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Regional diversity patterns in African bovids, hyaenids, and felids during the past 3 million years: the role of taphonomic bias and implications for the evolution of *Paranthropus*

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ABSTRACT

Reconstructing patterns of Plio-Pleistocene mammalian faunal exchange between eastern and southern Africa may help us to better understand patterns of evolution within the hominin clade. However, differences in geological context, taphonomic history and collection methods, as well as a lack of a precise chronology in one of the regions, complicate attempts to compare the faunas of the two regions, but access to new comprehensive datasets encouraged us to re-examine this critical time period in the African paleontological record. In this study, we examine the biogeographic histories of three terrestrial African mammalian families whose fossil records span the past 3 million years to test hypotheses related to the evolutionary history of the hominin genus *Paranthropus*. We used presence/absence data for 117 species from 38 genera within the family Bovidae and 34 species from 15 genera within the families Hyaenidae and Felidae from 52 eastern African and 40 southern African fossil localities. These assemblages were placed into 500 ka time slices and compared at both the genus and species level using the Jaccard index of faunal similarity. Our findings indicate that sampling biases have more effect on the patterns of interchange between eastern and southern African Bovidae than they do the patterns of interchange seen in the Hyaenidae and Felidae. However, even when these biases are taken into account there are persistent differences in the degree of interchange within and between these families. These findings suggest that mammalian groups (including hominins) can have very different histories of exchange between eastern and southern Africa over the past 3 million years.

There is no *a priori* reason why any of the three families we examined is a suitable proxy for the eastern and southern African hyper-megadont and megadont hominin taxa presently included in *Paranthropus*, but of the three we suggest that the Bovidae is likely to come closest to being an appropriate proxy. The results of this comparative study are consistent with relatively independent evolutionary trajectories in the two regions for the hominins that are presently included in the genus *Paranthropus*.

1. Introduction

There have been several attempts to reconstruct the phylogenetic relationships, ecology and biogeography of one of two hyper-megadont hominin taxa from eastern Africa and the single megadont hominin taxon from southern Africa (Wood, 1988; Strait and Wood, 1999; Wood and Constantino, 2007; Wood and Leakey, 2011). But the different geological and chronological contexts, plus differences in the taphonomic histories and collection methodologies of the two regions combine to make any evidence about the faunal similarities and differences between the two regions difficult to decipher.

The ultimate question addressed in this contribution is whether the eastern and southern African “robust” taxa evolved from a recent common ancestor exclusive to themselves and thus form a monophyletic group, or did the taxa evolve independently in the two regions? This is not a trivial question, for if these two taxa evolved from a recent common ancestor, then because the less derived “robust” form (*Paranthropus robustus*) is apparently more recent than the more derived form (*Paranthropus boisei*), this would

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either imply several reversals in cranial morphology, or that *P. robustus* existed for several hundred thousand years prior to its current first appearance datum. Alternatively, if the two regional variants arose independently, then it would be a striking example of homoplasy, with at least two hominin lineages independently acquiring postcanine megadontia and masticatory hypertrophy. The outcome also has taxonomic consequences, for it makes no sense to use the genus *Paranthropus* for these taxa if they arose independently. This is because they would not comply with one of the two criteria, monophyly and adaptive coherence, for a genus (Wood and Collard, 1999).

Several different studies have found support for *Paranthropus* monophyly. Wood (1988) reviewed fifteen hominin cladistic studies that had treated the eastern and southern African "robust" taxa separately in phylogenetic analyses and all of them concluded that the two regional variants were sister taxa (but some of the studies used the same datasets, so these results are not quite as impressive as they appear). In a separate review of the results of early hominin cladistic analyses Corruccini (1994) concluded that one of the few reliable parts of the hominin cladogram is the *Paranthropus* clade. Strait et al. (1997) carried out a phylogenetic analysis on 60 traits derived from five previous studies, but they did adjust several character state distributions on the basis of their own observations. They then subjected the 60 traits to eight parsimony analyses "that differed with respect to the number of characters examined and the manner in which the characters were treated" (Strait et al., 1997, p. 17). In all of the analyses the "robust" taxa formed a single separate clade. In a more recent analysis, Strait and Grine (2004), who used 109 non-metrical traits plus 89 traits based on linear measurements and two different in-groups, also found that the "robust" taxa consistently forming an independent clade. In a separate study published the same year Kimbel et al. (2004) also found consistent support for a "robust" australopith clade.

