



Patterns of resource use in early *Homo* and *Paranthropus*

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Abstract

Conventional wisdom concerning the extinction of *Paranthropus* suggests that these species developed highly derived morphologies as a consequence of specializing on a diet consisting of hard and/or low-quality food items. It goes on to suggest that these species were so specialized or stenotopic that they were unable to adapt to changing environments in the period following 1.5 Ma. The same conventional wisdom proposes that early *Homo* species responded very differently to the same environmental challenges. Instead of narrowing their niche it was the dietary and behavioral flexibility (eurytopy) exhibited by early *Homo* that enabled that lineage to persist. We investigate whether evidence taken across eleven criteria supports a null hypothesis in which *Paranthropus* is more stenotopic than early *Homo*. In six instances (most categories of direct evidence of dietary breadth, species diversity, species duration, susceptibility to dispersal, dispersal direction, and non-dietary adaptations) the evidence is inconsistent with the hypothesis. Only one line of indirect evidence for dietary breadth—occlusal morphology—is unambiguously consistent with the null hypothesis that *Paranthropus*' ability to process tough, fibrous food items (e.g., leaves) was reduced relative to early *Homo*. Other criteria (habitat preference, population density, direct and indirect evidence of dietary breadth related to incisor use) are only consistent with the hypothesis under certain conditions. If those conditions are not met, then the evidence is either inconsistent with the hypothesis, or ambiguous. On balance, *Paranthropus* and early *Homo* were both likely to have been ecological generalists. These data are inconsistent with the conventional wisdom that stenotopy was a major contributing factor in the extinction of the *Paranthropus* clade. Researchers will need to explore other avenues of research in order to generate testable hypotheses about the demise of *Paranthropus*. Ecological models that may explain the evolution of eurytopy in early hominins are discussed.

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Introduction

There is still considerable debate and dispute about the details of human evolutionary history. Some of this disputation focuses on the number of

species in the hominin fossil record with some workers willing to accept as many as 17 species (e.g., Wood, 1996a; Foley, 1999; Tattersall, 2000) while others consider the same fossil evidence samples only nine (Wolpoff et al., 1994), or even fewer species (Henneberg and Thackeray, 1995; Thackeray et al., 1997; Eckhardt, 2000). The other focus of discussion is whether hominin evolution is

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mainly ‘transformational’ (i.e., dominated by anagenesis) or ‘taxic’ (i.e., dominated by cladogenesis) (Eldredge, 1979). Yet, proponents on both sides of these debates (e.g., Wolpoff et al., 1994; Wood, 1996a; Asfaw et al., 1999), despite their fundamentally different interpretations of hominin alpha taxonomy and macroevolution, agree that between three and two million years ago a major cladogenetic event resulted in two adaptively distinct hominin lineages. It is also generally agreed that the hominins immediately antedating this major cladogenesis belong to a grade of hominin we will refer to informally as the australopiths. However, the taxa presently subsumed into *Australopithecus sensu lato* are probably paraphyletic and may exhibit more adaptive diversity than is generally recognized (e.g., Chamberlain and Wood, 1987; Skelton and McHenry, 1992; Strait et al., 1997; Wood and Collard, 1999; Lieberman, 2001).

One of the two lineages postdating the australopiths includes the only extant hominin species, *Homo sapiens*. The other lineage, which has no extant representative, includes hominin species some workers retain in *Australopithecus*, but which others have returned or transferred to the genus *Paranthropus*. Whatever the details of the taxonomy (reviewed in Wood and Richmond, 2000) most researchers accept that the taxa incorporated in *Homo* and *Paranthropus* respectively comprise the best evidence we have for hominin clades. It is thus not surprising that the *Homo/Paranthropus* dichotomy has been a consistent feature of hominin phylogenies for nearly half a century (e.g., Robinson, 1954a, pp. 197; Campbell, 1962, pp. 228 and 231, and see below).

Since the acceptance and widespread recognition of the *Homo/Paranthropus* dichotomy the dominant explanatory paradigm has been that these genera diverged from each other, and from other hominins, because the component species of each genus adopted very different adaptive strategies. *Paranthropus* species were considered to be “specialists”, whereas *Homo* species and *A. africanus* (which he later included in *Homo* [Robinson, 1965]) were judged to have adopted a “generalist” strategy (Robinson, 1954a). This dichotomy was most explicitly expressed with respect to the dentition. Nearly four decades ago

Robinson (1963: 391–392) referred to the *Paranthropus* dentition as “unbalanced” and “specialized” with an “emphasis on crushing and grinding”, whereas the more “balanced pattern of tooth size” seen in *Homo* was said to be indicative of omnivory. Subsequently, the labels ‘stenotopy’ and ‘eurytopy’ (*sensu* Eldredge, 1979; Vrba, 1980) were applied to the respective dietary adaptations of *Paranthropus* and *Homo* (Vrba, 1988).

Robinson’s (1954a) ‘Dietary Hypothesis’ has been enormously influential. Its basic premise that *Paranthropus* was a dietary specialist has been reinforced by numerous studies in craniofacial functional morphology (e.g., Du Brul, 1977; Hylander, 1979a; Rak, 1978, 1983; Ward and Molnar, 1980; Sakka, 1984), dental microwear (Grine, 1981, 1986; Kay and Grine, 1988), comparative dental anatomy (Robinson, 1956; Lucas and Luke, 1983a,b, 1984; Lucas et al., 1985; Luke and Lucas, 1983) and primate ecology (Jolly, 1970). Although some studies have presented evidence that *Paranthropus* may not be a dietary specialist (Walker, 1981; Demes and Creel, 1988; Peters, 1987; Sillen, 1992; Sillen et al., 1995; Lee-Thorp and van der Merwe, 1993; Lee-Thorp et al., 1994), they have made little impression on the conventional wisdom as originally set out by Robinson (1954b). As a result, for much of the past 40 years the fates of *Homo*, the more flexible eurytope, and *Paranthropus*, the narrow-niched stenotope, have been contrasted. The paradigm referred to above suggests that whereas the dietary and other flexibility shown by the members of the *Homo* lineage allowed it to survive the climatic vicissitudes of the Plio-Pleistocene, the specialized dietary niche of *Paranthropus* species ultimately proved unequal to the same challenge.

We have re-examined the evidence for interpreting *Homo* as a eurytope and *Paranthropus* as a stenotope. We conclude that equally, if not more, convincing arguments can be put forward for *Paranthropus* being a eurytope. As for *Homo*, while overall its earliest members appear to have been eurytopes, they may have been stenotopic in at least some of their adaptations.

In this paper we set out the background to the existing explanatory paradigm, review the criteria

for stenotopy and eurytopy, and then apply these criteria to the relevant fossil and other evidence for *Homo* and *Paranthropus*. Lastly, we discuss the implications of this re-examination of the adaptations of these two hominin genera.

Paleoclimate and paleohabitat

In an effort to better understand the *Paranthropus/Homo* dichotomy some researchers have concentrated on reconstructing the paleoclimatic context of these early hominins. Brain (1958) concluded that the microscopic lithology of the Swartkrans Member I sediments indicated a wetter environment than that of Member 4 at Sterkfontein, or of Members 2 and 4 at Makapansgat (Brain, 1958: 121, Fig. 16). Robinson (1963) interpreted these data as being consistent with the Dietary Hypothesis. Subsequently Vrba (1974, 1975) interpreted the bovid assemblages at the sites as suggesting there was better evidence for nearby woodland during the formation of Member 4 at Sterkfontein than during the deposition of Swartkrans Member 1 and the Kromdraai B site breccia. The inference that the predominant climate signal at Swartkrans indicated more arid conditions than those that prevailed at Sterkfontein has recently received support from an examination of the micromammal evidence (Avery, 2001). Meanwhile, in East Africa, paleosol, paleobotanical and microfaunal evidence from the Omo group deposits (Bonnefille, 1976, 1985, 1995; de Heinzelin et al., 1976; Haesaerts et al., 1983; Wesselman, 1984, 1985, 1995) consistently supported a change in vegetation between Members B and C. Thus, by the time Members E and F of the Shungura Formation were being deposited a more xeric habitat had become established. Later research would show that the timing of this ‘habitat shift’ corresponds approximately to the earliest evidence for *Paranthropus boisei sensu stricto* (Suwa, 1988; Wood et al., 1994; Suwa et al., 1996; Alemseged, 2003). Thus, in both of the geographical regions where relevant fossil evidence has been recovered at least some environmental interpretations suggest the appearance of *Paranthropus* apparently coincided with a shift to a more xeric regime.

This ‘climatic forcing’ hypothesis to explain the origins of *Paranthropus* and *Homo* (Coppens, 1975; Vrba, 1985a, 1988) was an important component of the evidence supporting what Vrba termed the ‘Turnover Pulse Hypothesis’ (TPH) (Vrba, 1985b). This hypothesis proposed that between 3 and 2 Ma there was a link between global and regional climate change (summarized in Partridge et al., 1995a,b, and Shackleton, 1995) and patterns of mammalian species origination and extinction (i.e., macroevolution). The TPH has subsequently been refined (Vrba, 1992, 1993, 1995a), elaborated (Vrba, 1994, 1995b), tested (e.g., Bobe and Eck, 2001; Bobe et al., 2002) and challenged (Foley, 1994; McKee, 1995, 2001; Behrensmeyer et al., 1997; Prothero, 1999). Nonetheless, it remains the most influential of the ‘scenario-level’ (*sensu* Tattersall and Eldredge, 1977) hypotheses put forward to explain the origin of the *Paranthropus* and *Homo* clades (e.g., Stanley, 1992; Turner and Wood, 1993; de Menocal, 1995; Wood, 1995; Conroy, 1997, pp. 37–41; Bilsborough, 1999; Klein, 1999, pp. 251–253).

Potts’ (1998a) ‘Variability Selection Hypothesis’ (VSH) takes a different view of the influence of climate on human evolution. It focuses on the influence of a combination of the scale and rapidity of climate change (de Menocal, 1995; Kennett, 1995; Peizhen et al., 2001), and suggests that this combination of factors during the Plio-Pleistocene was responsible for adaptations that “enhanced behavioral versatility and ultimately ecological diversity in the human lineage” (Potts, 1998a, p. 93). Crossing a crucial threshold in cultural complexity may have been a critical component of that versatility and the implications of the VSH need to be tested against appropriately taphonomically-controlled (Bobe and Eck, 2001) fossil and archeological records.

Eurytopy and stenotopy

A little over half a century ago Simpson (1950) reminded human origins researchers of what he termed the ‘principles of historical biology’. In the section of that paper devoted to adaptation he

Table 1

Variables predicted to be correlated with stenotopy and eurytopy (*sensu* Eldredge, 1979; Vrba, 1980)

Variables	Stenotopy	Eurytopy
1. Dietary breadth	Narrow	Broad
2. Habitat preference	Function of key resource	No strong preference
3. Species diversity	High	Low
4. Species duration	Short	Long
5. Sympatry among sister-species	Possible	Not possible
6. Population density	Function of key resource	Function of total carrying capacity of region
7. Susceptibility to vicariance and dispersal	High	Low
8. Dispersal direction	Function of environmental change	Unconstrained
9. Continuity of range	Can be discontinuous	Continuous
10. Degree of apomorphy	Apomorphic	Apomorphic or plesiomorphic
11. Morphological adaptation	Narrow	Broad

referred to the types of “basic adaptive processes” researchers might expect to observe in the evolutionary history of any group, including hominins. One of the possible adaptive responses he referred to was the “narrowing or specialization of adaptive type from more general to more specific, or ecologically from a wide to a narrow niche” and another was the “converse broadening of adaptive type” (Simpson, 1950: 63). These types of adaptations are what we now refer to as ‘stenotopy’ and ‘eurytopy’. Eurytopic species, or ‘generalists’, exhibit broad utilization and tolerance of a range of environments, whereas stenotopic species, or ‘specialists’, exhibit narrow utilization and limited environmental tolerance (Eldredge, 1979; Vrba, 1980, 1989). These definitions have long been conventional in evolutionary ecology (e.g., Pianka, 1978; Morse, 1980; Rosenzweig, 1995; Maurer, 1999). Species can be specialists with respect to certain environmental variables, and generalists with respect to others, but typically species are characterized as being predominantly stenotopic or eurytopic.

As a result of these differential patterns of environmental tolerance, generalists and specialists are predicted to have different evolutionary histories (Table 1). Some of these predictions concern species-level properties (e.g., duration, distribution, morphology, etc.). Other predictions concern clade-level properties (e.g., species diversity). Each property, or criterion, has a different

expression in stenotopes and eurytopes. However, an important caveat regarding the predicted differences concerns the preferred resource of the specialist. A stenotope has essentially the same tolerance of environmental change as this resource. If the resource itself can tolerate extreme change, then so may the specialist. In cases like this, the specialist will have the evolutionary profile of a generalist. Thus, when attempting to evaluate whether an extinct organism is a generalist or specialist, one should also consider the ecological tolerances of the resources available to it.

This review tests the hypothesis that differences in the evolutionary histories of two hominin clades (and their included species) are due to different adaptive strategies, eurytopy dominating in early *Homo* and stenotopy in *Paranthropus*. The properties of the two clades (and when data are available, for species within the clades) are assessed to see whether they are consistent, or inconsistent, with the hypotheses of eurytopy and stenotopy, respectively, for *Homo* and *Paranthropus*.

Obviously, evaluations at the level of the clade assume robust taxonomic and phylogenetic hypotheses. Although the details of early hominin phylogeny remain controversial we accept for the purposes of this paper that *Paranthropus* and *Homo* are each monophyletic. We acknowledge that ‘early *Homo*’ (*H. habilis sensu stricto*, *H. rudolfensis*, *H. ergaster*, *H. erectus sensu stricto*)

is adaptively heterogeneous and may be paraphyletic. Indeed, these are the factors that prompted one of us to suggest that *H. habilis s.s.* and *H. rudolfensis* be attributed to *Australopithecus* (Wood and Collard, 1999). Nonetheless, for the purposes of this study we retain the traditional taxonomy and employ the widely used informal taxonomic group ‘early *Homo*’ to refer to the species named above. We recognize three taxa within the genus *Paranthropus*, *P. boisei sensu stricto* (hereafter referred to as *P. boisei*), *P. aethiopicus* and *P. robustus*. Species-level and clade-level predictions are evaluated relative to other early hominins. We have made no attempt to characterize these hominin taxa as being stenotopic or eurytopic relative to other mammals.

The hypothesis of early *Homo* eurytopy and *Paranthropus* stenotopy focuses primarily on diet. Although we examine other aspects of early hominin paleobiology we concentrate on evidence that is directly or indirectly germane to the dietary manifestations (i.e., euryphagy and stenophagy) of eurytopy and stenotopy. In part, this focus derives from the fact that teeth, jaws and other cranial remains are disproportionately well-represented in the hominin fossil record, but it is also highly probable that selection acting on dietary regimes has played a major role in shaping the different evolutionary histories of these genera. The other non-dietary criteria (Table 1) are considered to see if their evidence supports, or runs counter to, the deductions made on the basis of the dietary evidence.

