

The Macroevolution of our Ancient Lineage: What We Know (or Think We Know) about Early Hominin Diversity

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Received: 17 January 2007 / Accepted: 20 March 2007 / Published online: 17 July 2007
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Abstract Quantitative, evolutionary models that incorporate within- and between-species variation are critical for interpreting the fossil record of human diversity, and for making taxonomic distinctions. However, small sample sizes, sexual dimorphism, temporal trends, geographic variation, and the limited number of relevant extant models have always made the consideration of variation difficult for paleoanthropologists. Here we provide a brief overview of current early hominin diversity. We then argue that for many species our limited understanding of within species variation hampers our ability to make taxonomic decisions with any level of statistical certainty. Perhaps more significantly, the underlying causes of between-species variation among early hominins are poorly studied. There have been few attempts to correlate aspects of the phenotype with meaningful evidence for niche differentiation, to demonstrate the selective advantage of traits, or to provide other evidence for macroevolutionary divergence. Moreover, current depictions of vast pattern (but not size) diversity are inconsistent with expectations derived from most other extant primate clades that have adaptively radiated. If indeed the early hominin record is highly speciose, the reasons for this remain unclear.

Keywords Hominin evolution · Interspecific and intraspecific variation · Adaptive radiation · Australopith · Species recognition

Introduction

Scientists often have a naive faith that if only they could discover enough facts about a problem, these facts would somehow arrange themselves in a compelling and true solution.

Theodosius Dobzhansky

A fundamental assumption of the paleoanthropological research agenda is that the path of human evolution will be clarified by the discovery of more fossil evidence, and that major gaps in our understanding are due at least in part to gaps in the fossil record. If this is true, the extraordinary successes of the past decade should have greatly illuminated our understanding of hominin evolution. Certainly in many ways they have—for example, by providing firm fossil evidence of hominins before 5 million years ago. And yet, in other respects, the picture is more muddled than ever. How many of us who study and teach human evolution currently find ourselves at a loss to communicate a coherent picture of phylogenetic diversity prior to the evolution of our own genus? Why is this? In this review we provide an overview of our current understanding of early hominin diversity, and explain our view of why the plethora of new fossil taxa seems to have done little to improve our understanding of the human past. We suggest that it is largely because evolutionary models that incorporate our understanding of intra- and inter-specific variation in extant species have been applied unevenly to the consideration of early hominin diversity, leading us far too

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often to draw unsupportable inferences. Although poor sampling of much of the hominin fossil record—and the associated statistical and methodological problems—continues to be partly responsible for this, of greater concern is the lack of a conceptual framework that firmly grounds interpretations of inter-specific patterns of phenotypic diversity within an understanding of evolutionary process. For the most part, the links between proposed phenotypic diversity and the underlying causes of macroevolutionary divergence remain to be demonstrated.

When Things were Simpler

In the early 1990s, all early hominins¹ were referred to as ‘australopithecines,’ and were placed into five species, which were rather neatly divided by many into two groups (Table 1). The more ‘robust’ group—designated so on the basis of its massive masticatory complex—consisted of *Australopithecus aethiopicus* and *A. boisei* from east Africa, and *A. robustus* from South Africa. There was (and is) general agreement that this lineage emerged around 2.5 million years ago, lived contemporaneously with early members of the genus *Homo*, and then went extinct approximately one million years ago. The other, earlier group consisted of *Australopithecus africanus* from South Africa, and *A. afarensis* from east Africa. East African *A. afarensis* lived from about 3.6 to 2.9 million years ago (mya), followed by the reign of South Africa’s *A. africanus* (circa 2.5 mya; the actual duration of this species is poorly known). Although the relationship between these last two species was a matter of debate, it was generally accepted that at least one of them was a direct ancestor of *Homo*. Today, many researchers have accepted generic distinction for the ‘robust’ forms, in acknowledgement of their unique dietary adaptations and ultimate fate, placing them all in the genus *Paranthropus*—a sidebranch and evolutionary dead end (we will use this generic distinction here for ease of reference). The term ‘australopithecine’ has also been replaced in the literature by many authors with the more colloquial ‘australopith,’ which is rather loosely used to refer to the group comprised of *Australopithecus* and *Paranthropus*.

These ‘australopiths’ are united by some general similarities, despite temporal and geographic variation. Like all hominins, they were bipedal, although earlier species may

¹ The term ‘hominin’ is used to refer to all members of our lineage following the split from a common ancestor shared with the chimpanzee. ‘Early hominin’ is used here to refer to those members of our lineage that are not members of the genus *Homo*. We recognize that early members of the genus *Homo* and other early hominins overlapped temporally for in excess of 1 million years, rendering this terminology flawed, if convenient.

have retained some climbing ability (we have little data on the postcranial morphology of robust forms)—as evidenced by traits such as curved finger bones and the gorilla-like scapula of the new *A. afarensis* juvenile (Alemseged et al. 2006)—which suggests that they were not yet fully committed to terrestrial bipedalism. They generally had small (chimp-sized) bodies and brains (McHenry, 1993) and patterns of development that tend to align more closely with modern chimpanzees than modern humans. Their faces were generally large and prognathic (associated with varying degrees of megadontia), reducing through time towards a flatter condition in the later forms.

This fairly straightforward picture has been changed considerably by fossil finds and other empirical research over the past fifteen years. We will now consider the new picture of early hominin diversity, focusing on relatively recent finds which have broadened the temporal and geographic range of hominins during the Miocene and Pliocene, and will begin to outline some of the issues which make interpretations of this diversity so challenging.

The Late Miocene

There are currently three hominoids² known from the terminal Miocene in Africa, all of which have been argued to represent early members of the hominin lineage: *Orrorin tugenensis* from the Baringo region of Kenya (Senut et al., 2001), *Sahelanthropus tchadensis* from Chad (Brunet et al., 2002; Brunet et al., 2005), and *Ardipithecus kadabba* from the Middle Awash in Ethiopia (Haile-Selassie, 2001; Haile-Selassie, Suwa, & White, 2004). The dating of the three sites would not prevent them from representing a single anagenetic lineage, though differences in habitat and morphology might. These species are separated geographically by approximately 2500 km from east to west, and 1000 km from north to south. In all cases, they occupied an environment that was at least partially wooded. Associated faunal remains suggest that *Sahelanthropus* was living in a mosaic environment, with gallery forest, savannah, grassland, and an extensive aquatic habitat, in close proximity to desert conditions (Vignaud et al., 2002); within this eclectic environment the exact habitat of *Sahelanthropus* is unknown. The remains of *Orrorin* and other associated fauna were probably accumulated by a carnivore, making paleoenvironmental reconstruction more difficult, but the abundance of small ruminants and colobine monkeys suggests open woodlands with some denser forested components, possibly fringing water (Pickford & Senut, 2001). Conversely, *Ar. kadabba* appears to have occupied more closed wooded environments (WoldeGabriel et al., 2001). Although none of

² Hominoids are apes and humans, and their ancestors.