In the face of all of this support for a "robust" clade why would anyone question the hypothesis of *Paranthropus* monophyly? The first reason is that if consistency indices (CI) are any guide to homoplasy, the *c.*0.65 average CI for hominin cladistic analyses means that approximately 35% of the characters used in the analyses must have been independently acquired (i.e., they are homoplasies). Second, many, but by no means all, of the characters that link *Paranthropus* taxa in the same clade are related to the masticatory system. There is empirical evidence that these characters are likely to be functionally integrated and thus potentially they violate the requirement that the characters in a cladistic analysis are independent, and there is comparative evidence from other groups of African mammals (e.g., Maglio, 1973; Vrba, 1979, 1984) that the masticatory system might be the equivalent of a "homoplasy ghetto." However, when Strait et al. (1997) excluded masticatory characters from one of their cladistic analyses they still found strong support for a *Paranthropus* clade.

2. Testing the hypothesis of *Paranthropus* monophyly

Relatively few studies have looked beyond cladistic analysis to test the hypothesis of *Paranthropus* monophyly. Wood (1988) used Patterson's (1982) similarity and ontogenetic criteria to devise two tests. The logic of the first test was that for any character state morphocline the apparently more derived eastern African hyper-megadont taxon should be a scaled-up variant of the less derived megadont southern African taxon, but when this logic was put to the test using ten morphoclines based on mandibular postcanine crown morphology, only two were consistent with the null hypothesis. The logic of the second test was that if *P. boisei* and *P. robustus* are sister taxa, with *P. boisei* being generally more derived than *P. robustus*, then the morphology of *P. robustus* should be closer to the primitive state of a shared character state morphocline. However, the predominant P_3 root forms of *P. robustus* (2T) and *P. boisei* (2R: M and D) suggest that the taxa are not on the same morphocline (Wood, 1988).

Turner and Wood (1993a) also looked beyond cladistic evidence to test the hypothesis of *Paranthropus* monophly, but they took a different, comparative, tack and assessed the probability of monophyly by examining the biogeographic patterns of African Plio-Pleistocene large mammals. They concluded that during the time range of *Paranthropus* there was evidence in at least one mammalian group of faunal dispersal between regions, with several monophyletic groups having representatives in both regions. They suggested that while this lends credibility to the hypothesis of *Paranthropus* monophyly, it does not refute a polyphyletic origin for this group. In their second test of the *Paranthropus* monophyly hypothesis, Turner and Wood (1993b) worked on the assumption that the well-developed masticatory system of *Paranthropus* was an adaptation to enable the consumption of tough food items in response to environmental aridity. They found that similar trends were detectable in the craniodental anatomy of other terrestrial mammals from this time period, and parallels in lineage turnover suggest that a large-scale response to environmental changes was occurring. Although this second study by Turner and Wood did not contradict the first one, it did suggest there are comparative precedents for regional mammalian lineages independently evolving similar masticatory adaptations in response to changing environmental conditions.

In their analysis of the taxonomic and biogeographic distribution of mammalian families from eastern and southern Africa, Turner and Wood (1993a) suggest that during the time period spanning the duration of the existence of *Paranthropus* there was considerable contact between the two regions. Although this pattern was used to support a monophyletic *Paranthropus* clade, perhaps the most interesting pattern that emerged from this study was the differential degree of exchange among the mammalian families analyzed.

3. Comparative paleoecological context

The complex topography of the African Rift creates an extraordinary diversity of terrestrial biomes (White, 1983; Bailey et al., 2011). These highly variable ecosystems serve as centers of endemism as well as facilitate the vicariance of mammalian taxa (Grubb et al., 1999). Although these processes drove the distribution of mammalian taxa over the past 3 million years, due to a host of potentially confounding factors understanding their implications for interpreting the eastern and southern African hominin fossil records is difficult. However, with the discovery of new hominin taxa as well as an increased interest in paleoecology we are beginning to place hominins within the context of the larger mammalian community. As a result, we can begin to formulate hypotheses about how hominins used the landscape and their patterns of distribution in different regions of Africa over the past 3 million years.

Paleoecological analyses of the abundant and well-dated eastern African Plio-Pleistocene fossil record indicate drastic alterations in mammal communities over the past 3 million years (Behrensmeyer et al., 1997). Although there is considerable debate about the tempo of these changes (see Behrensmeyer et al., 1997; Vrba, 1985, 1992), it has become clear that communities were subjected to dynamic environmental conditions that likely affected mammalian lineages differentially. Using data from the Shungura Formation of southern Ethiopia, Bobe and Behrensmeyer (2004) document periods of faunal turnover and alterations in the abundance of bovids, suids, cercopithids, and hominids from 4 to 1 million years ago, with a relative expansion of taxa characteristic of grassland-dominated ecosystems.