It is important to note that the terms “generalist” and “specialist” are being used here in a strict ecological sense, in that they refer specifically to the breadth or narrowness of a given species’ ecological niche. The common informal uses of these terms are not employed here. In particular, the use of the term “specialized” is not equivalent to “derived” (i.e., apomorphic) or “well adapted for”. With respect to degree of apomorphy, many specialized features may be derived, but not all derived features are specialized in that they result in a narrow use or tolerance of environmental variables. Regarding adaptation, specialist features may in fact be well adapted to performing particular behavioral roles, but if a given adaptation

has the effect of broadening the overall ecological niche of the species, then it is effectively a “generalist” feature.

The differences between the formal and informal definitions of these terms can be significant. For example, it is conventional to consider *Alouatta* species dietary specialists because they have evolved morphological adaptations that allow them to efficiently process one of their major resources (leaves). Although leaves are, indeed, a major component of their diet throughout the year these primates also consume a wide variety of food resources, including fruits and flowers (e.g., Crockett and Eisenberg, 1987; Fleagle, 1999). It is only during certain seasons (when other resources are not available) that these species exclusively exploit leaves. Their adaptations for eating leaves may allow them to remain in their territories during parts of the year when other species lacking those adaptations must leave (Garber, pers. comm.). Thus, although these species are so-called “seasonal specialists” and even though they have adaptations that allow them to perform certain behaviors exceptionally well (i.e., eating leaves) they are nonetheless ecological generalists in that they have a broad usage of the resources in their environment and a high tolerance of environmental change. Indeed, their flexible diets and their ability to exploit ‘fall-back’ food items are likely to be the reason these species occupy a broad geographic range across a variety of habitats. Thus, the ability to seasonally shift one’s diet is a key generalist adaptation (Rosenzweig, 1995).

Among living primates, there are probably relatively few examples of true stenotopes. Most species generalize to one degree or another. However, *Tarsius* is an example of an ecological specialist. From a dietary standpoint, it relies entirely on insects throughout the year (although its dependence on particular insect species shifts seasonally, see Gursky, 2000) and its locomotor skeleton makes it fully dependent on arboreal substrates (e.g., Fleagle, 1999). If either of these components were to be removed from their environment, it is difficult to see how tarsiers could persist without structural adaptation. Callitrichinae and *Daubentonia* are also good examples of primates that are relatively specialized.

Null hypothesis

The null hypothesis to be evaluated by this review posits that the species of *Paranthropus* were substantially more stenotopic, or specialized, than those of early *Homo*. We examine each of the criteria set out below to determine whether they are consistent or inconsistent with this proposal. Note that this hypothesis can be rejected in several ways: (1) if, with respect to a given criterion, *Paranthropus* displays the eurytopic condition and early *Homo* displays the stenotopic condition, (2) if both *Paranthropus* and early *Homo* display the eurytopic condition, and (3) if both *Paranthropus* and early *Homo* display the stenotopic condition. Note that possibilities (2) and (3) represent simplified interpretations insofar as it is assumed that if both groups of taxa share a broadly similar adaptive strategy, then one group cannot be substantially more generalized, or more specialized, than the other. Examination of possibilities (1) and (2) above reveals that whenever *Paranthropus* exhibits the eurytopic condition, the hypothesis is rejected with respect to the given criterion. Similarly, possibilities (1) and (3) indicate that the hypothesis is rejected whenever early *Homo* shows the stenotopic condition. Furthermore, possibility (3) indicates that rejection of the hypothesis does not necessarily mean that *Paranthropus* is a generalist.

Criteria

Eleven criteria are examined in which stenotopes are expected to differ from eurytopes. Of these, the first two (dietary breadth and habitat preference) are probably the most directly related to ecology, and, for certain species, the best documented in the fossil record. Thus, dietary breadth and habitat preference should be given the most weight when interpreting the adaptive strategies of *Paranthropus* and early *Homo*, and the remaining criteria should be viewed as secondary, supporting, evidence.

In order to evaluate the criteria it is necessary to assume that the hominin fossil record as currently known is a reliable reflection of human evolutionary history. Obviously, the possibility that the

fossil record has been affected by taphonomic bias, and that fossil preservation and the stratigraphic record are better in East than in southern Africa, means that any conclusions about hominin adaptive strategies must be drawn cautiously. New fossil discoveries may overturn the conclusions of the present study, but this is true of all paleontological research. The goal of this study, therefore, is to attempt to interpret the data at hand. Any conclusions will serve as hypotheses that can be tested by future discoveries of hominin fossils, or by using new methods of analysis.

Dietary breadth

Insofar as the availability of food resources is tied to other environmental variables (e.g., temperature, seasonality, humidity) dietary breadth is often a key variable in assessing whether a species is stenotopic or eurytopic. With respect to early hominins, the presumed difference in adaptive strategy between early *Homo* and *Paranthropus* is explicitly a “Dietary Hypothesis” (Robinson, 1954a). Certainly, other variables must be considered, but, for example, it is difficult to argue that *Paranthropus* is a stenotope if it is not also stenophagic (i.e., has a narrow diet). Dietary breadth in early hominins can be assessed using either direct or indirect evidence.

Direct evidence

Dental microwear and trace element and stable isotope ratios can potentially provide direct evidence about dietary preferences. However, these three methods of analysis have important limitations. First, different dietary combinations may result in the same microwear signal and trace element or isotope ratio (Schoeninger, 1995). Second, in order to control for ecological variation specimens from the same species should be sampled from fossil localities known to have different paleoenvironments. For reasons discussed below, this is difficult to do for fossil hominin sites. Finally, relatively few hominin species have been examined using these techniques, with most research concentrated on *A. africanus* and *P. robustus*. For all of these reasons, this study interprets microwear, trace element and isotope evidence

conservatively. Rather than infer the particular types of food ingested (e.g., nuts, tubers, graze, browse, meat) the discussion below focuses on whether early hominins were eating many, or just a few, types of food.

Microwear

Dental microwear studies of early hominins have focused on the molars of southern African australopiths. Grine (1981) qualitatively examined Phase I (shearing) and Phase II (grinding) facets in the deciduous molars of *A. africanus* and *P. robustus*. On the basis of wear patterns, Grine (1981) surmised that jaw movements during both Phase I and Phase II were steeper in the ‘gracile’ than in the ‘robust’ species. Moreover, at high magnification, the images suggested a higher incidence of both pits and total number of microwear features on *Paranthropus* molars. Grine (1981) interpreted these results to mean that habitual mastication in *A. africanus* consisted of shearing leaves and fleshy fruits, while *P. robustus* was designed for grinding hard, small, or “gritty” objects. The results of subsequent quantitative analyses of microwear on adult maxillary molars (Grine, 1986; Kay and Grine, 1988) were consistent with these conclusions. Walker (1981) made a detailed examination of *P. boisei* and found that the pattern of dental microwear could not be distinguished qualitatively from those of primate frugivores (e.g., chimpanzees, mandrills, and orangutans).

Thus, the molar microwear pattern of *P. boisei* appears to differ from that of *P. robustus*. There are several possible explanations for this difference: (1) the diets of these species differ, (2) the diets are comparable, but the microwear signals reflect paleoecological differences at the respective sites from which the fossils were sampled, and (3) the then contemporary methods for comparing quantitative and qualitative microwear patterns were inadequate. It is difficult at present to choose between these alternatives. If it is confirmed that the two species have different microwear signals, then, with respect to the question of eurytopy vs. stenotopy, one can conclude that the two *Paranthropus* species are, at a minimum, not specialized for the same type of diet. Whether they are specialized for different diets, or are dietary generalists

capable of eating whatever is presented, cannot at present be determined on the basis of microwear alone. More quantitative hominin molar microwear studies are needed before the null hypothesis of the present study can be rejected.

In addition to molar microwear, Ungar and Grine (1991) have examined patterns of incisor microwear in *A. africanus* and *P. robustus*. They found that these species were similar with respect to several microwear patterns (scratch orientation, the size of microwear features, and the ratio of pits to scratches), but that *A. africanus* had a higher density of microwear features. They interpret these results to mean that *A. africanus* used its teeth more extensively to process food items. Ungar and Grine (1991) further suggest that the observed differences in microwear pattern indicate that *A. africanus* may have ingested a wider variety of foods. Such a conclusion might imply that *Paranthropus* had a narrower, stenotopic, diet. However, a complication with this interpretation is that *Paranthropus* may have processed food with tools, rather than incisors. Such a behavioral pattern could conceivably explain the low density of microwear features observed in *P. robustus* without implying that the species had a narrow diet. Without better evidence regarding tool-use in *Paranthropus*, incisor microwear data are not by themselves a valid test of the null hypothesis. The most that can be concluded is that incisor microwear is consistent with *Paranthropus* stenophagy only if *Paranthropus* did not use tools for food preparation.

Trace element analysis

Strontium/calcium ratios are diet-sensitive because bone preferentially absorbs ingested Ca rather than Sr. Thus, as one moves up the food chain from plant to herbivore and then to carnivore the ratio of Sr/Ca should decrease (Table 2). However, Sr levels are partitioned in plants. They are lower in leaves (including grass leaves) than in roots, stems, seeds and fruits. Thus, high Sr/Ca ratios are indicative of a non-leaf-eating herbaceous diet, while low ratio values are consistent with either folivory (leaf eating) or carnivory. Interpretation is further complicated because Sr concentrations in the geological substrate vary

Table 2
 $\delta^{13}\text{C}$, Sr/Ca and microwear signatures expected from various food items

Food item	$\delta^{13}\text{C}^1$	Sr/Ca ²	Molar microwear ³
<i>Plant food:</i>			
Soft, fleshy fruit	Low	High	Few features
Tree leaf	Low	Low	Scratches
Fruit seed/Nut	Low	High	Pits
Tuber	Low	High	Pits
Grass leaf	High	Low	Scratches ⁴
Grass root/stem	High	High	Pits ⁴
Grass seed	High	High	Scratches ⁴
<i>Animal food⁵</i>			
Grazer (grass leaf)	High	Very low	Few features ⁶
Grazer (grass root/stem)	High	Low	Few features ⁶
Browser (tree leaf)	Low	Very low	Few features ⁶
Browser (fruit, berry, etc.)	Low	Low	Few features ⁶
Mixed feeder	Medium	Low	Few features ⁶

¹Lee-Thorp et al. (1994); Schoeninger (1995); Sponheimer and Lee-Thorp (1999).

²Sillen (1992); Sillen et al. (1995).

³Walker et al. (1978); Teaford (1985, 1988, 1993); Kay and Grine (1988); Daegling and Grine (1999); Grine (pers. comm.); Solounias (pers. comm.).

⁴The microwear signals of different parts of grass (leaf, stem, seed) are not well established. *Theropithecus gelada* seasonally shifts its diet among all parts (Iwamoto, 1993), and has a microwear signal of scratches (Teaford, 1993). However, Solounias (pers. comm.) finds that grit adhering to grass roots may produce pitting.

⁵Refers to vertebrates only.

⁶Unless diet includes bone crunching behavior.

from location to location. Thus, Sr/Ca ratios are difficult to interpret in migratory animals and in the carnivores that eat such animals. The first trace element analysis of early hominins found that two Omo specimens attributed to *Homo* sp. (L 427-7 and 894-1) had elevated Sr/Ca ratios compared to *P. boisei* (L 71-125) and folivorous herbivore comparators (Boaz and Hampel, 1978). However, the results of this initial study included apparently anomalous values for certain mammalian species. Sillen (1992) has since noted that researchers had yet to appreciate the complexity of the pattern by which Sr/Ca ratios reflect trophic level.

The most comprehensive studies of Sr/Ca ratios in early hominins are those of Sillen and colleagues (Sillen, 1992; Sillen et al., 1995) on *P. robustus* and *Homo* specimens from Swartkrans. Sillen (1992)

established that fossils of non-hominin mammals from Swartkrans exhibited Sr/Ca ratios consistent with their place in the food web. Thus, carnivores and folivores had low ratio values, non-leaf-eating herbivores high values, and omnivores or mixed-feeders intermediate values. Sr/Ca ratios in *P. robustus* were moderately low (Sillen, 1992), but greater than those observed in carnivores and folivores, and less than those observed in baboons, an omnivore. In contrast, the Sr/Ca ratios of early *Homo* specimens (including SK 847) were higher (Sillen et al., 1995), being comparable to those of baboons. The pattern of elevated values in *Homo* and lower values in *Paranthropus* is consistent with the observations of Boaz and Hampel (1978) regarding the East African fossil record. Sillen et al. (1995) suggested that the most likely cause of the low Sr/Ca ratio value in *P. robustus* was meat in its diet. They ventured that the elevated ratios in early *Homo* were due to the latter's exploitation of underground food resources, such as tubers.

Regardless of whether or not Sillen's interpretations are correct, several points are clear. Neither *P. robustus* nor early *Homo* ate exclusively seeds or tubers. If they had done so, their Sr/Ca ratios would have been much higher. Thus, although these food items may have been significant components of the *Paranthropus* diet, one cannot conclude that *Paranthropus* specialized in eating them. Moreover, the ratio values in *P. robustus* are somewhat higher than those of specialized carnivores or folivores (but as Sillen [1992] noted the functional morphology of this species is inconsistent with exclusive carnivory or folivory). Thus, trace element analysis is inconsistent with *P. robustus* being stenophagic. Instead, the results are consistent with the hypotheses that both *P. robustus* and early *Homo* were euryphagic. Thus, trace element data appear to be inconsistent with the null hypothesis.

Stable carbon isotope analysis

Stable carbon isotope analysis (Lee-Thorp et al., 1994) is based on the premise that the two main photosynthetic pathways (dubbed C₃ and C₄) produce molecules that differentially incorporate the ¹³C and ¹²C isotopes. The C₃ pathway, found in trees and shrubs, discriminates against the ¹³C

isotope, thus $^{13}\text{C}/^{12}\text{C}$ ratios are lower in C_3 plants than in C_4 vegetation such as grasses (Table 2). These isotopic differences are passed to the herbivores that eat the plants, and the carnivores that eat the herbivores. When extracted from bone, stable carbon isotope ratios, expressed as $\delta^{13}\text{C}$ (Lee-Thorp et al., 1994), are expected to range from -16 to -10 per mil in browsers (and the animals that eat them) and from -2 to 2 per mil in grazers (and their predators) (Sponheimer and Lee-Thorp, 1999).

Stable carbon isotope analysis has been performed on teeth belonging to *P. robustus* and *A. africanus*. Lee-Thorp and van der Merwe (1993) and Lee-Thorp et al. (1994) observed that *P. robustus* from Swartkrans has intermediate $\delta^{13}\text{C}$ values ranging from -10 to -6.8 , with an average of -8.5 per mil. These results indicate that *P. robustus* obtained approximately 75% of its food from C_3 plants (or from browsers that eat such plants) and 25% from C_4 plants (or from grazers). Sponheimer and Lee-Thorp (1999) obtained similar results for four *A. africanus* teeth from Makapansgat, which had $\delta^{13}\text{C}$ values ranging from -10.7 to -5.3 per mil., and a separate study (van der Merwe et al., 2003) of ten *A. africanus* teeth from Sterkfontein yielded $\delta^{13}\text{C}$ values between -8.8 and -4.4 per mil. Lee-Thorp and colleagues (Lee-Thorp and van der Merwe, 1993; Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999; Lee-Thorp et al., 2000; Lee-Thorp et al., 2003) suggest that the C_4 component of the diets of these species may have come from the consumption of grazing animals, but they point out that there are other dietary pathways by which these hominins could have obtained their $\delta^{13}\text{C}$ values. Again, regardless of whether or not these species ate meat, it is clear that both *P. robustus* and *A. africanus* were consuming a range of foods. Taken overall, the results of stable carbon isotope ratio studies are inconsistent with a hypothesis of *P. robustus* stenophagy and allow the null hypothesis to be rejected.