Table 1 Early hominin diversity. Species known prior to 1994 are shown in bold

Species	Reference	Approximate age (mya)	Distribution
<i>Sahelanthropus tchadensis</i>	Brunet et al. (2002)	7–6	Chad
<i>Orrorin tugenensis</i>	Senut et al. (2001)	6	Central Kenya
<i>Ardipithecus kadabba</i>	Haile-Selassie et al. (2004)	5.8–5.3	Middle Awash Valley, Ethiopia
<i>Ardipithecus ramidus</i>	White et al. (1994)	4.4	Middle Awash Valley, Ethiopia
<i>Australopithecus anamensis</i>	Leakey et al. (1995)	4.2–3.9	Northern Kenya, Ethiopia
<i>Australopithecus afarensis</i>	Johanson, White, and Coppens (1978)	3.6–2.9	Across eastern Africa (especially Ethiopia, Tanzania)
<i>Kenyanthropus platyops</i>	Leakey et al. (2001)	3.5	Northern Kenya
<i>Australopithecus bahrelghazali</i>	Brunet et al. (1996)	3.5–3.0	Chad
<i>Australopithecus africanus</i>	Dart (1925)	3–2	South Africa
<i>Australopithecus garhi</i>	Asfaw et al. (1999)	2.5	Middle Awash, Ethiopia
<i>Paranthropus aethiopicus</i>**	Arambourg and Coppens (1968)	2.5	Northern Kenya and Ethiopia
<i>Paranthropus boisei</i>*	Leakey (1959)	2.3–1.4	Across eastern Africa (Ethiopia, Kenya, Tanzania)
<i>Paranthropus robustus</i>	Broom (1938)	1.7–1.1	South Africa

*Originally named *Zinjanthropus boisei*, this was later renamed *Paranthropus boisei* (Robinson, 1960)

**Originally named *Australopithecus aethiopicus*, the generic name *Paranthropus* has been resurrected by many authors

these fossils have yet been thoroughly studied by the broader scientific community, all three species are considered by their discoverers to be bipeds—a defining trait of the human lineage. In fact, the primary purpose of the original descriptions of each species was to describe them in terms of their unique morphological patterning, and to document bipedalism. Evidence for this is direct in the case of *O. tugenensis*, in the form of two proximal femora (BAR 1002-00 and BAR 1003-00) (Pickford, Senut, Gommery, & Treil, 2002). For *S. tchadensis*, the holotype (TM 266-01-060-1) is a nearly complete cranium, which is interpreted as having a basicranium consistent with later bipeds (Guy et al., 2005). *Ar. kadabba* bipedalism has been tentatively diagnosed based on a proximal foot phalanx argued to be similar to those of later *A. afarensis* (Haile-Selassie, 2001).

Pliocene Diversity

Following on the chronological heels of *Ardipithecus kadabba* comes the second member of this genus, *Ar. ramidus* (4.4 mya) (White, Suwa, & Asfaw, 1994), followed by the earliest known australopith, *Australopithecus anamensis* (4.2–3.9 mya) (Leakey, Feibel, McDougall, & Walker, 1995). *Ar. ramidus* derives from the Middle Awash of Ethiopia, and is essentially a temporal continuation of *Ar. kadabba*. Like *Ar. kadabba*, *Ar. ramidus* displays ape-like features, such as relatively thin tooth enamel and large canines, and may serve as a good morphological bridge between *Ar. kadabba* and later australopiths, although the

species has not yet been described fully, making further diagnosis difficult. The high percentage of colobine monkeys and relative rarity of aquatic species and large mammals suggests that *Ar. ramidus* (like *Ar. kadabba*) may have lived in a closed woodland environment (Wolde-Gabriel et al., 1994), perhaps something like modern-day Kibale forest in western Uganda, where chimpanzees and many canopy-dwelling primates abound. *A. anamensis* is well-known from Kanapoi and Allia Bay in the Lake Turkana region of Kenya, and was discovered recently in Ethiopia. This species marks the first of the well-sampled hominins. The hypodigm consists of approximately 80 largely craniodental fossils (Kimbel et al., 2006; Leakey et al., 1995; Leakey, Feibel, McDougall, Ward, & Walker, 1998; Ward, Leakey, & Walker, 2001; White et al., 2006), which display a mixture of primitive, ape-like features and derived, human-like features (such as thick tooth enamel). Although temporally contiguous with *Ar. ramidus*, *A. anamensis* inhabits a somewhat different environment, with a mixture of open wooded or bushland conditions with some riverside gallery forest (Coffing, Feibel, Leakey, & Walker, 1994; Leakey et al., 1995; Ward et al., 2001), although the new Ethiopian specimens are interpreted to have a “tight spatial and temporal placement” in a vertebrate assemblage from a wooded environment (White et al., 2006).

