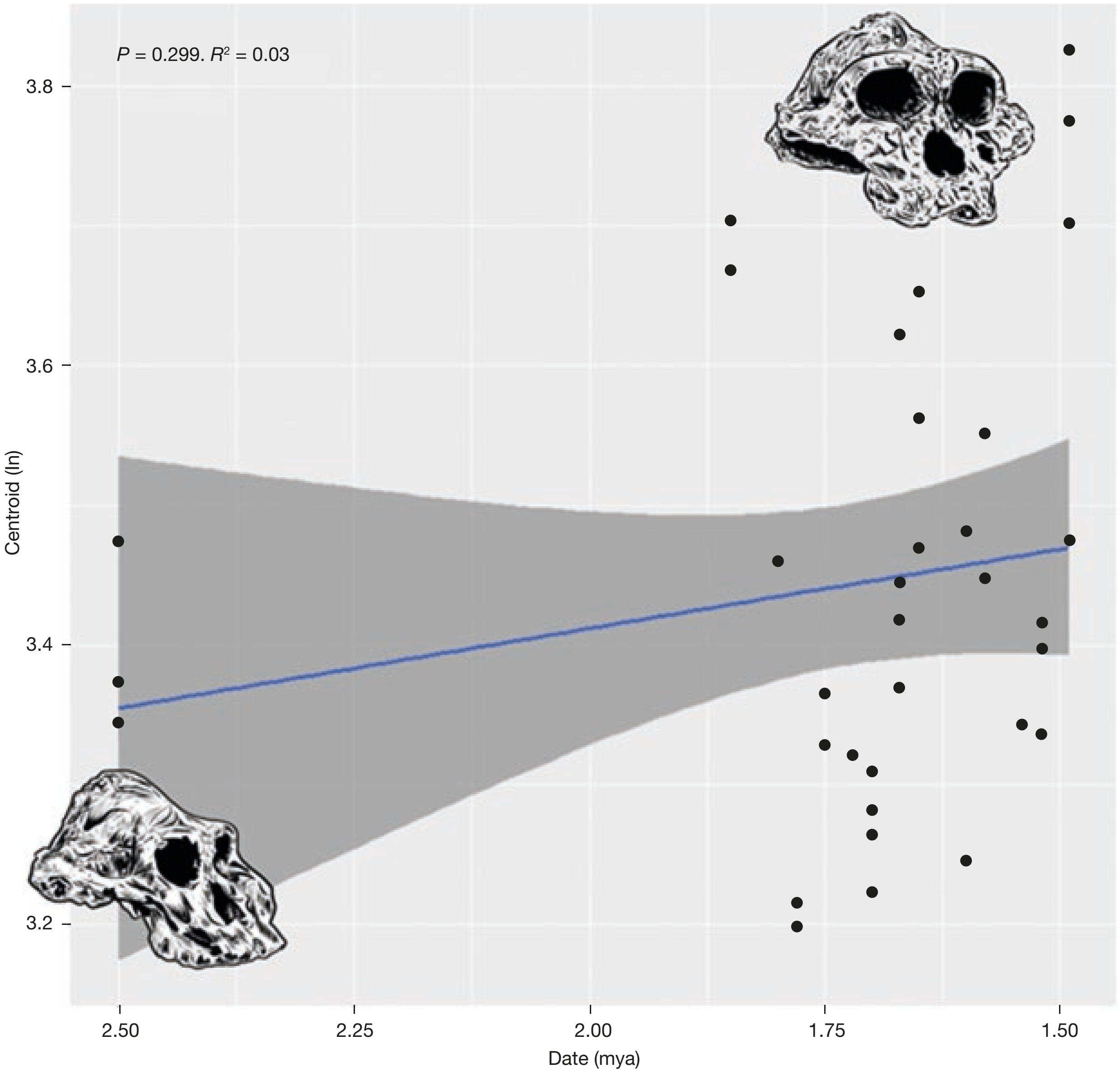

FIG. 6. — Size (centroid (ln)) through time in *Paranthropus* specimens included in the **closed circle landmark** scheme of Uluutku (2024). There is a significant change in size through time in early *Homo* (p = 0.005) (see above) when using the **closed circle landmark** scheme but not in *Paranthropus* (p = 0.299). This is more consistent with the pre-sympatric niche divergence hypothesis than with competitive exclusion.

post-canine teeth, sagittal crest, and broad zygomatic arches, were specializations that allowed it to consume hard objects as its preferred food, has been rejected (Marcé-Nogué *et al.* 2020; Constantino & Konow 2021), but these derived morphological traits may have enabled *P. boisei* to consume hard-objects as a fallback food, thus adding to the breadth of its dietary niche (Wood & Strait 2004; Laden & Wrangham 2005).