Summary of the direct evidence

There is only one early hominin species, *P. robustus*, in which dental microwear, Sr/Ca ratios, and $\delta^{13}\text{C}$ values have been assessed. This species

exhibits a high incidence of pitting on its molars, a low density of microwear features on its incisors, a moderately low $\delta^{13}\text{C}$ value and a low Sr/Ca ratio. When compared with the major food items likely to be available to *P. robustus* (Table 2), it is clear that no single food item can be responsible for the conditions observed in that taxon. It is probable that only seeds, nuts, or tubers could be responsible for the high incidence of pitting observed on *P. robustus* cheek teeth. However, Daegling and Grine (1999) have recently examined molar microwear patterns in the tuber-eating *Papio ursinus* and found that the incidence of pitting in this species far exceeds that seen in *P. robustus* and in seed- and nut-eating primates (Kay and Grine, 1988). The pitting in *P. ursinus* is apparently caused by exogenous grit adhering to the tubers. Daegling and Grine (1999) doubt that exogenous grit associated with ingested tubers is responsible for the pitting pattern observed on *P. robustus* teeth. Thus, we may conclude that if tubers were consumed by *P. robustus* they did not leave any obvious microwear signal.

If seeds, nuts and tubers of C_3 plants comprised the majority of *P. robustus*' diet then one could perhaps conclude that this species was a stenophage. However, because *P. robustus* specimens have low Sr/Ca ratios, seeds, nuts and tubers are likely to have been, at most, a modest component of their diet (Table 2). This implies that 1) the rest of the diet would have been composed of a mixture of C_3 and C_4 based foods (i.e., plants and/or the animals that eat them), 2) such foods must be consistent with a low Sr/Ca value, and 3) their molar microwear signal should not override that imposed by the hard items mentioned above. Meat and marrow fit these criteria, but so do other food items. Rather than attempt to be specific about the nature of the *P. robustus* diet we simply note that several types of food were apparently consumed by this species, with the caveat that these foods were not extensively prepared using incisors. This result is consistent with euryphagy and is inconsistent with stenophagy. Consequently, in this respect the null hypothesis can be rejected.

Indirect evidence

Functional morphology has traditionally been an important line of evidence for assessing whether

taxa are generalists or specialists. A critical difficulty, however, in discriminating specialist from generalist morphology is that while a novel anatomical feature might be designed to exploit a very specific resource or perform a specific behavior, if it does not also limit the ability of the organism to exploit other resources or perform other behaviors, then it can have the effect of broadening the adaptations of its possessor. Such a possibility speaks to the difference between what [Bock and von Wahlert \(1965\)](#) termed the “*faculty*” (or form-function relationship) of a feature and its “*biological role*”. In particular, the biological role of a feature may incorporate several form-function relationships. Thus, in order to discriminate generalist from specialist morphology one must consider not only what the morphology allows an organism to do (i.e., the function for which it is designed) but also what it restricts an organism from doing. Morphology that appears to be designed for a specific function, but that does not preclude other functions, does not necessarily indicate stenotopy. For example, bilophodont teeth are well designed for a folivorous diet, but they do not prevent certain cercopithecoids (e.g., *Papio*) from eating a wide range of food items.

If one considers the classic examples of eurytopes and stenotopes, then it becomes clear that the most compelling evidence for stenotopy consists of specialist features that exclude behaviors other than the preferred one. For example, the premaxilla of browsing ruminants, especially bovids, comes to a point such that the incisor rows on either side of the skull are oblique to each other ([Solounias et al., 1988](#); [Solounias and Moelleken, 1993a,b](#); [Spencer, 1997](#)). This morphology allows a browser to select specific leaves on a bush to eat. In contrast, grazers have a premaxilla that is flattened anteriorly with the incisors arranged in line, thereby maximizing the amount of grass that can be cropped with each bite. Each morphology excludes the other type of behavior thus browsers and grazers can each be recognized as specialists. Among bovids, generalists (i.e., mixed feeders) exhibit an intermediate morphology.

Such clear-cut morphological examples are rarely found in early hominins. For example, much of the debate about *Paranthropus* adaptations con-

cerns the function for which various morphological features are best suited. Less attention has been paid to whether those features limit other functions. Here we consider inferences about both the primary function and the potential functional limitations of the characteristic diet-related morphology of *Paranthropus* and early *Homo*. Note, however, that the likelihood that some or all of these hominins used stone tools complicates our ability to draw conclusions regarding the dietary implications of morphology. For example, an examination of morphology alone might lead to the conclusion that certain food items were unavailable to a given species, but if those food items could have been exploited using tools, then that conclusion would be erroneous.

Dentognathic proportions and facial morphology

The face of *Paranthropus* has been described as being “*buttressed*”. Buttressing refers to bony features of the face whose configurations or contours are thought to be designed to resist the high stresses imposed by chewing hard food ([Robinson, 1954b](#); [Rak, 1983](#)). Such features in *Paranthropus* include anterior pillars, dished zygomatics, sloping supraorbital tori, rounded inferolateral margins of the orbits, inflated zygomatics, anteriorly positioned zygomatic roots, and a thick palate. If these features are indeed designed to resist stress, then they might indicate that *Paranthropus* species fed on hard or tough food items that would require either high bite forces or repetitive chewing, respectively. However, although the functional relationships of these features have been widely assumed, they have only rarely been rigorously tested. This shortcoming is due largely to the complex geometry of the face, which precludes attempts to examine facial function using simple biomechanical models. Experimental studies (e.g., [Hylander et al., 1991](#); [Ross and Hylander, 1996](#); [Hylander and Johnson, 1997](#)) have provided information about how the primate face is loaded during mastication, but the functional role(s) of small-scale facial features have yet to be tested. As a result, the degree to which these features resist stress remains hypothetical. Moreover, none of these features exclude the consumption of any particular food type. It is therefore possible that

stress-resisting features in the *Paranthropus* face may have served to add hard or tough foods to an already broad diet. Although the consumption of these foods was sufficiently adaptively significant as to stimulate the evolution of buttressing features, there is no way of directly evaluating how great a proportion of the total diet these foods represented. Thus, the facial buttressing seen in *Paranthropus* is consistent with both stenotopy and eurytopy.

Although many (Robinson, 1954b; Jolly, 1970; Rak, 1983) interpret the masticatory system of *Paranthropus* as being specialized for a hard- or tough-food diet, less emphasis has been placed on the facial and dental reduction seen in members of the genus *Homo*. The dental and facial morphologies of both *Homo* and *Paranthropus* are likely to have been derived from an ancestral condition that approximates that of *A. afarensis* and/or *A. africanus*. Such ancestral morphology would most likely have included relatively large cheek teeth, robust mandibles compared to non-hominins, a moderate to pronounced degree of facial prognathism and a facial skeleton lacking extensive buttressing (e.g., Strait et al., 1997). *Paranthropus* obviously deviates from this condition, and thus is derived. *Homo rudolfensis* and at least some specimens of *H. habilis s.s.* approximate this general ancestral condition (Wood and Aiello, 1998; Wood and Collard, 1999) and thus they are not exceptionally derived in this regard. However, *H. ergaster* and later hominins are clearly derived, albeit in the opposite direction to the dentognathic morphocline within *Paranthropus*.

The derived dentognathic morphology of *H. ergaster* is arguably more ecologically specialized than that of *Paranthropus*. As argued above, the masticatory system of *Paranthropus* does not limit, and may even have broadened, the range of food items that can be ingested. In contrast, reduction in the size of the teeth and jaws could potentially limit the types of food available to *H. ergaster* and later members of the genus *Homo*. A complication with such an interpretation is that it is possible that *H. ergaster* was processing its food extraorally. Thus, foods that would have been in their raw state inaccessible to *H. ergaster* might nonetheless have

been exploited. Thus, the derived dentognathic reduction seen in *H. ergaster* and later members of the genus *Homo* is consistent with stenotopy, but is not necessarily inconsistent with eurytopy.

In summary, the facial features of *Paranthropus* might be adaptations for eating hard or tough food items, but they are not obviously stenotopic features. The facial features of some early *Homo* species appear to be stenotopic, but this conclusion is mitigated by the likelihood that these species used tools. Thus, facial features are not diagnostic with respect to the null hypothesis.

Mandibular corpus size and robusticity

Functional explanations for the massive and robust mandibles seen in *P. boisei* and other hominin taxa are similar to those of facial buttressing. Namely, the robust corpora and symphysis of the mandible may be designed to resist high stresses (e.g., Robinson, 1956; Tobias, 1967; Wolpoff, 1973; White, 1977; Rak, 1983; Wood and Aiello, 1998). The mandible is easier to model biomechanically than the face and thus more is known about how it withstands biomechanical stresses associated with feeding (Hylander, 1979a,b, 1981, 1984, 1985; Hylander and Crompton, 1986; Hylander et al., 1987). In particular, a deep corpus resists bending moments in the sagittal plane and a thick corpus and symphysis resists torsion and the wishboning stresses that are generated when high bite forces and high muscle forces are simultaneously applied to the working and balancing sides, respectively (Hylander, 1988; Daegling and Grine, 1993). However, just as in the case of facial buttressing features, reinforcement of the corpus and symphysis might be needed to avoid fatigue due to repetitive chewing, so the ultimate adaptive explanation for the feature remains unclear (Hylander, 1988). Indeed, insofar as the mandible houses the tooth roots, one could argue that a robust mandible is simply a non-functional consequence of having large teeth (but see Daegling and Grine, 1993). Regardless, a robust mandible does not preclude any particular diet type. Thus, this feature, too, is consistent with both eurytopy and stenotopy. The much smaller mandibular corpus of the *H. ergaster* component of early *Homo* (Wood and Aiello, 1998; Wood and Collard, 1999)

suggests a diet devoid of hard items that need to be crushed within the mouth. However, this morphology does not exclude hard items that could be processed extra-orally (e.g., nut cracking in *Pan*). As was the case with facial features, mandibular morphology is not diagnostic with respect to the null hypothesis.

Masticatory musculature

Ectocranial morphology suggests that species of *Paranthropus* had relatively massive masticatory muscles (e.g., Robinson, 1954b; Tobias, 1967; Rak, 1983). This is particularly evident from the large rugosities on the zygomatic arch and mandibular ramus for the attachments of the masseter muscle, and the sagittal and temporonuchal crests marking the origin of temporalis. The masseter is also relatively anteriorly-positioned, thus increasing its mechanical advantage. In addition, the relatively anteriorly-placed sagittal crest in *P. boisei sensu stricto* has led some to argue that the anterior fibers of temporalis were especially well developed (Tobias, 1967; Wolpoff, 1974; Kimbel et al., 1984; Kimbel and Rak, 1985). These factors led to the conclusion that the masticatory musculature of *Paranthropus* species was able to generate high, vertically oriented forces on the posterior part of the tooth row. This has been interpreted by some as indicating a hard-food diet for this species (e.g., Jolly, 1970), but other researchers have suggested that bite forces relative to occlusal area are no higher in *Paranthropus* than in other hominins (Walker, 1981; Demes and Creel, 1988). This latter interpretation is consistent with a diet in which a large amount of food is being processed with each bite (Walker, 1981). The two interpretations are not mutually exclusive. The conclusion that bite force relative to occlusal area in a megadont species is the same as in a non-megadont species is also consistent with the notion that when the megadont species applies its bite force to a restricted bite point (as when a hard, round object is loaded by flat teeth), then the stress experienced by the food item will be extremely high. Thus, a high muscle force can be applied to various types of food items and is consistent with the predictions of both eurytopy and stenotopy.

The reduction in masticatory musculature of *H. ergaster* relative to that of earlier hominins is consistent with either a switch to softer foods, or if hard foods did form part of its diet, then these would have been prepared extra-orally using tools. Masticatory musculature is apparently not diagnostic with respect to the null hypothesis.

Anterior tooth size

Incisors in *P. robustus* and *P. boisei* are both absolutely and relatively smaller than those in other early hominins (Tobias, 1967; Wood and Stack, 1980; Ungar and Grine, 1991). Large, spatulate incisors are used by primates to reduce large food items into bite-sized chunks (e.g., Hylander, 1975). Generally, primates with small incisors ingest only those food items that are already bite-sized (e.g., Hylander, 1975). Thus, small incisors are probably related to the absence or removal of selection pressure for large incisors (Teaford and Ungar, 2000). Szalay (1976) has suggested that the peg-like incisors of *P. boisei* were adaptations for carnivory, but this hypothesis has not received support. Rather, this morphology probably indicates that *P. boisei* and *P. robustus* were not processing large food items with their anterior teeth. Such an inference is consistent with patterns of incisor microwear in *P. robustus*. In nearly any other primate this would further imply that large food items were not part of the diet, but in the case of *Paranthropus* there is the possibility that such food items were processed not with the incisors, but with tools (Susman, 1994; Wood, 1997). Thus, although small incisors suggest that *Paranthropus* was not directly ingesting large items, they do not exclude the possibility that large items were being processed in other ways. However, incisors in early *Homo* species are neither exceptionally large or small. Considering that these species presumably used tools at least as, and probably more, extensively than *Paranthropus*, it is clear that tool-use alone does not fully explain the extreme incisal reduction seen in *P. robustus* and *P. boisei*. Whether there was selection pressure favoring small incisors in *Paranthropus*, or if reduced size was simply a result of removing selection favoring large incisors is difficult to determine. One can certainly conclude that if *Paranthropus* did not

use tools extensively, then small incisor size may be indicative of stenophagy and consistent with the null hypothesis. However, if tools were used to prepare food, then incisor size would not necessarily be indicative of dietary breadth.

Canine size reduction has been linked with the facilitation of the side-to-side jaw movements that allow the grinding of hard or high-grit food items (Broom and Robinson, 1949). A potential flaw in this argument is that large canines apparently do not interfere with mastication in other primates with hard-object diets (e.g., mangabeys). Regardless, canine size is also known to be related to non-masticatory social behaviors (see Plavcan, 2001 for a review) and thus one cannot be certain that canine reduction reflects a dietary adaptation. Although some primates (e.g., pitheciines) use their canines to open hard-shelled fruits and nuts (Fleagle, 1999), the small canines of *Paranthropus* are not obviously more unsuited for this function than are those of early *Homo*. Thus, even if one makes the assumption that small canines had the effect of restricting dietary breadth *Paranthropus* would not be more specialized than early *Homo*.

Postcanine tooth size

Premolar “molarization”—enlargement of the mandibular premolar occlusal area by expanding the talonid—has been interpreted as an adaptation for crushing hard food objects. Presumably, hypotheses pertaining to hard-object feeding should also entail biomechanical modifications allowing the maximization of the bite force. However, models of jaw biomechanics (e.g., Du Brul, 1977; Smith, 1978; Rak, 1983; Greaves, 1978; Spencer, 1995, 1998) indicate that the maximization of bite force is unlikely to have involved the premolars. As a generalization, bite forces should decrease as the bite point moves anteriorly because the load arm of the bite force increases. This would indicate that maximum bite forces at the premolars should always be less than those on the molar teeth. This conclusion is tempered by the observation that in order to keep the working-side temporomandibular joint from experiencing tension (which it is poorly designed to withstand) it is necessary to reduce balancing-side muscle force. This might imply that bite forces along the molar and,

possibly, premolar row remain relatively constant regardless of mesiodistal position. Bite forces at the premolars will, therefore, always be less than, or equal to, bite forces at the molars. Thus, for processing hard foods molar mastication will always be equally, if not more, advantageous than premolar mastication. Thus, one must ask why premolars are molarized if such teeth provide no biomechanical advantage. A possible explanation is that premolar molarization is related to processing more food with each bite or to increasing the functional life of the molar teeth by incorporating the premolars into the molar row. Such functions do not specify whether few, or many, types of food resource were being consumed.