From approximately 4 to 3 million years ago, multiple, contemporaneous species inhabited the landscape. As already discussed, the most well-known of these is *A. afarensis*, comprised of approximately 400 specimens,

best known from Laetoli, Tanzania and Hadar, Ethiopia. It is suggested that *A. afarensis* is a direct descendent of *A. anamensis*, and that it represents a good example of anagenetic evolution within the hominin lineage (White, 2002; Kimbel et al., 2006). Paleoenvironmental evidence suggests that *A. afarensis* lived in a mixed and changing habitat, with grassland, scattered trees and woodland (Johanson, Lovejoy, Kimbel, White, & Ward, 1982; Harris, 1987; Grine, Ungar, Teaford, & El-Zaatari, 2006b). In addition to *A. afarensis*, less well known taxa from Chad, Kenya, and South Africa, each represented by only a single individual, are dated to this time period. The first of these, *A. bahrelghazali*, is represented by a single mandible (Brunet et al., 1995). Announced in 1995, this individual was noteworthy at the time because it extended the range of australopiths to Chad (the finds of *Sahelanthropus* have further confirmed the importance of looking for early hominins west of the Great Rift Valley); whether it is taxonomically distinct from *A. afarensis* is debatable (e.g. Kimbel et al., 2006; White, 2002). The second individual, from Sterkfontein, South Africa, was announced in 1995, and nicknamed “Little Foot” because the first bones found were from a foot (Clarke, 1998; Clarke & Tobias, 1995). This hominin has not yet been fully analysed, and it may represent a geographic variant of *A. afarensis*, a temporal extension of *A. africanus*, or some new hominin. Faunal associations place this hominin at circa 3.3 mya—extending the geographic range of australopiths southward during this time period—although it may be significantly younger at 2.2 mya (Walker, Cliff, & Latham, 2006). A third individual also adds diversity of a different sort to this time period; with its flat face, derived facial features, and smallish molars, *Kenyanthropus platyops* (3.5 mya) has been argued to represent a genus closely linked to *Homo*, possibly representing the early, smaller-brained ancestor of *Homo rudolfensis* (Leakey et al., 2001; Lieberman, 2001), though there is some disagreement on this matter (see below). Taxonomic affinities aside, these fossil finds suggest that hominins during this time period were significantly more mobile and diverse than previously understood. The presence of hominins far afield is not surprising given the presence of earlier Miocene apes in places like Namibia (Conroy, Pickford, Senut, Van Couvering, & Mein, 1992), and emphasizes the fact that the known distributions of hominins are to a large extent an artifact of geology (Fig. 1).

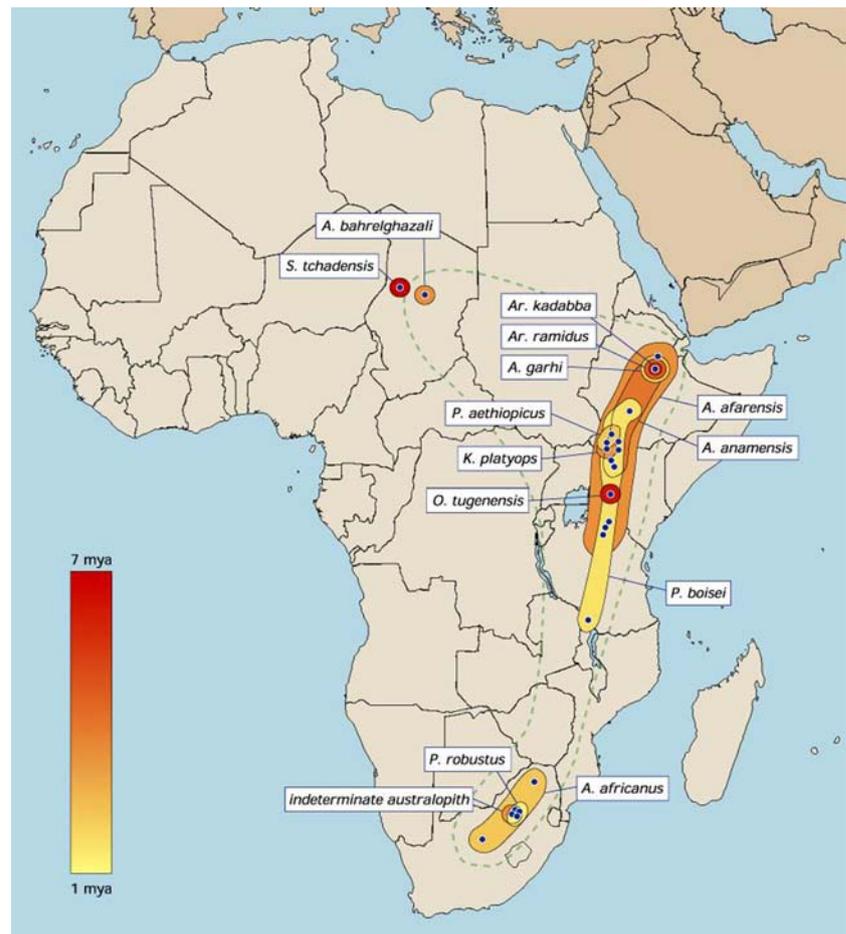
From 3 to 2 million years, two representatives of the genus *Australopithecus* are present, and in addition two new genera emerge—*Paranthropus* and early *Homo*. The best-known hominin is *A. africanus*, represented by in excess of 600 specimens from South Africa (Lockwood & Tobias, 1999; Moggi-Cecchi, Grine, & Tobias, 2006; Pickering, Clarke, & Moggi-Cecchi, 2004). During this time

in South Africa, grasslands were generally increasing, although bushland and some riparian forest persisted (Reed, 1997; Vrba, 1980; Vrba, 1985). In east Africa, the poorly sampled *Australopithecus garhi* from the Middle Awash, Ethiopia (Asfaw et al., 1999) represents a contemporaneous gracile australopith (~2.5 mya), considered distinct from *A. africanus* due to a more primitive facial morphology, which is nonetheless derived relative to *A. afarensis* (Asfaw et al., 1999). Like other Plio-Pleistocene sites in this region, the *A. garhi* locality is associated with a lake margin environment (de Heinzelin et al., 1999), probably not unlike that seen in the Great Lakes region of east Africa today. Interestingly, evidence of food processing in the form of cut and hammerstone marks on long bones (de Heinzelin et al., 1999) suggests possible (but not definitive) tool use by this australopith; this is unusual as tools have largely been considered the realm of *Homo*, and this may represent the only example of tool use in all of the early hominins. Also at approximately 2.5 million years ago, *P. aethiopicus*—the first of the robust australopiths—emerged, followed by *P. boisei* in eastern Africa and *P. robustus* in South Africa. As discussed above, this genus is generally considered to have evolved as a specialized feeder in an increasingly arid Africa, and the lineage likely went extinct at around 1 mya. The genus *Homo* also appears around the same time; we will not consider this lineage further here.