Dietary specialization is only one element (aka dimension) of an organism's niche. The physical coexistence of two or more species is driven by niche differences (e.g. diet) and by competitive ability (Hurlbert 1981; Mayfield & Levine 2010). In fossil species, depositional environment has been used as a proxy for the type of paleoenvironment favored by an organism (Behrensmeyer & Boaz 1980), but studying niche differences without including competitive ability leaves us with ambiguous results that support more than one hypothesis. For example, a recent study shows that eastern African *Paranthropus* is found in a more limited set of palaeoenvironments than *Homo*, leading researchers to conclude it was an environmental specialist (O'Brien *et al.* 2023). But the occupation of a smaller range of environments does not always imply environmental specialization, and if *Paranthropus* was restricted to a smaller subset of palaeoenvironments than *Homo* in eastern Africa, this could imply: 1) dietary restriction (O'Brien *et al.* 2023); or 2) *Paranthropus* is able to maintain its preferred niche by possessing a higher competitive ability in those environments despite pressure from *Homo*. Depositional environments *and* relative competitive ability need to be considered when trying to narrow down potential scenarios.

EXPLORING ALTERNATIVE EXPLANATIONS

Ecosystems and biological organisms are complex, with the added challenge that when they are studied in deep time we cannot control any of the variables that could be affecting the ecosystems. In this final section, we explore alternative explanations for any differences between *Paranthropus* and early *Homo* through time. Compared to character displacement and ecological niche incumbency, these explanations do not have as clear predictions, but individually, or in combination, they could influence morphological change. It is likely that any competition between *Paranthropus* and early *Homo* was driven by multiple factors, either simultaneously or sequentially. Our goal is not to identify a single cause of morphological change, but to parse out, using evidence from as many proxies as possible, what types of competition may have occurred between these genera, and if so, when and what circumstances any competition occurred. Specifically, what factors – or combinations of factors – could mimic evidence for competition?

Taphonomy and taxonomy could potentially mimic the effects of competition. Differences between the size of the post-canine teeth and the mandibular corpus of *P. boisei* and early *Homo* may influence how many specimens of each are recovered, and sex ratio and differences in depositional environments may also influence the nature of the two fossil records. Taxonomic misallocations could also potentially affect the outcome, but while this is possible for early *Homo*, it is less likely for *P. boisei* because the latter is so distinctive (Wood & Constantino 2007). Canalization, when a species loses the capacity to modify its phenotypes in response to different environments due to extreme morphological specialization, could also be relevant given the apparently highly-derived morphology of *P. boisei*.

Finally, it is possible that key cultural innovations played a role in determining the nature and course of any morphological change in the two lineages, but assessing any such influences is challenging for at least two reasons. First, there is usually a time lag between behavioral and morphological change. Second, while it is conventional to attribute any evidence of stone tool manufacture to *Homo*, we are reluctant to assume that early *Homo* was the only hominin with cultural capabilities, especially given the recent discovery of *Paranthropus* with Oldowan tools at a 2.6-3 Ma site in Kenya (Plummer *et al.* 2023).

CONCLUSION

There is impressive comparative evidence for interspecific interactions between the two extant taxa that are most closely-related to early hominins (Sanz *et al.* 2022), and equally impressive trace fossil evidence that early *Homo* and *Paranthropus* were potentially interacting in lake-shore environments in the Omo-Turkana Basin (Hatala *et al.* 2024). Although the East African Rift System, of which the Omo-Turkana Basin is a component, is the source of nearly all of the information we have about human evolution north of the Zambesi, that is due to geological contingency and not because that region was necessarily the focus of early hominin populations in the region (Barr & Wood 2024).

It is especially critical in palaeoanthropology, where researchers' interpretations directly frame the public narrative of human evolution, to challenge conventional wisdom. While it is true that *Paranthropus* in eastern Africa disappears from the fossil record without leaving any likely descendants, that does not mean it did not influence the course of human evolution. We should be careful to explore and test alternative hypotheses before we deem any species, clade, or time period, inconsequential.

Yves Coppens was well-known for questioning conventional wisdom, and it is our honor to follow in his footsteps.

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