A large molar occlusal area could be functionally related to hard- or tough-object feeding in the sense that a large platform would be available for grinding food items (Robinson, 1954b; Jolly, 1970; Grine, 1981; Lucas et al., 1985; Wood and Ellis, 1986). Alternatively, large tooth size might also allow large quantities of food of any type to be processed quickly and efficiently (Walker, 1981). The former function implies a specialist adaptation, while the latter does not necessarily do so. There is no obvious way to choose between these alternatives. Moreover, large molar area does not necessarily preclude any type of food item from the diet. Thus, we conclude that neither molarized premolars nor large molar teeth are diagnostic with respect to eurytopy or stenotopy. In the absence of any evidence of technology the reduction in postcanine crown size in *H. ergaster* and *H. erectus s.s.* might reduce the dietary options of these taxa. Given that tool-use in these species is very likely, little can be concluded from their small cheek teeth. The null hypothesis cannot therefore be evaluated on the basis of occlusal area.

Occlusal morphology

There is a well-known association between occlusal morphology and diet type in primates (Kay, 1981; Maier, 1984). Among hominins, *Paranthropus* has relatively bunodont teeth with little evidence of functional shearing crests. Thus, *Paranthropus* teeth were most likely used to mash or grind food items, but they are unlikely to facilitate (or, in fact, may even hinder) the

consumption of leaves (Teaford and Ungar, 2000). It is fair to conclude, therefore, that leaves were not a substantial component of the *Paranthropus* diet. The exclusion of leaf eating underscores a specialization for crushing and grinding food items, and thus in at least that sense the occlusal morphology of *Paranthropus* appears inconsistent with the predictions of eurytopy, and may be indicative of stenotopy. Early *Homo* teeth are less bunodont than those of *Paranthropus*, but not to the extent that anyone has proposed that fibrous items like leaves were a substantial component of the early *Homo* diet. However, it seems likely that the occlusal morphology of early *Homo* would exclude fewer food items from the diet than would that of *Paranthropus*. Thus, occlusal morphology appears to be consistent with the null hypothesis.

Enamel cap

Paranthropus species possess enamel caps that are relatively thicker than those of any other hominoid (Beynon and Wood, 1986; Grine and Martin, 1988; Schwartz et al., 1998). Thick enamel may serve either, or both, of the following functions (e.g., Kay, 1981). First, it may act as a structural support to prevent the tooth crown from fracturing in response to high stresses imposed by the application of a high bite force onto a hard food item (Macho and Spears, 1999). Second, it may extend the life of the tooth by prolonging the time until occlusal enamel is completely removed by an abrasive, high-grit, diet. Note that the two functions are compatible with each other; both abrasive and high-resistance food objects could be masticated by such teeth. Moreover, there is nothing about thick-enamel that would preclude low-grit or low-resistance (i.e. soft) food items from the diet. Thus, although hyperthick enamel can be functionally related to two types of specialized diets, it is also compatible with a generalized diet. Thus, this feature is consistent with the predictions of both stenotopy and eurytopy and is not diagnostic with respect to the null hypothesis.

Habitat preference

Habitat preference is a key variable in Vrba's (1992) Habitat Theory. In general, steno-

topes, who exhibit narrow utilization and tolerance of one or a few environmental variables, will also have a narrow habitat preference (i.e., they will be stenobiomic). This will be particularly true when the key resource of the stenotope also has a narrow habitat preference. Exceptions are when the key resource of the specialist occurs in multiple habitats (e.g., anteaters; Vrba, 1992).

Establishing habitat preference for an extinct species requires relatively precise knowledge about paleoecology. Although this might appear to be straightforward, debates persist as to the habitat preferences of early hominins, particularly *Paranthropus*. There are a number of reasons for this. First, although the broad strokes of African paleoecology during the Plio-Pleistocene are well established, disagreement remains concerning the paleoecological reconstructions of particular fossil localities or horizons. Second, it is inherently difficult to establish a strong habitat preference, because such a conclusion ultimately rests on negative evidence. In other words, a habitat preference is inferred because a species is found in fossil assemblages representing one habitat, but is absent from assemblages representing other habitats. Such a conclusion might be warranted, but the possibility always exists that better sampling will disprove the hypothesis. In comparison, the lack of a habitat preference is easy to demonstrate. Once fossils are known from sites with different paleohabitats, then a hypothesis of strict habitat preference is falsified (Vrba, 1988). Thirdly, taphonomic processes limit our ability to assemble comparable samples of fossils from the full range of environments. For example, many East African fossil hominin sites are associated with lake or river margins. The presence of water necessarily constrains the number of paleohabitats that might be represented at these sites (e.g., Vrba, 1988; White, 1988). In contrast, the southern African hominin fossils are preserved in karst caves in which many of the bones may have been accumulated by carnivores (Brain, 1981), whose own habitat preferences may be driving the paleoecological signal of the sites. Adding to the complexity, karst cave sites bearing fossil hominins are unknown in East Africa and fossil-hominin-bearing sedimentary basins of a comparable age to those in East

Africa are unknown in southern Africa. Thus, the glimpses into hominin paleoecology provided by the southern and East African fossil sites are not strictly comparable.

It is well established that between 3.0 and 2.0 Ma, Africa experienced the effects of a global cooling trend (Shackleton, 1995). This climatic change ultimately led to a decline in mesic environments in favor of more xeric ones (e.g., Bonnefille, 1983; Wesselman, 1995). In southern Africa, this change is best documented in the faunal assemblages of Makapansgat, Sterkfontein and Swartkrans. In particular, the representation of grazing, open-country bovids is larger in Swartkrans Member 1 than in the chronologically earlier Sterkfontein Member 4 (Vrba, 1974, 1975, 1985a). In East Africa, evidence of this climate change is best preserved in the fauna and flora from the Omo Shungura Formation (e.g., de Heinzelin, 1983). The timing and rate of this change, as well as its effect on mammalian fauna (including hominins) remains controversial (e.g., Vrba, 1995a; White, 1995; Behrensmeyer et al., 1997). However, regardless of exactly how and when the change took place, the appearance of both the *Paranthropus* and early *Homo* clades are roughly correlated with ecological change in the late Pliocene.

Table 3 summarizes paleoecological reconstructions of most of the major geological units preserving early *Homo* and *Paranthropus* fossils in the Plio-Pleistocene of Africa. It is striking how many of these site complexes are reconstructed as being mosaics of multiple types of habitats. One interpretation is that early hominins had access to, and exploited, multiple environments, and thus were eurybiomic. However, an equally plausible interpretation would be that hominins had a preference for one of the habitats common to the various mosaic environments, but presently that habitat cannot be identified. A third interpretation would be that the mosaic “signal” is an artifact of time averaging.

With respect to particular hominin species, *P. robustus* is currently only known from relatively open and arid environments in the vicinity of a permanent stream (Table 3: Kromdraai, Swartkrans). This evidence is based on both faunal (e.g., Vrba, 1975, 1985a,b; Shipman and Harris,

1988; Avery, 2001) and $^{87}\text{Sr}/^{86}\text{Sr}$ stable isotope analysis (Sillen et al., 1998). These results are consistent with the hypothesis that *P. robustus* was an open habitat specialist, but arguably this species is not known from enough sites to establish whether it had a strong habitat preference (Vrba, 1988). Indeed, all known *P. robustus* sites are in close geographic and temporal proximity. It is not surprising, therefore, that they preserve evidence of similar habitats. More sites of varying age and location, preserving different paleoenvironments, need to be found before habitat preference in *P. robustus* can be established.

There has been disagreement concerning the habitat preference of East African *Paranthropus* taxa. Behrensmeyer (1975, 1978) noted that at Koobi Fora, although both *Homo* and *P. boisei* were found in lacustrine deposits, *P. boisei* predominated in fluvial deposits. Behrensmeyer (1975, 1978) was cautious about assigning particular hominins to particular habitats, but she suggested that perhaps *P. boisei* was associated with riverine gallery forests. Shipman and Harris (1988) examined the representation of bovid tribes in many early hominin sites and concluded that *P. boisei* (and what is now recognized as *P. aethiopicus*) preferred closed, wet habitats. Vrba (1988) criticized the methods of Shipman and Harris (1988), even though the same methods successfully categorized the habitats of modern game reserves. White (1988) suggested that bias due to taphonomic effects was likely to frustrate attempts at categorizing the habitat preferences of early hominins. Recently, Reed (1997) examined the ecomorphology and ecological structure of modern African faunal communities and compared them to hominin fossil bearing localities in East and southern Africa. Although she reconstructed many *P. boisei* and *P. aethiopicus* sites as being mosaics, she noticed a consistent association of these species with edaphic grasslands. Her results appear to be indicative of a preference for open, wet habitats. A similar conclusion was reached by Alemseged (1998) with respect to an analysis of the fossil assemblage of a single locality, Omo-323, in unit G-8, of the Shungura Formation that included a fragmentary cranium, Omo-323-1976-896, that has been assigned to *P. boisei*.

Table 3

Paleoecological reconstructions of relevant early hominin fossil assemblages preserving early *Homo* and *Paranthropus*

Site (member) ¹	Age (Ma)	Paleoecological reconstructions	Species
<i>Southern Africa:</i>			
Sterkfontein (Member 4)	~2.6–2.4	Medium density woodland (Vrba, 1974, 1975) Moderately open savanna (Vrba, 1985a) Dry, open habitat (Shipman and Harris, 1988) Open woodland to forest (McKee, 1991) Open savanna (Benefit and McCrossin, 1990) Open woodland with bushland and thicket (Reed, 1997)	<i>A. africanus</i> , <i>H. habilis</i> ?, <i>Paranthropus</i> sp. indet.?
Sterkfontein (Member 5)	~1.8	Open savanna (Vrba, 1974, 1975, 1985a; Shipman and Harris, 1988; McKee, 1991; Reed, 1997)	<i>H. habilis</i>
Kromdraai (B East)	~1.8–1.7	Open savanna (Vrba, 1975) Dense woodland along river margin (Vrba, 1981) Open grassland with patches of riparian woodland (Reed, 1997)	<i>P. robustus</i>
Swartkrans (Member 1)	~1.8–1.7	Open savanna (Vrba, 1975; Shipman and Harris, 1988) Mesic, closed woodland (Benefit and McCrossin, 1990) Savanna woodland with riparian woodland and edaphic grassland (Watson, 1993; Reed, 1997)	<i>P. robustus</i> , <i>H. ergaster</i> ?
Swartkrans (Member 2)	~1.7 or ~1.5 or ~1.1	Moderately open savanna (Vrba, 1975) Open, dry habitat (Shipman and Harris, 1988) Wooded grassland with wetlands (Reed, 1997)	<i>P. robustus</i> , <i>H. ergaster</i> ?
Swartkrans (Member 3)	~1.65 or ~0.85 or ~0.7	Open grassland, with river supporting edaphic grassland (Reed, 1997)	<i>P. robustus</i>
<i>East Africa, north of Turkana region:</i>			
Hadar (Kada)	2.33	Open, dry habitat (Kimbel et al., 1997)	<i>H. habilis</i>
Hadar, BKT-3			
Konso (between KRT and TBT)	1.43–1.41	Dry grassland (Suwa et al., 1995)	<i>P. boisei</i>
<i>East Africa, Turkana region:</i>			
Omo (Shungura C)	<2.95–2.52	Wooded savanna with riverine woodland (Bonnefille, 1976; Bonnefille and Deschamps, 1983) Riverine forest and savanna (de Heinzelin, 1983) Closed, dry habitat (Shipman and Harris, 1988) Mesic woodlands and dense thickets, with some forest and savanna (Wesselman, 1995) Bushland/woodland with riverine forest and edaphic grassland (Reed, 1997)	<i>Australopithecus</i> sp. indet., <i>P. aethiopicus</i>
Omo (Shungura D)	2.52–~2.45	Mesic plant communities, with large forest galleries and some woodland savanna (Bonnefille and Deschamps, 1983; Wesselman, 1995) Riverine forest (de Heinzelin, 1983) Woodland (Bonnefille, 1984) Closed, dry habitat (Shipman and Harris, 1988) Woodland/bushland with riverine forest and edaphic grassland (Reed, 1997)	<i>P. aethiopicus</i>
Omo (Shungura E)	~2.45–2.34	Grassland (Bonnefille, 1976, 1984; Bonnefille and Deschamps, 1983; de Heinzelin, 1983; Wesselman, 1995) Closed, dry habitat (Shipman and Harris, 1988) Well-watered woodland/bushland with riparian forest or woodland (Reed, 1997)	<i>P. aethiopicus</i> , <i>Homo rudolfensis</i> ?

Table 3 (continued)

Site (member) ¹	Age (Ma)	Paleoecological reconstructions	Species
Omo (Shungura F)	2.34–2.32	Dry savanna, open savanna/woodland, steppe, with few mesic woodlands (Jaeger and Wesselman, 1976; Wesselman, 1995) Open savanna (Boaz, 1977) Dry savanna with riverine forest galleries, steppe (Bonnefille and Deschamps, 1983; de Heinzelin, 1983) Grassland (Bonnefille, 1984) Desertic steppe (Bonnefille, 1985) Closed, dry habitat (Shipman and Harris, 1988) Open woodland/bushland with few edaphic grasslands (Reed, 1997)	<i>P. aethiopicus</i> , <i>Homo rudolfensis</i> ?
Omo (Shungura G)	2.32–~1.9	Savanna, riverine forest (Bonnefille and Deschamps, 1983; de Heinzelin, 1983) Closed, wet habitat (Shipman and Harris, 1988) Arid <i>Acacia</i> grassland (Wesselman, 1995) Open woodland, edaphic grassland (Reed, 1997)	<i>P. boisei</i> , <i>P. aethiopicus</i> ?, <i>H. habilis s.s.</i> , <i>Homo rudolfensis</i> ?
Koobi Fora (Upper Burgi)	~2.0–1.88	Grassland and desertic steppe (Bonnefille, 1985) Closed, wet habitat (Shipman and Harris, 1988) Mosaic of bushland, savanna, grassland and some gallery forest (Feibel et al., 1991) Open woodland with edaphic grassland and riparian woodland (Reed, 1997)	<i>P. boisei</i> , <i>H. habilis s.s.</i> , <i>H. rudolfensis</i> , <i>H. ergaster</i>
Koobi Fora (KBS)	1.88–~1.6	Closed, wet habitat (Shipman and Harris, 1988) Wet and dry grasslands, semi-arid savanna, some woodlands (Feibel et al., 1991) Scrub woodland, arid shrubland (Reed, 1997)	<i>P. boisei</i> , <i>H. habilis s.s.</i> , <i>H. rudolfensis</i> , <i>H. ergaster</i>
Koobi Fora (Okote)	~1.6–1.39	Closed, wet habitat (Shipman and Harris, 1988) Wet grassland with dry grassland, woodland, scrub and some gallery forest (Feibel et al., 1991) Wetlands and edaphic grasslands (Reed, 1997)	<i>P. boisei</i> , <i>H. rudolfensis</i> , <i>H. ergaster</i>
West Turkana (upper Lomekwi = Shungura C9)	>2.52	Grassland and marsh (Walker et al., 1986) Open woodland with bushland thickets, edaphic grasslands and wetlands, and riparian woodland or forest (Reed, 1997)	<i>P. aethiopicus</i>
West Turkana (Lokalalei)	2.52–2.34	Closed, wet habitat (Shipman and Harris, 1988)	<i>P. aethiopicus</i>
West Turkana (Kaitio)	1.86–~1.6	Closed, wet habitat (Shipman and Harris, 1988)	<i>P. boisei</i>
West Turkana (Natoo)	~1.6–1.33	Closed, wet habitat (Shipman and Harris, 1988) Woodland and edaphic grasslands with marsh (Reed, 1997)	<i>H. ergaster</i>
<i>East Africa, south of Turkana region:</i>			
Tugen Hills (upper Chemeron)	~3–~1.6	Mosaic of C ₃ and C ₄ plants (Hill, 1995)	<i>Homo s.l. sp. indet.</i>
Lake Malawi (Chiwondo 3A)	~2.5–2.3	Open environment at Malema (Kullmer et al., 1999) Wooded savanna and open grassland with more closed vegetation near permanent water. At the hominin-bearing Uraha site, closed thicket to dry woodland with nearby grassland (Schrenk et al., 1995)	<i>P. aethiopicus</i> or <i>P. boisei</i> ?, <i>H. rudolfensis</i>
Olduvai (Bed I)	1.97–1.74	Lake-margin woodland and forest changing to open grassland higher in the Bed (Hay, 1973; Kappelman, 1984) Open, arid and closed, wet habitats (Shipman and Harris, 1988)	<i>P. boisei</i> , <i>H. habilis s.s.</i> , <i>H. rudolfensis</i> ?