Early Hominin Relationships

The above overview should make one thing apparent—that early hominins are currently considered by many to come in myriad forms. Interpretations of this lineage diversity and ancestor-descendant relationships vary widely, particularly for the most recent and therefore less well understood and contextualized taxa. For example, in the 3–4 mya time period, some researchers suggest that *Homo rudolfensis* should be renamed *Kenyanthropus rudolfensis*, which would relegate all big-toothed australopiths to a side branch not leading directly to *Homo* (Leakey et al., 2001). Others question the validity of *Kenyanthropus* as a valid genus distinct from *Australopithecus* (White, 2003). At the same time some researchers consider *A. bahrelghazali* merely a western member of *A. afarensis* (Kimbel et al., 2006; White, 2002). The earliest hominins also spark disagreement, with some suggesting that *Orrorin* was not well evaluated, and that *Ardipithecus* represents the earliest representative of the true hominin lineage (Haile-Selassie, 2001), perhaps even the genus into which both *Orrorin* and *Sahelanthropus* should be subsumed (Haile-Selassie et al., 2004). Still others argue that *Sahelanthropus* is not a human ancestor at all, but instead allies more closely with

Fig. 1 Estimated species ranges of the early hominins based on current fossil sites, colored to indicate time depth. As can be seen fairly clearly, these distributions are determined largely by geological circumstance, rather than representing the likely actual ranges of these hominins; as a result new finds can alter these ranges considerably. For example, the Chad specimens have dramatically expanded the known hominin range westwards. Different taxonomic interpretations can also change this picture. For example, if *A. bahrelghazali* is placed in *A. afarensis*, as proposed by some, the range of the latter species would grow considerably. Finally, only two genera (*Australopithecus* and *Paranthropus*) can truly be considered widespread; the dashed line represents the approximate range of the furthest-ranging, *Australopithecus*. All other genera are known from a single region or locality



the apes (Wolpoff, Senut, Pickford, & Hawks, 2002). And we could go on. The variety of interpretations is not merely a function of professional disagreements within the field either; researchers peripheral to the field have also weighed in with their interpretations of early hominin diversity (Cela-Conde & Ayala, 2003). What we are left with is a picture that is decidedly unclear, with probably as many phylogenetic interpretations of diversity as there are purported fossil species.

Many of the disagreements regarding phylogenetic relationships, particularly with regards to the earliest fossil genera (*Sahelanthropus*, *Orrorin*, *Ardipithecus*), have centered on the understanding (and/or assumption) of what is primitive versus derived in the hominin lineage. One of the greatest impediments to understanding the earliest evolution of the human lineage is the blank slate we are confronted with at the end of the Miocene in Africa. There are no clear candidates for ancestry to any living African ape or hominin during this time (the only known fossil ancestral to an African ape is the recent find of three middle Pleistocene chimpanzee teeth (McBrearty & Jablonski, 2005)), and therefore no direct knowledge of what constitutes ‘the primitive condition’ (Pilbeam & Young,

2004). This severely limits our ability to gauge primitive versus derived characteristics, and to ascertain the affinities of the earliest hominins. For example, *O. tugenensis* is said to have relatively thick molar enamel, a feature which characterises later hominins (Senut et al., 2001), implying that thick enamel represents the primitive condition, and by extension the thinner-enameled later hominin *Ardipithecus* is not on the hominin lineage. But leaving arguments about the validity of these thickness measurements aside (Haile-Selassie, 2001; Haile-Selassie et al., 2004), how do we know whether thick or thin enameled molars are primitive? Apes from the earlier Miocene have variable molar thickness, providing little guidance (Begun, 2004). If we assume that the primitive state is more likely to be modern ape-like (i.e., like the chimpanzee), then molar enamel should be thin, such as seen in *Ardipithecus*. Do we have good reason to make this assumption? With the exception of *Ardipithecus*, the environment these early hominins were living in appears to be decidedly unlike that in which most chimpanzees live. It has also been suggested that the developmental underpinnings of enamel thickness may vary considerably (Schwartz, 2000), signifying that ‘thickness’ or ‘thinness’ might not be biologically meaningful (e.g.,

homologous) across organisms. Similar issues plague postcranial comparisons. We don't know whether late Miocene ancestors were primarily tree-dwelling gibbon-like hangers, African ape-like knuckle-walkers, or something else. Resolving this question is essential to understanding these early hominins (McHenry, 2002). Even one of the most commonly cited hominin traits—a reduced canine—is of questionable phylogenetic value. Sarmiento, Stiner, and Mowbray (2002) argue that reduced canines are present in other, earlier hominoids, and that canine size is variable within species, thereby making it a poor 'diagnostic' trait. As this example of the problems with character polarity determination shows, interpretations of phylogenetic relationships can be difficult, especially when such interpretations hang on a single character or a handful of characters.

Variation Within and Between Species

Yet, despite varied interpretations of the relationships among early hominins, researchers generally have accepted the idea of a fairly speciose lineage, with hominin species most likely living contemporaneously at multiple points in the last six million years. Paradoxically, despite this acceptance of wide diversity, there has been a noticeable lack of attention paid to one of the basic themes in evolutionary biology—understanding variation. In early hominin systematics we believe that the problem is twofold, involving: (1) our lack of knowledge of within-species variation for many poorly sampled hominin species, and (2) a lack of consideration of the evolutionary underpinnings of variation between species.

As was detailed above, a number of early hominin species have fairly large hypodigms, especially *A. afarensis*, *A. africanus*, and *P. boisei*. For these species, our understanding of intraspecific variation is good (e.g., Constantino & Wood, 2004; Kimbel et al., 2006; Lockwood, Richmond, Jungers, & Kimbel, 1996; Wood, Wood, & Konigsberg, 1994), and generally taxonomic interpretations—including assessments of acceptable levels of within-species variation—are well grounded within a firm understanding of variation in extant primate species. However, for a number of early hominins the patchy fossil record makes understanding the magnitude and pattern of intraspecific variation impossible. This greatly affects our ability to assess fossil diversity, and therefore draw taxonomic conclusions, as data-poor science allows for significant error in interpretation. Many early hominin species have been diagnosed based on very small effective sample sizes of as few as one individual; this is particularly true for the early hominins