Table 3 (continued)

Site (member) ¹	Age (Ma)	Paleoecological reconstructions	Species
Olduvai (Bed II)	1.71–1.33 or 1.1	C ₄ plants and a gallery woodland in the vicinity of a stream (Blumenschine et al., 2003)	<i>P. boisei</i> , <i>H. habilis s.s.</i> , <i>H. erectus</i>
		Lake-margin woodland changing to open grassland higher in the Bed (Hay, 1971; Kappelman, 1984; Cerling and Hay, 1986)	
Peninj (Humbu) Chesowanja (Chemoigut)	1.7–1.3?	Open, arid and closed, wet habitats (Shipman and Harris, 1988)	<i>P. boisei</i>
	~1.4	Deltaic environment (Dominguez-Rodrigo et al., 2001) Bushed grassland habitat, with riverine and lacustrine elements (Bishop et al., 1978)	<i>P. boisei</i>

¹Sites are organized by region, and within each region, are arranged in approximate chronological order.

A more comprehensive study of changes in the abundance of ecologically sensitive taxa from the Shungura Formation also concluded that “edaphic grasslands became more prevalent in the lower Member G” (Alemseged, 2003, p. 475). As Alemseged points out, this is also the time *P. boisei sensu stricto* is first recognized in the hominin fossil record.

Adding to the confusion, several conflicting paleoecological reconstructions have been proposed for certain of the geological members in the Turkana basin (Table 3: Omo Shungura: E, F, G; Koobi Fora: and KBS and Okote Members). Rather than favor one reconstruction over the other, this study explores what apparently contradictory analyses have in common. Conflicting studies are often based on different types of evidence (e.g., pollen, bovids, micromammals and mammalian communities) and each is likely to be at least partially correct. For example, there is broad agreement that habitats become drier and more open over the course of Olduvai Bed II (see Hay, 1990), but Shipman and Harris (1988) reconstruct site BK (a *P. boisei* site located near the top of Bed II) as having a closed, wet habitat because the bovid fauna is dominated by *Pelorovis*. These reconstructions appear to contradict each other, but given that one reflects a general trend, while the other refers to a particular locality, the reconstructions are compatible. Similarly, the micromammals from Shungura G indicate an open, arid habitat (Jaeger and Wesselman, 1976; Wesselman, 1995), while bovids from the same member

apparently indicate a closed, wet habitat (Shipman and Harris, 1988). Insofar as the micromammals and bovids preserved in this member are associated with particular habitat types, both lines of evidence are likely to be generally true, indicating evidence of either a mosaic habitat, time averaging of different habitats, or perhaps some poorly understood taphonomic processes.

Certain units from which *P. boisei* is known (Omo Shungura: G; Koobi Fora: KBS, Upper Burgi and Okote) have been reconstructed as mosaics thus making them difficult to interpret (Table 3). However, there is consensus that, at least at some localities, *P. boisei* was exploiting wet and wooded environments. In particular, multiple lines of evidence (Table 3; see also Hay, 1971, 1973, 1990), including an analysis of the bovid assemblage from the Olduvai Bed I FLK Zinj site (Shipman and Harris, 1988), indicate that at least some *P. boisei* populations were probably living in wet, densely-vegetated habitats.

The discovery of *P. boisei* fossils at Konso (Suwa et al., 1995) adds significantly to the picture of *P. boisei* paleoecology. The fossil horizon from which *P. boisei* fossils were found (KGA 10) is thought to represent an alluvial fan adjacent to a lake and mammalian taxa recovered from this horizon indicate the presence of open, dry grassland. Interestingly, other horizons at Konso indicate the presence of more closed and wet habitats, but as yet *P. boisei* fossils are absent from those horizons. Suwa et al. (1995) argued that the Konso fossils demonstrate that *P. boisei* was not restricted

to closed, wet habitats. Notably, at least one locality at another *P. boisei* site, Peninj, is linked with a deltaic environment (Dominguez-Rodrigo et al., 2001). Tentative though they may be, these results are inconsistent with the predictions of stenotopy, unless *P. boisei* was exploiting a specific key resource present in a range of habitats. Reconstructions of *P. boisei* paleoecology are, however, consistent with the predictions of eurytopy.

Paranthropus aethiopicus is known from several units with mosaic but generally mesic paleohabitats (Omo Shungura: C, D; West Turkana: Upper Lomekwi, and Lokalalei), and several others with conflicting paleoecological reconstructions (Omo Shungura: E, F, G). Certainly, one can conclude that habitats during Shungura E and F were probably drier than those in C and D, indicating at least some level of ecological flexibility, but beyond this, firm conclusions about the habitat preference of *P. aethiopicus* cannot be drawn.

There is nothing about the ecomorphology of *Paranthropus* species that suggests different habitat preferences. Yet, when viewed collectively, the non-morphological evidence suggests that one species (*P. robustus*) is associated with dry, open habitats, a second (*P. aethiopicus*) is known from both wet and somewhat drier habitats, and the third (*P. boisei*) is known from a variety of habitats. Thus, the genus *Paranthropus* is apparently not specialized ecologically.

With regard to early *Homo*, *H. habilis* s.s. is known from several units with dry, open habitats (Sterkfontein: Member 5; possibly Swartkrans: Members 1 and 2; possibly Hadar: near BKT-3), one unit with a mosaic habitat (Koobi Fora: Upper Burgi), three with conflicting habitat reconstructions (Omo Shungura: G; Koobi Fora: KBS and Okote) and from some localities that had wet, wooded habitats (Olduvai: Lower Bed I). This species was apparently able to subsist in both dry and open, and closed and wet environments. This is indicative of eurybiome, and is consistent with a hypothesis of eurytopy.

The principal fossil evidence for *H. rudolfensis* is associated with a mosaic habitat (Koobi Fora: Upper Burgi). The species is less well known from several units with conflicting habitat reconstructions (Omo Shungura E, F, G; Koobi Fora: KBS

and Okote), and one (Lake Malawi Chiwondo 3A) that indicates a closed, lake-margin habitat. The recently discovered OH 65 (Blumenschine et al., 2003), which the authors claim shares morphological affinities with KNM-ER 1470, was recovered from Olduvai's upper Bed I. The paleoenvironmental setting at this locality indicates the presence of C₄ plants and a gallery woodland in the vicinity of a stream. Collectively, and given the uncertainty over the taxonomic attribution of OH 65, these data are not sufficient to evaluate habitat preference in this species.

Homo ergaster is known from one unit with a wet habitat (West Turkana: Nattoo), two with conflicting habitat reconstructions (Koobi Fora: KBS and Okote), one with a mosaic habitat (Koobi Fora: Upper Burgi) and possibly two (Swartkrans: Members 1 and 2) with dry, open habitats. Thus, *H. ergaster* appears to have been eurybiomic. On the basis of the evidence reviewed above the taxa included in early *Homo* had no strong habitat preference. This is consistent with a hypothesis of eurytopy.

In summary, neither *Paranthropus* nor early *Homo* appears to have a strong habitat preference. These data are inconsistent with the null hypothesis, unless *Paranthropus* specialized on a resource that itself had no habitat preference.

Species Diversity

Although there are exceptions, eurytopes are predicted to show lower speciation rates than stenotopes and thus they are expected to differ with respect to species diversity (Eldredge, 1979; Vrba, 1980). Stenotopes will thrive only under particular environmental conditions (i.e., when their preferred resource is available) and are susceptible to environmental perturbation. Thus, stenotopes are expected to experience natural selection related to resource availability more frequently and more intensely than would eurytopes (e.g., Pianka, 1978; Farrell and Mitter, 1993). It is hypothesized that the high frequency of selective pressures should translate into high speciation and extinction rates for stenotopes (Eldredge, 1979; Vrba, 1980). In contrast, eurytopes are not dependent on particular resources and are thus less

susceptible to environmental change. When faced with the depletion of one resource, the generalist switches to other resources. Thus, eurytopes should have low speciation and extinction rates (Eldredge, 1979; Vrba, 1980). Because of the differences in speciation rate, clades of stenotopes are expected to be highly speciose, whereas clades of eurytopes should show less taxonomic diversity.

Unfortunately, evaluating species diversity in the hominin fossil record is fraught with difficulty. Well-known philosophical differences exist among researchers regarding how best to identify and define hominin species (see Tattersall, 1986, 2000 and Wolpoff et al., 1994 for extreme opposing views). This paper recognizes multiple species within both early *Homo* and *Paranthropus*, but also assesses species diversity using a more conservative taxonomic philosophy.

Among researchers prone to recognize more, rather than fewer species, most agree that the *Paranthropus* clade contains three species (*P. boisei*, *P. robustus* and *P. aethiopicus*). The existence of a fourth species, *P. crassidens* (Broom and Robinson, 1949; Grine, 1982a,b, 1985a,b) is no longer widely recognized. Some workers (e.g., Walker et al., 1986; Walker and Leakey, 1988) conflate *P. boisei* and *P. aethiopicus* into *P. boisei sensu lato*, and thus only recognize two species. In comparison, although some researchers recognize only two taxa, *H. habilis sensu lato* and *H. erectus sensu lato*, in early *Homo* (e.g., Tobias, 1991; Suwa et al., 1996) others now recognize four nearly contemporaneous species of early *Homo* (*H. habilis s.s.*, *H. rudolfensis*, *H. ergaster* and *H. erectus*) (e.g., Wood, 1991) as well as possibly an as yet unnamed species from southern Africa, as represented by one, or more, of Sts 19, Stw 53 and SK 847 (Clarke, 1977; Hughes and Tobias, 1977; Kimbel and Rak, 1993; Grine et al., 1993, 1996).

In contrast, some workers (e.g., Wolpoff et al., 1994; Eckhardt, 2000) argue that all species of early *Homo* should be subsumed within *Homo sapiens*. This proposal requires a single species to accommodate substantial morphological variability, albeit variability that is distributed over time and space. These workers tend to focus on *Homo* rather than *Paranthropus*, but if all early *Homo*

specimens can be grouped into a single species, then surely all of the *Paranthropus* specimens would be attributed to a single species as well. Thus, if one applies comparable taxonomic criteria to each clade and makes the assumption that “undiscovered” taxa are as likely (or unlikely) in both clades, then *Paranthropus* is probably equally speciose, or perhaps slightly less speciose, than is early *Homo*. Thus, data on species diversity are inconsistent with the premise that *Paranthropus* is more specialized than early *Homo*, and the null hypothesis can be rejected.

Species duration

Narrow environmental specialization is hypothesized to induce high extinction rates because stenotopes have a low tolerance for environmental change (Wright, 1932; Eldredge, 1979; Vrba, 1980). Thus, even though stenotopic clades are likely to be more speciose, the species they contain are expected to be relatively short-lived. In contrast, eurytopic species should persist for longer periods of time because they are less susceptible to ecological change (Eldredge, 1979; Vrba, 1980). Hominins, in general, are short-lived relative to other large-bodied mammals. The average duration of a mammalian species is about 2 myrs (Vrba, 1992), but in all but the most conservative taxonomies hominin species do not approach this value. A complication in estimating species duration in hominins is that first (FAD) and last (LAD) appearance dates are often critically influenced by the taxonomic and stratigraphic allocations of particular hominin specimens (Table 4). Moreover, the southern African fossil record is not as well dated and sampled through time as the East African record. Because it is difficult to estimate durations of species endemic to southern Africa we consider both maximum and minimum estimated durations. The maximum and minimum estimated durations of *P. aethiopicus* are comparable to those of other early hominins. The duration of *P. robustus* probably cannot currently be assessed. Both the maximum and minimum durations of *P. boisei* are among the longest observed in any early hominin except *H. erectus sensu lato*. Although the durations of some early *Homo* species

Table 4
First and last appearance dates (FAD, LAD) of early hominin species

Species FAD/LAD	Age (Ma)	Site
<i>A. afarensis</i> :		
Min FAD	3.5	Laetoli (White, 1995)
Max FAD	3.9	Belohdelie, Middle Awash (Asfaw, 1987; White et al., 1993)
LAD	3.0	Hadar (Kimbel et al., 1994)
<i>A. africanus</i> :		
Min FAD	2.8	Makapansgat 3 (Vrba, 1995)
Max FAD	3.0	Makapansgat 3 (Partridge, 1986)
Min LAD	2.4	Sterkfontein 4 ¹ (Vrba, 1995)
Max LAD	2.3	Taung (Delson, 1988)
<i>P. aethiopicus</i> :		
FAD	2.7	Omo Shungura C (Suwa, 1990; White, 1995; Suwa et al., 1996)
Min LAD	2.3	Omo Shungura G (Suwa, 1990; Suwa et al., 1996)
Max LAD	1.9	Koobi Fora (Kimbel, 1995)
<i>P. boisei s.s.</i> :		
Min FAD	2.3	Omo Shungura G (Suwa, 1990; Suwa et al., 1996)
Max FAD	2.5	Lake Malawi (Kullmer et al., 1999)
Min LAD	1.4	Konso (Suwa et al., 1995)
Max LAD	1.1	Olduvai Bed II (Wood, 1991; Aiello et al., 1999; but see Tamrat et al., 1995)
<i>P. robustus</i> :		
Min FAD	1.8	Swartkrans 1/Kromdraai B (Vrba, 1995)
Max FAD	2.0	Drimolen (Keyser et al., 2000)
Min LAD	1.6	Swartkrans 3 (Delson, 1988, 1993)
Max LAD	0.7	Swartkrans 3 (Vrba, 1995)
<i>H. rudolfensis</i> :		
Min FAD	1.9	Koobi Fora ² (Wood, 1991)
Max FAD	2.4	Lake Malawi (Schrenk et al., 1993)
LAD	1.6	Koobi Fora (Wood, 1991)
<i>H. habilis s.s.</i> :		
Min FAD	1.9	Koobi Fora (Wood, 1991; Kimbel, 1995)
Max FAD (east) ³	2.3	Hadar ⁴ (Kimbel et al., 1997)
Max FAD (south) ³	2.6	Sterkfontein 4 ⁵ (Vrba, 1995)
LAD	1.67	Olduvai Bed II (White, 1995; Kimbel 1995)
<i>H. ergaster</i> :		
FAD	1.9	Koobi Fora (Wood, 1991)
LAD	1.5	Koobi Fora, West Turkana (Wood, 1991)
<i>H. erectus</i> :		
Min FAD	1.1	Olduvai Bed II (Hay, 1976; Delson, 1988; Delson, 1990; but see Tamrat et al., 1995)
Max FAD	1.8	Java (Swisher et al., 1994)
Min LAD	0.3	Zhoukoudian (Grün et al., 1997)
Max LAD	0.02	Ngandong (Swisher et al., 1996)

¹If Taung is considered undated (White, 1995). Vrba (1995) assigns Sterkfontein Member 4 a minimum age of 2.4 Ma.