named since 1994 (Smith, 2005).³ This trend may be due to the general tendency among paleoanthropologists over the past decade to interpret any diagnosable difference between new finds and previous hypodigms as reason enough to define a new species. However, this is not entirely the cause; *P. aethiopicus* is not a recent find, and yet has become embedded into our taxonomy, despite being represented by only a cranium and mandible. Tellingly, with the application of appropriate statistical methods for dealing with such small samples, many of species diagnoses would not be supportable (Smith, 2005). Perhaps more significantly, while many investigators dealing with very small fossil samples in their diagnoses present extinct and extant comparative data (particularly for dental metrics), even the comparative samples are generally quite small, and the effects of such small samples and disparate sample sizes (not to mention differences in body size dimorphism) on the interpretation of their data are generally not reported or discussed (Smith, 2005). In making judgments of similarity, difference, and group membership on the basis of small sample sizes, paleoanthropologists are susceptible to well-understood cognitive biases. People (whether laypersons or experts) tend to underestimate the importance of sample size and overestimate any observed differences or effects when they make all kinds of decisions that require judgment in the presence of uncertainty, including their interpretation of representativeness, chance effects, predictability, and validity (Tversky & Kahneman, 1974). These issues are serious stumbling blocks to the rigorous interpretation of fossil diversity, and on these methodological grounds alone it can be argued that speciose interpretations of early hominin evolution are premature at best.

The second issue—a lack of attention to variation *between* species—reflects more of a conceptual shortcoming, rather than a statistical/methodological one. What is lacking is a consideration of *why* high levels of interspecific diversity might exist, if indeed they do⁴. The vast bulk of the recently announced species are

³ Effective sample size is an expression of known trait variability. Early hominin species with very limited trait variability at the time full species rank was proposed include: *O. tugenensis* (N = 1, except N = 2 for maxillary and mandibular third molars and a proximal femur); *S. tchadensis* (N = 1, except N = 2 for maxillary third molar); *Ar. kadabba* (N = 1, except N = 2 for a few dental dimensions); *Ar. ramidus* (N = 1, except N = 2 for humerus and a few teeth); *A. anamensis* (N = 1, except N = 2–4 for several posterior teeth); *A. bahrelghazali* (N = 1); *K. platyops* (N = 1, except N = 2 for some temporal bone features); *A. garhi* (N = 1); *P. aethiopicus* (N = 1). See discussion in Smith (2005).

⁴ There is reason for concern that these estimates are too high, as this level of diversity is unexpected for animals of a similar size—for a discussion of this issue in the genus *Homo*, see Conroy (2002).

named based on a descriptive, qualitative diagnosis (bigger, smaller, etc.) with almost no discussion of the evolutionary underpinnings of such lineage diversity. This may be the byproduct of the nature of many first-announcement publications (e.g. short, high-profile reports), rather than the intent of the researchers, but regardless the morphologically speciose scenario outlined above suggests several branching events in human evolution⁵, resulting either from the action of selectively neutral processes or because these organisms were adapting to distinct niches. In fact, various commentaries on this diversity have interpreted the “bushiness” as signaling an evolutionary history resplendent with adaptive radiations and innovations (Begun, 2004), resulting in a picture “in which anatomical features are ‘mixed and matched’ in ways that we are only beginning to comprehend” (Wood 2002: 134). Put another way, the different, mosaic combinations of traits that we see are interpreted as signaling the occupation of divergent niches.

In the remaining sections we wish to examine the evidence for such lineage divergence. We will focus first on whether there is any discernable signal of adaptive radiation(s) acting in early human evolution, especially clear evidence that early hominin genera occupied distinct adaptive zones (*sensu*) (Mayr, 1950) or show finer-scale evidence of niche differentiation. Much of this discussion will focus on evidence for differences in resource exploitation, as this is the most probable explanation for niche diversification within any group of primate. Because many of the descriptions of pattern differences between early hominin taxa hang on the notion that traits are being combined in unexpected, mosaic ways (e.g. ‘mixed and matched’ morphology), we will then ask whether this mosaic patterning is itself evidence for divergent adaptations within a single lineage. Unfortunately, these questions have not been asked of many species in the early hominin fossil record, and our intent is that this discussion serve as a foundation and stepping stone for future research directions in the field.⁶

⁵ Branching events do not, of course, preclude anagenetic change, and in fact there is good evidence for such an ancestor-descendent relationship from *A. anamensis* to *A. afarensis* (Kimbel et al., 2006). However, most interpretations of this diversity suggest that cladogenesis is also present (Begun, 2004).

⁶ In framing such research, we think it needs to be recognized that the literature on human evolution has tended to accept the possible implications of a very limited set of general processes that describe patterns of speciation (such as competitive exclusion) while essentially ignoring other important generalizations about species diversity (such as niche construction and self-organized similarity) (Laland & Sterelny, 2006; Scheffer & van Nes, 2006).

Whither Adaptive Radiation?

An adaptive radiation refers to the evolution of phenotypic and ecological diversity within a lineage that is rapidly multiplying (Schluter, 2002). According to Schluter (2002), four features may be used to detect an adaptive radiation: common ancestry, phenotype-environment correlation, trait utility, and rapid speciation. Let’s assume that we are sampling organisms that share a common ancestor (which they invariably do, at some point in time) and that speciation occurred rapidly (a reasonable assumption given the short time depth under consideration). The remaining two criteria are necessary for demonstrating that the phenotypic differences between taxa are adaptive and that these adaptations are related to the occupation of distinct ecological niches. So the questions become: (1) is there clear evidence among early hominins for links between morphology and aspects of the environment (phenotype-environment correlation), and, (2) do the traits under consideration provide some sort of fitness advantage (trait utility)?

Let’s first consider what we know about the early hominin environment. As discussed above, the bulk of the early hominins lived in a mixed environment, typically located near water (either rivers or lakes), with some combination of forest (generally located near the water sources, such as along the rivers), bush/scrub, and grassland. This is a classic environment along vast stretches of eastern Africa, from Ethiopia to South Africa, although there are many variations on this theme. Within such a varied environment it is difficult to tell precisely which micro-niche(s) the hominins occupied; this is further complicated at a number of localities where the hominins were often accumulated by predators. But there are a few hominin genera that may have been occupying very different environments. *Ardipithecus* has been reported to be a closed woodland genus, and as such it has been suggested that these hominins were “ecological apes” (Andrews, 1995), somewhat analogous to the chimpanzee in that respect. *Paranthropus* may also have occupied a distinct environment, emerging as it does towards the end of the Pliocene and persisting into the Pleistocene during what was a period of general aridification and increasing grasslands. Of course, broad differences in paleoenvironment alone are unlikely to be informative for considering the adaptive underpinnings of early hominin diversity. This is because primates are known to be ecological generalists under many circumstances, and as a result a single species of primate can live across a wide range of environments. For example, baboons range across most of sub-Saharan Africa, spanning a diversity of environments, including the harsh winter rainfall region of the Western Cape (South Africa), the mountainous Drakensberg in South Africa, the arid Namibian deserts, the riverine Okavango Delta of Botswana, the rugged Ethiopian Rift Valley, the gallery forests

of Ghana, and the Tanzanian savannah, to name a few. *Papio hamadryas*⁷, therefore, represents an example of a single primate species that occupies all of the ecological niches represented in early hominin evolution.