²If UR 501 is not allocated to *H. rudolfensis*.

³The maximum FAD of *H. habilis* depends on whether critical specimens in eastern and southern Africa are allocated to this species.

⁴If AL 666-1 is *H. habilis*, and if Sts 19 is neither *H. habilis*, nor from Sterkfontein Member 4.

⁵If Sts 19 is *H. habilis* and from Sterkfontein Member 4. Vrba (1995) assigns this member a maximum age of 2.6 Ma.

are difficult to assess, *H. habilis s.s.*, *H. rudolfensis* and *H. ergaster* did not obviously persist for a longer period than *Paranthropus* species. Thus, species duration data are inconsistent with the null hypothesis.

Sympatry

A fundamental distinction between generalists and specialists is the degree to which sister-species can be sympatric (Eldredge, 1979; Vrba, 1980). Sympatry should only rarely be observed among sister-species within a generalist clade, because the species would compete for the same (albeit diverse) resources. Ultimately, one species should exclude the other. Thus, eurytopic sister-species should have non-, or only minimally overlapping ranges. In contrast, sympatry among sister-species is possible in stenotopic clades because each species can be so specialized that even though they exploit the same basic resources, each manages to avoid direct competition with another.

Sympatry in a strict sense, of course, cannot be observed in the fossil record. Even if two species were found at the same site in the same stratigraphic level, the time-averaging nature of the fossil record would preclude the conclusion that the two taxa actually shared a range. Nonetheless, a minimal condition for a hypothesis of sympatry is that two fossil taxa are found in the same general area at the same general time. Although such chronological and geographical distributions are not proof of sympatry, they are at least consistent with sympatry.

There is no firm evidence that any of the three *Paranthropus* species overlapped with respect to geographical or temporal range. *P. robustus* is known only from southern Africa and thus does not overlap geographically with the East African *P. boisei* and *P. aethiopicus*. As shown in Table 3, it is possible that *P. boisei* and *P. aethiopicus* overlapped temporally (Wood et al., 1994; Kimbel, 1995). *P. aethiopicus* is well known from 2.7–2.3 Ma and *P. boisei* is known from after 2.3 Ma. It has been suggested that *P. aethiopicus* may persist until 1.9 Ma (Kimbel, 1995), but that possibility depends on the taxonomic attribution of a single

specimen, KNM-ER 1482. Similarly, Kullmer et al. (1999) have recently described a putative *P. boisei* specimen from Malawi (RC 911) dated to 2.5 Ma, but the specimen preserves little diagnostic morphology and could conceivably represent the contemporaneous *P. aethiopicus*. Even if these two attributions are correct, indicating that the species overlapped for several hundred thousand years, it is clear that *P. aethiopicus* predominated before 2.3 Ma and *P. boisei* thereafter. Thus, there is no compelling evidence for *Paranthropus* sympatry. The absence of sympatry is consistent with the predictions of *Paranthropus* eurytypy, but such a result does not allow us to reject *Paranthropus* stenotypy.

In contrast, species of early *Homo* overlap both chronologically and geographically. The taxa *H. habilis s.s.*, *H. rudolfensis* and *H. ergaster* are all found at sites in the Turkana basin between 1.9 and 1.7 Ma (Wood, 1991). Other early *Homo* fossil localities in East Africa span 2.4 to 1.5 Ma (Wood and Richmond, 2000). These data do not by themselves demonstrate sympatry, so a hypothesis of early *Homo* eurytypy cannot be rejected. However, it is clear that the data are consistent with early *Homo* eurytypy only if the overlapping geographic and temporal ranges described above are not indicative of sympatry. Ultimately, the data are not sufficiently diagnostic as to allow the evaluation of the null hypothesis.

Population density

The abundance, or density, of a stenotopic species in a given habitat depends critically on the abundance of its preferred resource (Pianka, 1978). If the resource is abundant, then the species can be abundant as well (e.g., grazers are abundant on grasslands). The density of a generalist will not be limited by any one resource, but may instead be a function of the total carrying capacity of the habitat and the presence of competitors for each of the several resources available to it (Pianka, 1978). Of course, population density is not something that can be observed directly in extinct taxa. The best one can do is to examine the relative abundance of species in the fossil record. This is problematic, because the representation of a species

may be affected by taphonomic bias. Despite this qualification, it is instructive to examine the relative abundances of *Homo* and *Paranthropus*.

Although early hominins are rare components of the African mammal fauna, the fossil record suggests that among hominins *Paranthropus* may have been substantially more abundant than contemporary hominins. This becomes particularly evident by tabulating the taxonomic affinities of hominin specimens found at the four sites (Swartkrans, Drimolen, Koobi Fora, Omo) with the most abundant evidence of fossil hominins during the time period in which *Paranthropus* is known. Of specimens classified to the genus level, *P. robustus* represents 87% (47 specimens) of specimens found at Drimolen (Keyser et al., 2000) while *Homo* sp. accounts for only 13% (7 specimens). At Swartkrans, the numbers are even more skewed (Howell, 1993). *Paranthropus robustus* comprises 96% of such specimens (275) compared to a representation of only 4% (11 specimens) of *Homo* sp. At the Omo (White, 1988; Suwa et al., 1996) specimens identified to the genus level include 51 specimens of *Paranthropus* (67%; this value includes both *P. boisei* and *P. aethiopicus*) and 25 specimens of *Homo* sp. (33%). *Paranthropus boisei* specimens comprise 50% of all hominin cranial fossils classified to the genus level at Koobi Fora (Wood, 1991: Table 7.1) and 58% (54 specimens) of those classified at the species level. In comparison, at the species level at Koobi Fora, *H. habilis* s.s., *H. rudolfensis* and *H. ergaster* comprise 7, 10, and 20% (i.e., 6, 9, 17 specimens) respectively, of the total hominin count. *Paranthropus* was apparently less abundant at Olduvai Gorge, where only three cranial specimens can be confidently attributed to the species (Wood, 1991: Table 7.2), with perhaps as many as three more belonging to the hypodigm (White, 1988).

A crude measure of abundance is the number of sites at which specimens of species have been recovered (Table 5). In this regard, *P. boisei* has been recovered from at least seven East African sites (Koobi Fora; West Turkana; Olduvai; Omo; Chesowanja; Peninj; Konso) and possibly Lake Malawi. In contrast, in East Africa, *H. habilis* s.s. is known from at least two, and possibly three or four, sites (Olduvai, Koobi Fora, and perhaps

Omo and Hadar), *H. rudolfensis* is known from at least three sites (Koobi Fora, Lake Malawi, probably Omo, and potentially at Olduvai), and *H. ergaster* is only securely known from two East African sites (Koobi Fora and West Turkana). Certainly, at least two early *Homo* species may be known from outside of East Africa (*H. habilis* in southern Africa, *H. ergaster* in southern Africa and Eurasia), but within the region from which *P. boisei* is known, they are less well represented.

On balance, during the time period following 2.3 Ma *P. boisei* is the most common hominin recovered from East African sites and *P. robustus* is the most common hominin recovered from southern African sites. Of course, abundance in the fossil record does not necessarily indicate abundance during life. It is possible that taphonomic processes have biased the record so that *Paranthropus* fossils are over-represented relative to those of its contemporaries. One obvious factor is that *Paranthropus* jaws and teeth are absolutely large, and thus might be more prone to fossilization than those of early *Homo*. However, the jaws and teeth of some early *Homo* species (particularly *H. rudolfensis*) are sufficiently robust that this explanation alone probably does not account for the large discrepancies in abundance described above. Another possibility might be that *Paranthropus* represents the preferred prey item of carnivores that may have been responsible for creating the fossil assemblage.

Barring taphonomic bias, if the population density of *Paranthropus* was higher than that of other contemporaneous hominins, this conclusion would be consistent with the predictions of both stenotopy and eurytopy. However, if *Paranthropus* taxa were abundant stenotopes, it would imply that key resource exploited by them was abundant as well (at least in comparison to the resources exploited by other hominins). Thus, abundance data do not definitively test the null hypothesis, but they do set conditions on the possibility that *Paranthropus* was a stenotope.

Susceptibility to dispersal or vicariance

Environmental change is one of several factors (geophysical change being another) that are likely

Table 5
Representation of early hominin species in geological units of African sites

Species	Site complex	Geological unit	Representative specimen ¹	References
<i>P. aethiopicus</i>	Omo	Shungura C	Omo 18-1967-18	Arambourg and Coppens (1967)
		Shungura D	L 296-1	Suwa et al. (1996)
		Shungura E	Omo 57.4-41	Suwa et al. (1996)
		Shungura F	L 860-2	Suwa et al. (1996)
		Shungura G	L 628-4 ²	Suwa et al. (1996)
	West Turkana	Upper Lomekwi	KNM-WT 17000	Walker et al. (1986)
		Lokalalei	KNM-WT 16005	Walker et al. (1986)
<i>P. robustus</i>	Swartkrans	Member 1	SK 48	Broom and Robinson (1952)
		Member 2	SKX 4446	Grine and Strait (1993)
		Member 3	SKX 21841	Grine (1989)
	Kromdraai	B East	TM 1517	Broom (1938)
	Drimolen	Drimolen Main Quarry	DNH 7	Keyser (2000)
<i>P. boisei</i>	Koobi Fora	Upper Burgi	KNM-ER 1469	Wood (1991)
		KBS	KNM-ER 406	Wood (1991)
		Okote	KNM-ER 729	Wood (1991)
	West Turkana	Kaitio	KNM-WT 17400	Walker and Leakey (1988)
	Olduvai	Bed I	OH 5	Tobias (1967)
		Bed II	OH 3	Howell (1978)
	Omo	Shungura G	L 7a-125	Suwa et al. (1996)
		Shungura L	F 203-1	Coppens (1980); Howell and Coppens (1974)
	Chesowanja	Chemeron	KNM-CH 1	Howell (1978)
	Peninj	Humbu Formation	Peninj	Leakey and Leakey (1964)
	Konso	Between TBT and KRT	KGA 10-525	Suwa et al. (1995)
Lake Malawi	Chiwondo 3A	RC 911	Kullmer et al. (1999)	
<i>H. rudolfensis</i>	Koobi Fora	Upper Burgi	KNM-ER 1470	Wood (1991)
		KBS	KNM-ER 1590	Wood (1991)
		Okote	KNM-ER 819	Wood (1991)
	Omo	Shungura E	Omo 177-4525 ¹	Suwa et al. (1996)
		Shungura F	Omo 33-5496 ¹	Suwa et al. (1996)
		Shungura G	Omo 75-14 ¹	Suwa et al. (1996)
	Lake Malawi (Olduvai??)	Chiwondo 3A	UR-501	Schrenk et al. (1993)
Bed I		OH 65 ¹	Blumenschine et al. (2003)	
<i>H. habilis s.s.</i>	Koobi Fora	Upper Burgi	KNM-ER 1813	Wood (1991)
		KBS	KNM-ER 1805	Wood (1991)
		Olduvai	Bed I	OH 24
	Olduvai	Bed II	OH 13	Tobias (1991)
		Omo	Shungura G	L 894-1 ¹
	Omo	Shungura I	Omo 74:-1969-18 ¹	Coppens (1980)
		Hadar	Kada Hadar	AL 666-1 ¹
	Sterkfontein	Member 4 or 5	Sts 19 ¹	Kimbel and Rak (1993)
		Member 5	Stw 53 ¹	Tobias (1978)
	Swartkrans	Member 1	SK 847 ¹	Grine et al. (1993, 1996)
<i>H. ergaster</i>	Koobi Fora	Upper Burgi	KNM-ER 2598	Wood (1991)
		KBS	KNM-ER 3733	Wood (1991)
		Okote	KNM-ER 992	Wood (1991)
	West Turkana	Natoo	KNM-WT 15000	Brown et al. (1985)
	Swartkrans	Member 1	SK 847 ¹	Clarke (1977)
		Member 2	SK 15 ¹	Broom and Robinson (1959)

¹Taxonomic affinities of early hominin specimens are controversial, particularly with respect to fossils of early *Homo*.

²Suwa et al. (1996) attribute L 698-4 to *Paranthropus aff. aethiopicus/boisei*.

to induce biogeographic events such as vicariance and dispersal. Vicariance refers to the splitting of a species' range, whereas dispersal refers to the movement of organisms across the landscape, and can entail range shift, range expansion or jump dispersal (crossing of a faunal barrier by a founding population). Because stenotopes are more sensitive to environmental perturbation than are eurytopes, it is predicted that they will likewise be more prone to dispersal and vicariance (Vrba, 1992). Specifically, short-term environmental instability should lead to vicariance of local habitats, whereas long-term environmental trends should lead to range shift. Thus, global cooling trends should induce mass dispersals towards the equator, while heating trends should spur dispersal in the opposite direction (Vrba, 1994, 1995a). Range expansion in stenotopes is possible so long as their specialized resource expands its range as well. All of these biogeographic events can occur in eurytopes, but at a reduced rate.

Dispersal can be difficult to observe in the fossil record. However, certain types of paleontological data can be interpreted in a biogeographic context. If a species is found in more than one region, then, presumably, a dispersal event between regions has taken place at some point in time. Moreover, phylogenetic patterns constrain biogeographic patterns. Namely, if an ancestor in one region gives rise to a descendant in another region, then a dispersal event has taken place. Of course, phylogeny is not observed directly, but rather is inferred, and so it is fair to say that inferences about phylogeny can inform inferences about biogeography. Each biogeographic hypothesis is therefore derived from a particular phylogenetic hypothesis, and if the latter is incorrect, then so will be the former. However, if one examines several alternative phylogenies, and observes commonalities in the biogeographic patterns implied by them, it is reasonable to have appropriate confidence in those patterns.