Accepting that it may be difficult to assign precise environments to any early hominin, do we see signs of a clear link between morphology and aspects of the environment? Moreover, do the traits under consideration provide some sort of fitness advantage? The early hominin genus for which we have the best information is *Paranthropus*. Considering the last question first, there is indirect evidence for cranial trait utility; analyses of morphological evolution of the face within this lineage have shown that natural selection (rather than drift) drove diversification (Ackermann & Cheverud, 2004a), in the form of positive selection in the lateral regions of the face. Combined with other morphological evidence (extremely large cheek teeth, flaring zygomatic arches, sagittal cresting, etc.) (Grine, 1988; Wood, 1991; Wood & Chamberlain, 1987), this confirms a longstanding hypothesis that selection has acted on aspects of morphology that are tied to diet. Turning to the first question, traditional interpretations have linked these aspects of the phenotype directly to the changing environment, suggesting that *Paranthropus* species were specialized, hard-object feeders, evolving huge masticatory apparatuses during a time of increased aridification. Yet, at the same time dietary studies of South African hominins suggest that there are no substantial differences in isotopic composition between the diets of *P. robustus* and *A. africanus*, with both consuming significant proportions (~30%) of C₄ or C₄-derived foods such as grasses, sedges, or animals that ate these plants (see discussion in (Lee-Thorp & Sponheimer, 2006)). This suggests that the morphological adaptations in *Paranthropus* may reflect their fallback foods rather than differences in their typical dietary regime, a notion that is consistent with recent behavioral studies of chimpanzees and gorillas which also propose that dietary differences are primarily tied to fallback foods (Stanford, 2006). Taken together, the morphological and dietary evidence suggest that selection was acting to diversify paranthropines in terms of their diet, driving them into overlapping but nonetheless distinctive niches relative to other hominins. Interestingly, rather than becoming specialized, the phenotypic changes in this lineage probably reflect their ability to access a wider range of resources, perhaps as an adaptation to increasing seasonality (Sponheimer et al., 2006b).⁸

⁷ There is considerable debate surrounding baboon taxonomy, and whether the myriad forms are distinct at the subspecific or specific level. For a view representing the latter, see Grubb et al. (2003).

⁸ Given this, the cause of their subsequent demise is no longer clear (Wood & Strait, 2004).

With regard to the other early hominin genera, the picture is less clear. There has been no quantitative study of the fitness advantage of traits for any of the earlier hominins. Correlations between aspects of the phenotype and the environment are also not well established. As these studies of *Paranthropus* have highlighted, dietary adaptations are one of the key drivers in human evolution, and can be important indicators of differences in resource exploitation and niche differentiation. Although similar isotopic studies of earlier hominins have not been done, studies of dental morphology and microwear suggest that the movement towards a strategy of accessing a wider variety of dietary resources (e.g. the beginning of hard-object feeding) may well have started quite early on in the australopith lineage (Teaford & Ungar, 2000; Ungar, 2004; White et al., 2006). Recently, studies of molar microwear in *A. afarensis* and *A. anamensis* indicate that these species may have relied on terrestrial herbaceous vegetation (Grine, Ungar, & Teaford, 2006a; Grine et al., 2006b), in contrast to what their dental morphology suggests. How these findings correlate to differences in environments is unclear, although they do indicate that many early hominins may have similar strategies for obtaining food; further research combining such information with morphological and paleoecological evidence will provide needed insight into how hominins differ in their patterns of resource use. Similar studies have not been conducted on other early hominin genera outside of *Australopithecus* or *Paranthropus*, although they have the potential to help determine whether indeed these hominins were accessing distinctly different resources and were therefore adaptively divergent. It would be of great interest, for example, to know whether *Ardipithecus*, as a presumed closed woodland hominin, had an isotopic signature comparable to that of a chimpanzee, particularly because chimpanzee populations living in very different environments have consistent isotopic signatures, as they select similar foods (Sponheimer et al., 2006a). Similar questions could and should be asked of the other late Miocene species.⁹

⁹ Of course, there are other ways to detect niche differentiation as well. For example, because of the close relationship between absolute body size and diet across all primates (Fleagle, 1999), differences in body size among early hominins may themselves provide a signal of niche differentiation. In fact, size evolution in primates is a likely consequence of adaptation to fill empty dietary niches (Marroig & Cheverud, 2001, 2005). Unfortunately, reliable estimates of body weight are unavailable for the earliest hominin taxa, leaving researchers to compare other aspects of morphology—such as tooth size—as a surrogate for overall size differences. From about 4.2 million years, we have somewhat better size estimates (Jungers, 1988; McHenry, 1992), which indicate that these australopiths are generally comparable in body size. Similarly, correlations between different locomotor adaptations and environments would indicate that these hominins occupied a diverse range of habitats. However, substantial postcranial material is not available for a number of early hominin genera, making comparative studies difficult.

To sum, combined morphological and dietary information has offered a complicated picture of the evolutionary underpinnings that drove the diversification of *Paranthropus*, suggesting that this genus may occupy a different niche or adaptive zone relative to the other hominins. Explanations for diversification among other genera are less clear. We will now examine whether pattern differences (mosaic morphology) are indicative of an adaptive radiation in early hominin evolution.

Pattern Differences and Mosaic Morphology

“...It can hardly be emphasized too strongly that, in assessing the taxonomic position of a fossil specimen, account must be taken of the total morphological pattern (and not its individual units) that provides the reliable morphological evidence on which zoological relationships can be determined. Comparing individual characters independently as isolated abstractions, instead of treating them as integrated components of a complex pattern, is perhaps one of the main reasons a multiplicity of systems of classification of the Primates are still to be found in the literature” (LeGros Clark, 1978: 51).

W.E. LeGros Clark was an early and adamant advocate for assessing the total morphological pattern instead of focusing on trait-based approaches (LeGros Clark, 1955). Part of the reason why he did this is because he was fully aware that phenotypic traits are not independent, but instead part of an integrated complex. This perspective has become commonplace in biology, especially in recent years as our understanding of the evolution of development has shown that much phenotypic change results from underlying regulatory changes (Carroll, Grenier, & Weatherbee, 2005). Within living primates, studies of cranial integration have shown that adults of closely related species share an overall pattern of trait integration and covariation; this is true within very speciose groups such as New World monkeys as well as within less taxonomically diverse (but arguably more relevant) groups such as humans and apes (Ackermann, 2002; Ackermann, 2003; Ackermann, 2005; Ackermann & Cheverud, 2000; Ackermann & Cheverud, 2004b; Cheverud, 1996; Marroig & Cheverud, 2001; González-José, Van Der Molen, González-Pérez, & Hernández, 2004). This suggests that across primates common developmental or functional processes, or both, have operated to keep covariance structure stable.

In light of this, the frequent description of pattern differences in early hominin morphology as ‘mosaic’ deserves further consideration. Most commonly, the term is used by investigators to indicate the piecemeal acquisition of

derived traits. For example, *Ardipithecus kadabba* teeth are described as showing a “mosaic of primitive and derived morphological features” (Haile-Selassie, 2001: 179), including thin enamel relative to *Ar. ramidus* and details of molar cusp morphology (both primitive), with canines that anticipate the morphology of later hominins (derived). Similarly, in the case of *Sahelanthropus*, the mosaic nature refers to the claim that this hominin displays a mixture of primitive (small brain size) and derived (small canines, intermediate tooth thickness) features (Brunet et al., 2002). But the term has also been used more generally to describe the variation between hominins, especially with reference to unexpected combinations of traits. In the case of *Sahelanthropus*, the primitive, chimpanzee-like neurocranium is expected for a hominin of such antiquity, while the more advanced (*Homo*-like?) face is not (Guy et al., 2005). Another example is in *Orrorin*, which has a pattern (small molars, big body) different from the australopithecids (big molars, small body). *Kenyanthropus*, with a flat *Homo*-like face and small brain is another example. In fact, Wood (2002: 134) predicted that future early hominin finds will consist of “creatures with hitherto unknown combinations of hominid, chimp and even novel features.”

What is most interesting about this mosaic depiction is that it implies that from 6 to 1 million years we are sampling a picture of diversity in which the overall morphological pattern differs greatly between closely related organisms (Fig. 2). For example, genera living in close temporal proximity can have small brains with either large faces or small faces; small molars with thick or with thin enamel; thick enameled molars that are either large or small; small canines that are diamond or V-shaped, and so on. Assumedly, this implies that different aspects of the phenotype—and particularly the cranium and dentition, as the bulk of comparisons are among craniodental characters—are independently modularized at quite a small scale, and can therefore evolve independently, producing very different patterns in different individuals. However, unlike size changes, *pattern* changes are very difficult indeed from an evolutionary point of view (Björklund, 2003). Moreover, the presence of very different morphological patterning is inconsistent with what we know about the evolution of the primate skull; as discussed above, studies of integration in living primates have shown that primate skulls are highly integrated, and that closely related species *share* an overall pattern of trait integration and covariation.¹⁰ In other words, when considering the relative patterning of trait covariation, the crania of even closely

¹⁰ There are, of course, exceptions to this. For example, the primary contributors to facial integration in apes and humans are the zygomatic and oral regions, while studies of both Old and New World monkeys indicate integration in the oral region alone. Nevertheless, the overall pattern of covariation is similar.

related primate species—which nonetheless diverged as long as 30 million years ago—tend to differ most often in degree, not in kind.¹¹

Moreover, we also know from studies of living primates that evolutionary divergence, including adaptive radiations, occurs most often along the line of least evolutionary resistance—e.g. size (Marroig & Cheverud, 2005). For example, in a study of 110 New World monkey species, Marroig and Cheverud (2005) showed that the vast bulk of their cranial diversification has been size-related (Marroig & Cheverud, 2005). Furthermore, when evolutionary change does not occur along the size dimension (in this example four genera), morphological change tends to be small and slow (Marroig & Cheverud, 2005). Other primates, including baboon subspecies (Frost, Marcus, Bookstein, Reddy, & Delson, 2003; Jolly, 1970; Jolly, 2003), and African apes (Shea, 1983) have also diverged cranially primarily in size and size-related shape.

What are the implications of this discordance between the typical primate pattern and current interpretations of early hominin diversity? It's not entirely clear. Early hominin diversity does not appear to be characterized primarily by size differences, and yet at the same time interpretations of this diversity imply large pattern changes during macroevolution. What we could be seeing is a very different patterning of interspecific diversity than typically exists in living primate clades, due to the fact that this is special (i.e., human) evolution.¹² But this seems highly unlikely. It is more likely that interpretations of pattern diversity are flawed. One possible explanation for this relates back to sample sizes and the skewed perspective poor sampling can provide. Ranges of variation within many of these species are unknown, and therefore inter-individual differences can easily be misinterpreted as inter-species differences. It is noteworthy that better sampled early

¹¹ Here too, cognitive biases affect our interpretations, as the placing of objects into categories (differentiated by degree, or kind) is not only a method of taxonomy and phylogenetic modeling, but a fundamental process by which all humans organize the world. As summarized by Murphy (2003: 514):

...people are far too willing to latch onto a possible category for objects and then to rely on it even when it is uncertain...there is a strong drive from early childhood to categorize entities and to assume that such categories reflect deep and important regularities...not only do we rely on categories when they are uncertain, simply asking about a category results in our using categorical information.

¹² Humans are not just apes at a different size, so some reorganization of morphological patterns has occurred at some point. We acknowledge that there are exceptions to the primate rules, however, multiple exceptions within a highly-branched lineage are unlikely.