Strait and Wood (1999) examined the biogeographic implications of recent hypotheses of hominin phylogeny. Geography was treated as a cladistic character, and for each phylogeny, parsimony was used to reconstruct the pattern by which taxa dispersed between regions. Results suggested

that regardless of which phylogeny was selected, hominin dispersals were more frequent than had previously been supposed (Foley, 1994, 1999; Turner and Wood, 1993; Bromage et al., 1995; Suwa et al., 1996). In each of the phylogenies examined by Strait and Wood (1999: Table 1) a greater number of dispersals are observed within early *Homo* than in *Paranthropus*. Strait and Wood's results must be modified to reflect the fact that *Paranthropus* is now known from Malawi (Kullmer et al., 1999). Depending on the taxonomic affinities of this specimen (RC 911), an additional one, or two, dispersals must have taken place within the *Paranthropus* clade. Nonetheless, there is no evidence that species of *Paranthropus* were more prone to dispersal than were species of early *Homo*. Indeed, many phylogenies imply that species of the latter group dispersed more frequently. These results are inconsistent with the null hypothesis that *Paranthropus* was more stenotopic than early *Homo*.

Dispersal direction

Vrba's (1992) Habitat Theory predicts that large-scale environmental changes will cause large-scale dispersals of mammalian taxa. Thus, depending on the magnitude and nature of the environmental changes, representatives of several mammalian orders should disperse in the same direction at approximately the same time. However, generalists and specialists are expected to differ in the manner in which they participate in these waves of dispersal. Stenotopic species tend to be much more sensitive to environmental conditions, and thus they are forced to track the movement of vegetational zones. During cooling trends, habitats at high latitudes will tend to move towards the equator, whereas during heating trends habitats at low latitudes will tend to move towards the poles. Thus, a cooling trend should be associated with an equatorward wave of mammalian dispersals, within which most of the species are specialists. Specialists are never expected to disperse in the direction opposite that of the prevailing mammalian trend, because such dispersal would imply that the species was moving outside its preferred habitat. Generalists, however, are not

tied to a particular vegetational zone (unless a preponderance of their many resources are so tied), and therefore can disperse either with the mammalian trend or against it (of course, they can also remain in place, and thus do not have to disperse at all). Consequently, a wave of mammalian dispersal can contain both specialists and generalists, but only generalists can oppose the wave.

Turner and Wood (1993) identified three waves of mammalian dispersal between East and southern Africa during the late Pliocene and early Pleistocene. The first wave comprises a southward dispersal (from East to southern Africa) of *Canis* sp., *Diceros bicornis*, and *Metridiochoerus andrewsi* at approximately 3.0 Ma. The second wave, corresponding to a global cooling trend, is a northward dispersal between 2.7 and 2.0 Ma of *Cercopithecoides williamsi*, *Connochaetes taurinus*, *Parmularius braini*, *Tragelaphus pricei* and *Antidorcas recki*. Finally, a third wave, consisting of southward dispersals, takes place between 1.8 and 1.5 Ma. Non-hominin taxa in this wave include *Theropithecus oswaldi*, *Nyctereutes terblanchei*, *Equus burchelli*, *Metridiochoerus modestus*, *Kobus ellipsiprymnus*, *Hippotragus gigas*, and two species of *Tragelaphus* (*T. scriptus* and *T. strepsiceros*). Note, however, that *Hipparion lybicum* disperses northward at 1.7 Ma when other mammals are dispersing southward.

Strait and Wood (1999) found that all published phylogenies imply that most hominin dispersals conformed to the three-wave pattern described above. That is, most hominin dispersals were in the same direction as contemporaneous mammals. According to most phylogenies, *Homo habilis* s.s. and *P. robustus*, or their ancestors, are the only hominin species that may have dispersed in a direction opposite that of contemporaneous mammals. However, these possibilities are contingent on the taxonomic and stratigraphic allocations of particular hominin specimens (e.g., Sts 19 and hominins from Drimolen; see Strait and Wood, 1999). Because these allocations are unresolved, Strait and Wood's (Strait and Wood, 1999) published observations do not allow a rejection of the null hypothesis.

The discovery of a *Paranthropus*-like maxilla in Malawi requires an important modification to be

made to Strait and Wood's (Strait and Wood, 1999) results. The new Malawi specimen (RC 911) has been attributed to *P. boisei* (Kullmer et al., 1999). If correct, this would imply that *P. boisei* dispersed northward from Malawi at approximately 2.3 Ma, along with the prevailing mammalian trend. This result, by itself, is not particularly noteworthy. However, parsimony indicates that in nearly every phylogenetic hypothesis, *P. boisei* is descended from an East African ancestor. Thus, the presence of *P. boisei* in Malawi at 2.5 Ma implies a southward dispersal of *Paranthropus* at a time when other mammals are moving northward. Of course, the RC 911 specimen is fragmentary, and it potentially could represent the contemporaneous *P. aethiopicus* rather than *P. boisei*. Even if this were the case, the presence of this specimen in Malawi would likewise imply a southward dispersal of *P. aethiopicus* at 2.5 Ma. Thus, there is evidence that at least one, and perhaps two, *Paranthropus* dispersals opposed prevailing mammalian trends. This is inconsistent with the hypothesis that *Paranthropus* was a stenotope, and thus allows for the rejection of the null hypothesis.

Range continuity

Although the biogeographic processes described above (i.e., vicariance, dispersal) are difficult to directly document in the fossil record, one might be able to indirectly infer their presence by examining a species' range. Vrba (1992) predicts that because stenotopes are more prone to vicariance than eurytopes, their ranges will tend to be discontinuous and widespread. Discontinuity is expected not only in the ranges of populations of a single species, but also in the ranges of sister species as well. In contrast, eurytopes are less prone to vicariance, and thus should exhibit a continuous range, even if widespread. The nature of paleontology is such that fossils are discovered where erosion has exposed them on the surface, or in the case of cave deposits, where natural erosion or mining has provided access to cave sediments. These are circumstances independent of the ranges of fossil taxa. Thus, a prudent conclusion is that

this prediction cannot be adequately evaluated with respect to early hominins.

Degree of apomorphy

Stenotopes specialize on one, or a few, environmental resources, and thus may have derived morphological features designed to exploit those resources. Thus, specialist morphology will tend to be apomorphic. In contrast, eurytopes should exhibit morphology that allows them to exploit many resources. It is intuitive to consider such generalized morphology as being primitive, but it need not be. Eurytopes conceivably could have derived features that allow them to generalize. Anatomical features related to the human precision grip are an example of such derived, generalist traits (broad apical tufts, separate tendon for flexor pollicis longus, phalanx dimensions, e.g., Napier, 1962; Susman, 1988a,b, 1994). Thus, a generalist morphology could be either apomorphic or plesiomorphic.

With respect to cranial morphology, cladistic studies that have included *Paranthropus* conclude that much of its craniodental morphology is derived with a substantial proportion of it being autapomorphic (Chamberlain and Wood, 1987; Wood, 1988, 1991, 1992a,b; Skelton and McHenry, 1992; Lieberman et al., 1996; Strait et al., 1997; Strait and Grine, 1999). Putting aside, for the moment, the adaptive reasons for why such features might have evolved, it is clear that the genus overall is apomorphic. Early *Homo*, especially *H. ergaster*, is also apomorphic albeit with respect to a different suite of features (e.g., cranial capacity, dentognathic reduction; Wood and Collard, 1999). As such, the degree of apomorphy in both taxa is consistent with the predictions of both stenotopy and eurytopy and are thus not diagnostic with respect to the null hypothesis.

Non-dietary adaptations

Obligate terrestriality

The evolution of obligate terrestriality in hominins is unique among primates. As a generalization, non-human primates represent a radiation

of arboreal mammals. Even species with advanced terrestrial adaptations (e.g., *Papio* and *Pan*) retain the ability to move competently through the trees. Such species are therefore afforded the opportunity of exploiting resources both in the trees and on the ground. Indeed, the ability to move on arboreal substrates can often prove critical to “terrestrial” primates, because trees provide a source of food, and an important refuge from many types of predators. The loss of the ability to easily exploit arboreal resources therefore represents a considerable narrowing of a primate’s niche-space. Among living primates, modern humans are arguably the only species that are obligate ground-dwellers, and thus the point during human evolution at which advanced arboreal competency was lost represents the advent of a specialist adaptive strategy.

The origin of obligate terrestriality in hominins was not necessarily coincident with the origin of bipedality (Stern and Susman, 1983). Morphological adaptations to terrestrial bipedalism are generally found in the hindlimb, but large-bodied primates tend to adopt forelimb-dominated locomotor behaviors when traveling arboreally (e.g., Fleagle, 1985, 1988, 1999). Thus, the evolution of derived features related to terrestrial bipedalism does not necessarily preclude the possibility of arboreal locomotion unless forelimb features related to suspension are lost. Given these criteria, the earliest hominin taxa for which the postcranial skeleton is well known are not obviously obligate ground-dwellers, because they retain suspensory features in the forelimb. For example, *A. afarensis* has long, curved phalanges, a relatively long upper limb, a long hook of the hamate, and a long pisiform (Susman et al., 1984, 1985; Stern, 2000), while it is claimed that *A. africanus* exhibits limb proportions (using joint morphology as a proxy) that are even more ape-like than those of *A. afarensis* (McHenry and Berger, 1998). The behavioral interpretation of these and similar features has been controversial, with some researchers (e.g., Latimer, 1991) arguing that the suspensory traits are non-functional and present in early hominins simply as a result of phylogenetic inertia (Ward, 2003). However, their presence, at a minimum, makes it difficult to discount with certainty the

possibility that these early hominins were partially arboreal.

The postcranial skeleton of *H. habilis s.s.* is only partially known, but in this species, too, bipedal features in the hindlimb (particularly the foot) may be found in combination with forelimb features consistent with arboreality, namely, the partial retention of a power-grip (Susman and Stern, 1982) and relatively long upper limbs (Hartwig-Sherer and Martin, 1991).

The locomotor behavior of *Paranthropus* is unclear. Almost nothing is known of the postcranial skeletons of *P. boisei* and *P. aethiopicus*, and the attribution (Susman, 1988a,b, 1994) of human-like postcranial remains to *P. robustus* is conjectural. Similarly, postcranial remains have yet to be attributed with confidence to *H. rudolfensis*. Arguably, the only early hominin species to qualify as an unambiguous obligate ground-dweller is *H. ergaster*, as represented by KNM-WT 15000 (Wood and Collard, 1999). This specimen possesses a generally human-like postcranial skeleton (Walker and Leakey, 1993) and lacks obvious adaptations to arboreal locomotion. Thus, it is possible, if not probable, that the earliest hominins were generalists in the sense that they exploited both arboreal and terrestrial resources. By the latest Pliocene, at least one hominin species, *H. ergaster* (and the subsequent members of the *Homo* clade) had lost morphological adaptations allowing them to travel competently using arboreal substrates. These traits were lost despite the fact that *H. ergaster* presumably had as much access to wooded environments as did other contemporaneous hominins. This does not necessarily mean that *H. ergaster* entirely abandoned arboreal resources, but certainly their importance must have been reduced relative to that of terrestrial resources. Obligate terrestriality in *H. ergaster* and later members of the genus *Homo* should be interpreted as a stenotopic feature. The precise locomotor behavior of *Paranthropus* is unknown, but certainly it was not any more adapted to terrestriality than *H. ergaster*. Thus, it cannot be argued that *Paranthropus* was more specialized than at least this species, and the null hypothesis should be rejected.

Tool-use

Among the more impressive adaptations of the hominin lineage is the ability to extensively make and use tools. Insofar as tools expand the range of resources that can be exploited by the tool-user, tool use must be viewed as a generalist adaptation, even though any given tool might have a very specific application. Habitual tool making and use obviously requires an advance in cognitive powers, but, just as importantly, requires the ability to precisely manipulate objects. Napier (1962) identified several features related to what he called a “precision grip” in the hand of OH 7 and suggested that *H. habilis s.s.* was capable of making at least some of the stone tools found in contemporary sediments. It is presumed that a precision grip is retained in all members of the genus *Homo sensu stricto* although the hand is not well represented in the fossil records of many of the relevant taxa.

Susman (1988a,b, 1994) has identified features indicative of a precision grip in fossil hand bones from Swartkrans, a site from which both *Paranthropus* and *Homo sensu lato* have been recovered. Susman allocated most of these fossils to *P. robustus* on the grounds that the overwhelming majority of craniodental fossils from this site have been attributed to this species, and there is little reason to suspect that hand bones of *Homo s.l.* would be preferentially preserved. Some authors (Trinkaus and Long, 1990; McGrew, 1995; Hamrick and Inouye, 1995; Ohman et al., 1995; but see Susman, 1995) have objected to Susman’s morphological analysis. Nonetheless, although Susman’s logic regarding the taxonomic affinities of the hand fossils is persuasive, there is no way of being certain that *P. robustus* had a precision grip until relevant postcranial fossils are found in clear association with distinctive craniodental remains. Thus, while there is a consensus that early *Homo* was eurytopic in that it could make and use tools, there is less agreement as to whether *Paranthropus* had similar capabilities. However, researchers have cautioned that reliable inferences about the functional capability of these taxa require more data than are presently available (Marzke and Marzke, 2000). Thus, tool-use and dexterity data are not diagnostic with respect to the null hypothesis.

Brain size

There is no doubt that among mammals, modern humans possess a relatively large brain (e.g., Jerison, 1973; Martin, 1990). Moreover, it is often suggested that this large brain size is in some fashion related to intelligence, and that intelligence confers behavioral flexibility on an individual (e.g., Vrba, 1980; Potts, 1998a). A modern human brain might therefore be considered a eurytopic characteristic. However, the relationship between brain size and intelligence is sufficiently unclear that it is difficult to characterize the adaptive significance of relative brain size in early hominins. The brain of *H. habilis s.s.* is somewhat larger than that of a chimpanzee, but somewhat smaller than that of a modern human. Does it also have an intermediate level of intelligence? What, in any case, would such a characterization mean? Would such a brain necessarily confer greater behavioral flexibility to its possessor than that seen in chimpanzees? Could it be possible that the enlarged brain in fact reflects the enhancement of particular neural functions, which are in turn related to very specific behaviors? Answers to these questions are lacking. Moreover, even if 'intelligence' increases incrementally along with relative brain size (Kappelman, 1996; Aiello and Wood, 1994; Collard and Wood, 1999), brain size in *Paranthropus* apparently increases over time (Elton et al., 2001), although *Paranthropus* species do not attain the absolute brain size of the early *Homo* taxa. Are such data consistent with a hypothesis in which behavioral flexibility increases in both early *Homo* and *Paranthropus*? Again, the answer is unclear. Regardless, one should exercise caution when projecting aspects of modern human behavior back onto organisms with distinctly non-modern human sized brains. Although it is possible that the relatively large brains seen in *H. ergaster* and later hominins indicate the evolution of enhanced behavioral flexibility relative to other hominins, this hypothesis remains largely conjectural. In any case, even if large brain size in early *Homo* indicates increased behavioral flexibility, it is not as if the somewhat smaller brains of *Paranthropus* indicate a narrowing of behavior. That is, the brains may be less generalized, but they are not obviously more specialized. Ultimately, brain size data are not diagnostic with respect to the null hypothesis.