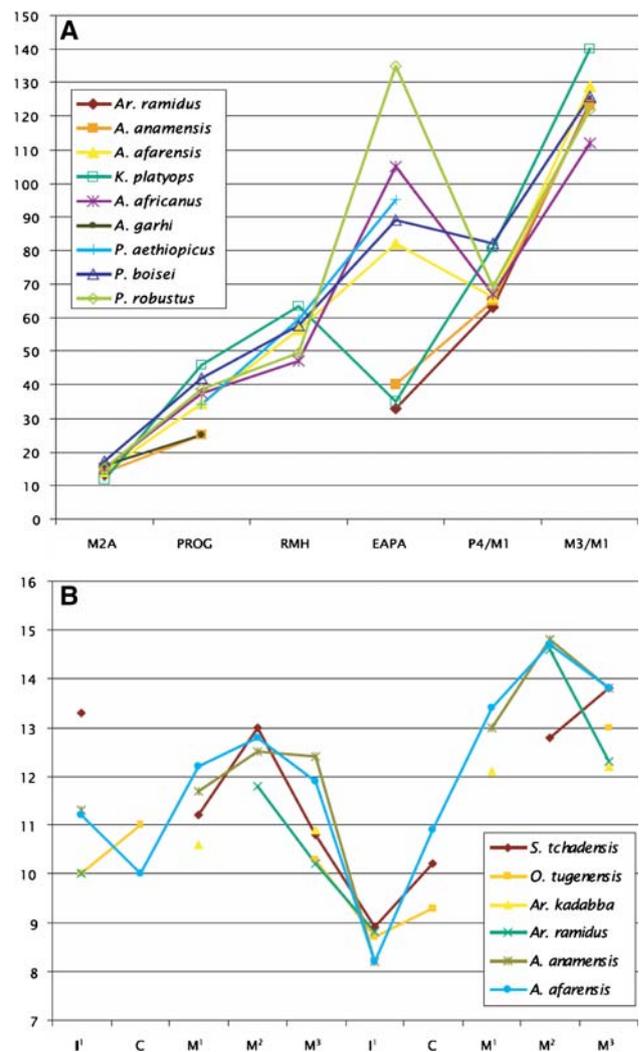


Fig. 2 Some pattern differences in early hominin craniodental measurements. (A) The mean values for the following six characters are estimated from Fig. 3 in (Leakey et al., 2001): M2A = Square root of the M² area; PROG = degree of subnasal prognathism; RMH = relative molar height, expressed as a percent; EAPA = external acoustic porous area; P4/M1 = P₄ area/M₁ area; M3/M1 = M₃ area/M₁ area. The data are graphed together for ease of comparison—as a result the Y-axis represents different things for different variables (e.g. mm², degrees, or percentages). (B) Buccolingual and mesiodistal tooth measurements in the upper dentition are taken from Table 2 in (Brunet et al., 2002); Y-axis is in millimeters. Note in both figures that even for this handful of characters there are distinct differences among the hominins in terms of their overall patterning. However, it is also important to note that few of the samples used to calculate these means have n>10 for any given trait, and most are represented by n < 5, undoubtedly making these poor estimates of true population means

hominins such as *A. afarensis* display high levels of intraspecific variation (Lockwood, Kimbel, & Johanson, 2000; Plavcan, Lockwood, Kimbel, Lague, & Harmon, 2005; Reno, Meindl, McCollum, & Lovejoy, 2003; Reno, Meindl, McCollum, & Lovejoy, 2005). However, it may

also be that we are sampling from very different lineages, where trait covariation has been altered dramatically due to divergent evolutionary adaptations. This needs to be seriously reconsidered and investigated, especially given the rather conspicuous lack of ape fossils during the late Miocene and early Pliocene. Either way, we believe that interpretations of mosaicism as indicating very different patterning, within a lineage of closely related organisms that have gone through a series of adaptive radiations, require further scrutiny.¹³

A Way Forward

Recently, a number of paleoanthropologists have interpreted early hominin evolution as bushy, with many branching events indicating adaptive radiations and subsequent niche-filling. As a result, the broader scientific community has been quick to accept the notion of an increasingly speciose early hominin lineage. This is frustrating to many of us in the field, as we ourselves find it difficult to evaluate many of these fossils; very little has been published on the most recent hominin discoveries outside of their original descriptive publications. Here we asked whether there is clear evidence, given the current state of knowledge, for such high levels of lineage diversity in early hominins. Sample sizes and related statistical issues alone make species delineation problematic for a number of these taxa, but beyond this we are confronted with numerous unanswered questions and unclear signals. The possible causes of adaptive radiation and associated between-species variation in morphology have not been considered at great length for most of these taxa. Given our understanding of living primates, the most probable explanation for such diversification within any group of primate is that they were occupying distinct niches driven by resource exploitation. We might be able to detect this in their diets, or perhaps more grossly by differences in size.

¹³ Another possible explanation for mosaicism that has received little attention is gene flow, an important shaper of diversity when one is dealing with small populations. Although a number of recent studies have suggested that hybridization is more common than previously appreciated in hominin evolution, these studies have overwhelmingly focused on the genus *Homo* (Brown et al., 2004; Reed, Smith, Hammond, Rogers, & Clayton, 2004; Stefansson et al., 2005; Swisher et al., 1996; Trinkaus, 2005; Zilhao & Trinkaus, 2002). Only one study has been concerned with earlier hominin evolution, and this focused on hybridization between chimpanzee ancestors and early hominins (Patterson, Richter, Gnerre, Lander, & Reich, 2006), rather than between early hominins. What does a tree look like if there is reticulation? This is not clear and needs to be tested, though assumedly hominin populations would diverge more slowly, and hybrid populations would display a wider range of phenotypic variation than you would see in the parental populations (Ackermann, Rogers, & Cheverud, 2006).

To date, we have little direct evidence for either in the earliest hominins, in part because the analyses have yet to be done, though there is good evidence within *Paranthropus* for adaptive diversification driven by diet. The description of early hominin morphology as “mosaic” is also enigmatic, as we know that closely related primates tend to be cranial variants, with divergent evolution occurring primarily (again) in size; this is not the pattern we see in these hominins. Given the current evidence, we suggest that evaluations of these hominins in terms of descriptive demonstrations of difference are of limited value in assessing adaptive divergence. Instead, more consideration needs to be given to approaches that evaluate species diversity in terms of what we know about the links between interspecific variation and the causes of macro-evolutionary divergence.

Acknowledgements We thank Benedikt Hallgrímsson for inviting us to write this review. Jim Cheverud, Charlie Lockwood, Matt Sponheimer, and three anonymous reviewers provided extremely helpful comments on previous versions of this manuscript.

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