Discussion

The evolutionary fates of *Paranthropus* and early *Homo*, extinction for the former and the founder membership of the *Homo* lineage for the latter, have been directly related to their contrasting responses to global and regional climate change. Terrigenous sediments recovered from deep-sea cores show that c. 2.8 Ma there was an approximate doubling of the periodicity of wet and dry climate cycles (de Menocal, 1995). This change coincides with evidence of global cooling (summarized in Kennett, 1995) and with a synchronic increase in aridity in Africa (de Menocal, 1995). It also occurred during a period when in many parts of the world sedimentation rates and sediment grain sizes were increasing, changes that have been interpreted as evidence for an escalation in both the frequency and abruptness of climate changes (Peizhen et al., 2001). Conventional wisdom suggests that early *Homo* adopted a eurytopic (i.e., generalist) adaptive strategy in response to these environmental changes, whereas *Paranthropus* responded by adopting a stenotopic (i.e., specialist) strategy. However, to our knowledge the morphological and other evidence for this hypothetical evolutionary scenario has never been tested against published criteria for eurytopy and stenotopy.

When we tested the null hypothesis against eleven criteria (Table 6) in six instances (direct evidence of dietary breadth, species diversity, species duration, susceptibility to dispersal, dispersal direction and non-dietary adaptations) the evidence is inconsistent with a hypothesis which interprets *Paranthropus* as being more specialized than early *Homo*. Only one definitive example (a category of indirect evidence for dietary breadth—occlusal morphology) can be found in which the criteria may be consistent with the null hypothesis. Three other criteria (evidence of dietary breadth related to incisor use, population density, habitat preference) are consistent with the null hypothesis under certain conditions, namely, that *Paranthropus* did not use tools to process its food, and that it specialized on a key resource that was both widely distributed across habitats and abundant relative to the resources of other early

Table 6

Degree to which evolutionary criteria are consistent or inconsistent with the null hypothesis that *Paranthropus* is more stenotopic than early *Homo*

Criteria	Consistency with null hypothesis	Notes
1. Dietary breadth		
Direct evidence		
Molar microwear	Not diagnostic	More data needed to evaluate apparent difference between <i>P. boisei</i> and <i>P. robustus</i> .
Incisor microwear	Conditionally consistent	Lower incidence of incisor wear in <i>P. robustus</i> than in <i>A. africanus</i> . Wear is relevant to dietary breadth only if <i>P. robustus</i> did not use tools to prepare food.
Trace elements	Inconsistent	<i>P. robustus</i> and early <i>Homo</i> values intermediate.
Stable carbon isotopes	Inconsistent	<i>P. robustus</i> values intermediate.
All direct evidence viewed collectively	Inconsistent	No single food item accommodates <i>P. robustus</i> data.
Indirect evidence		
Dentognathic proportions and facial morphology	Not diagnostic	<i>Paranthropus</i> features do not exclude foods from diet.
Mandibular corpus size and robusticity	Not diagnostic	<i>Paranthropus</i> features do not exclude foods from diet.
Masticatory musculature	Not diagnostic	<i>Paranthropus</i> features do not exclude foods from diet.
Anterior tooth size	Conditionally consistent	In the absence of technology, small incisors exclude large foods from <i>Paranthropus</i> diet.
Postcanine tooth size	Not diagnostic	<i>Paranthropus</i> features do not exclude foods from diet.
Occlusal morphology	Consistent	Extreme bunodonty excludes leaves from diet of <i>Paranthropus</i> .
Enamel thickness	Not diagnostic	<i>Paranthropus</i> features do not exclude foods from diet.
2. Habitat preference	Conditionally consistent	Lack of preference in both <i>Paranthropus</i> and early <i>Homo</i> . <i>Paranthropus</i> is stenotopic only if it specialized on a key resource that was widely distributed across habitats.
3. Species diversity	Inconsistent	<i>Paranthropus</i> not more speciose than early <i>Homo</i> .
4. Species duration	Inconsistent	Durations not obviously shorter in <i>Paranthropus</i> than in early <i>Homo</i> .
5. Sympatry	Not diagnostic	<i>Paranthropus</i> species allopatric, but cannot assess whether early <i>Homo</i> species were sympatric.
6. Population density	Conditionally consistent	<i>Paranthropus</i> fossils more abundant than early <i>Homo</i> . If abundance in fossil record is related to abundance in life, then <i>Paranthropus</i> is stenotopic only if its key resource was more abundant than those of other hominins.
7. Susceptibility to dispersal or vicariance	Inconsistent	<i>Paranthropus</i> does not disperse more frequently than early <i>Homo</i> .
8. Dispersal direction	Inconsistent	At least one <i>Paranthropus</i> dispersal opposes mammalian trend.
9. Range continuity	Not diagnostic	Fossil record too incomplete.
10. Degree of apomorphy	Not diagnostic	Both <i>Paranthropus</i> and early <i>Homo</i> are apomorphic.
11. Non-dietary adaptations		
Obligate terrestriality	Inconsistent	<i>Paranthropus</i> unlikely to be more terrestrial than <i>H. ergaster</i> .
Tool-use	Not diagnostic	Degree of tool-use in <i>Paranthropus</i> unclear.
Brain size	Not diagnostic	Meaning of increased brain size in early hominins unclear.

hominins. Regardless of how many criteria are ultimately found to be consistent with the null hypothesis, it is worth reiterating that consistency with an hypothesis does not necessarily constitute evidence that the hypothesis is true. In this light, it

is significant that six of eleven criteria do not support the null hypothesis, including several categories of dietary breadth (the criterion most directly related to Robinson's [1954a] Dietary Hypothesis).

Three interpretations are consistent with these data. First, *Paranthropus* is a eurytope. Second, *Paranthropus* is a stenotope, but its key resource is so abundant and broadly distributed in multiple habitats that it has the evolutionary profile of a generalist (e.g., anteaters; Vrba, 1992). Moreover, if that key resource is dietary, then the trace element and stable carbon isotope data must be incorrect. Third, *Paranthropus* is a stenotope, but the predictions about the evolutionary profile expected in a stenotope (Eldredge, 1979; Vrba, 1980, 1992) are wrong (Maurer, 1999). We consider the first option to be most probable. We suggest that although the masticatory features of *Paranthropus* are most likely adaptations for consuming hard or gritty foods, they had the effect of broadening, not narrowing, the range of food items consumed. It is possible that these adaptations allowed *Paranthropus* to become a “seasonal specialist” by exploiting previously unavailable fallback food items during periods of dietary stress (Conklin-Brittain et al., 1988). One of us (e.g., Wood and Ellis, 1986), and many others, have wrongly interpreted the derived morphology of the masticatory system of *Paranthropus* as evidence for stenophagy. Instead, the vast majority of the evidence suggests that the masticatory system of *Paranthropus* is more consistent with euryphagy. Thus, the extinction of *Paranthropus* species should not be considered a straightforward consequence of having an over-specialized diet.

Scenarios of *Paranthropus* extinction must also take into account the possibility that *Paranthropus* was present in large numbers relative to other hominins of the same time period. If true, then *P. boisei*, at least, would have had both longer species duration and a higher population density than its contemporaries. Insofar as these variables are used to measure the “success” of a species, one could pose the tantalizing, but essentially untestable, hypothesis that *P. boisei* was better suited for its habitat than were species of early *Homo*. One could apply the same argument to *P. robustus*, but less is known about the duration of this species. Regardless, although such a conclusion regarding the relative adaptations of early *Homo* and *Paranthropus* appears counter-intuitive, it is nonetheless a possibility that should be considered.

We are certainly not the first to suggest that one, or more, *Paranthropus* species may not be dietary specialists (e.g., Walker, 1981; Demes and Creel, 1988; Peters, 1987; Sillen, 1992; Sillen et al., 1995; Lee-Thorp and van der Merwe, 1993; Gordon, 1993; Brain, 1994; Lee-Thorp et al., 1994), but this is the first time such a wide range of evidence has been considered and collated. The results of our review of this evidence demonstrate that conventional wisdom about the proximate cause of *Paranthropus* extinction should be re-examined. The results of this review should not be interpreted as diminishing the importance of John Robinson’s seminal observations about the derived (Robinson, 1963) nature of the dentition of *Paranthropus*. Those observations still stand. However, evidence that has accumulated since Robinson first published his observations suggests that we need to revise our view of the dietary implications of that morphology.

The adaptive strategy of early *Homo* is more difficult to interpret. There is evidence that these species may have been stenotopic with respect to at least a few of the criteria examined here (Table 6). In particular, early *Homo* is possibly more speciose than *Paranthropus*, possibly more prone to dispersal and, with respect to *H. ergaster* and *H. erectus*, possibly more committed to a terrestrial lifestyle. Moreover, it is conceivable that species within early *Homo* were sympatric. The data associated with these possibilities are not conclusive but, at a minimum, they warrant further investigation. In contrast, there is also evidence that early *Homo* was eurytopic (Table 6). At least some direct evidence about dietary breadth (trace elements) is inconsistent with a hypothesis of *Homo* stenotopy, as is evidence of tool-use. One other criterion (habitat preference, tool-use) is inconsistent with stenotopy except under certain conditions. Thus, there is mixed evidence as to whether early *Homo* was eurytopic or stenotopic.

Would this conclusion be the same if we had opted for a less inclusive interpretation of the genus *Homo*? Excluding *H. habilis* s.s. and *H. rudolfensis* from *Homo* (Wood, 1996a,b; Wood and Collard, 1999) weakens the case for early *Homo* stenotopy by reducing species diversity within that clade, and by virtually eliminating the

possibility of *Homo* sympatry during the relevant time period. A more restrictive interpretation of *Homo* taxonomy leaves the majority of the remaining conclusions unaffected. However, in one case, changing the definition in the way suggested above actually strengthens the case for *Homo* stenotopy by removing a possible dispersal of a *Homo* taxon against the mammalian trend.

How, then, to interpret the adaptive strategy of early *Homo*? We postulate that unstable or changing environmental conditions in the late Pliocene may have driven early *Homo* species to reduce their reliance on arboreal resources and yet maintain a broad diet. As a result, species consolidated their adaptation to bipedal locomotion while expanding their exploitation of terrestrial food items. Thus, a specialist locomotor strategy was mediated by a generalist dietary strategy. Teaford and Ungar (2000) recently reviewed multiple lines of evidence suggesting that the australopiths were dietary generalists. Insofar as their results complement those of the present study, it appears that euryphagy has been characteristic of early hominins from the early Pliocene up through at least the early Pleistocene. However, this is not to say that all such hominins shared the same diet. As a generalization, australopiths lived in habitats that tended (with exceptions) to be more mesic than those of hominins from later time periods, such as *Paranthropus* and early *Homo*. Thus, although all early hominins had broad diets, the range of those diets may have shifted towards incorporating more resources from xeric habitats. In the case of *Paranthropus*, this shift may have entailed adding more hard food items to the diet. Regarding early *Homo*, the shift may have been towards a greater focus on meat. Undoubtedly, the australopiths could exploit resources from xeric habitats and *Paranthropus* and early *Homo* could exploit resources from mesic ones, but the relative proportions of these resources in the hominin diet may have changed over time.

Tool-use presumably played a critical role in facilitating early *Homo* euryphagy after the reduction of the masticatory apparatus. Indeed, the reason for the long-term success of the *Homo* clade almost certainly involves culture. However, the impact of tool-use is substantially more complex

than the simple, dichotomous, “presence” or “absence” of stone tools that researchers conventionally use to identify an early hominin as “culture-bearing” (Panger et al., 2002). It is probable that *Homo* and *Paranthropus* achieved their euryphagic strategies via very different functional routes. In the case of *Paranthropus* it was modifications to the dentognathic apparatus that enabled it to be a euryphage. The evolution of early *Homo* may also have been crucially affected by a dietary adaptation, but in this case towards an increased exploitation of meat. Later *Homo* species are associated with copious evidence of a culturally mediated adaptive strategy and much later in its prehistory the diet of at least one *Homo* taxon was apparently as dominated by meat ingestion as the diet of committed carnivores (Richards et al., 2000). However, with a very different dental inheritance, and thus without the help of blade-like carnassials, early hominins had to find another way of rendering carcasses, dismembered or otherwise, into digestible pieces. In that ‘second way’ to carnivory the burden of processing meat was shifted from the teeth and jaws to the brain and the hands. Certainly, early *Homo* species were unlikely to have been obligate carnivores, but meat may have been a critical supplement to their diet. Advances in intelligence and dexterity, including the deliberate manufacture of stone tools and intentional cooking (Collard and Wood, 1999; Wrangham et al., 1999) were probably crucial elements of *Homo*’s route to functional euryphagy.

Given that both *Paranthropus* and early *Homo* appear to be euryphagic, scenarios to explain the demise of the former and the persistence of the latter should not focus exclusively on dietary factors. Climate change, in and of itself, is not a satisfactory explanation, because both groups encountered the same changes, and yet experienced different outcomes. Other variables that might explain the differential success of these groups may include, but are not limited to, differences in 1) locomotor mode, 2) degree or mode of tool-use or production, 3) predator avoidance (Klein, 1988), 4) competition from non-hominin primates or non-primate mammals, 5) competition from each other (Klein, 1988), 6) social group structure, and 7) capacity for learned behavior. Obviously,

many of these variables are interrelated, and some are notoriously difficult to observe in the fossil record. Nonetheless, this partial list suggests various directions for future research related to the disparate evolutionary fates of *Paranthropus* and *Homo*.

The inference that all early hominin grades (australopiths, *Paranthropus*, and early *Homo*) may have been ecologically generalized is relevant to interpretations of broad-scale trends in hominin evolutionary ecology. It is widely assumed (see review in Potts, 1998a) that the cooling and drying experienced by African ecosystems during the late Miocene, Pliocene and early Pleistocene is broadly responsible for major patterns of hominin diversification and adaptation. If the last common ancestor of hominins evolved within a wooded habitat (e.g., Woldegabriel et al., 1994; Pickford and Senut, 2001; but see Vignaud et al., 2002), then the contraction of African forests can be viewed as a profound environmental degradation. One might expect that the preferred resources of the forest-dwelling hominins would become less abundant in these degraded habitats. Optimal foraging theory (e.g., Emlen, 1966, 1968; MacArthur and Pianka, 1966; Schoener, 1971; MacArthur, 1972; Charnov, 1976a,b) predicts that in a depleted environment an organism cannot afford to bypass secondary resources in the hopes that it will eventually locate a preferred one. As a result, generalists should be favored over specialists.

The above scenario posits that long-term directional selection related to lower temperatures and increased aridity favored ecological generalization in early hominins. However, during the same period in which the cooling trend occurred, climatic variability became increasingly more pronounced. In particular, the frequency and amplitude of oscillations between colder and warmer environments became greater (Potts, 1998a; see also Woodruff et al., 1981; Prentice and Denton, 1988; Wright and Miller, 1992; Shackleton, 1995; Miller et al., 1996). Given this climatic history, both Pianka (1978) and Potts (1998a) have proposed models that may be relevant to the evolution of hominin eurytopy.

Pianka's (1978) model is based on Fisher's (1930, 1958) mathematical model of adaptation.

Fisher (1930, 1958) viewed an organism's selective "environment" as being a multidimensional niche-space (Fig. 1). The axes of this space represent variables such as climate, competition, predation, and so on. Within that space is a point at which a given organism is perfectly adapted to its environment. In reality, organisms are not perfectly adapted, and thus they are located a certain distance d away from the "ideal" point. As d increases, the level of adaptation of the organism decreases. As environmental conditions change, so will the position of the ideal point relative to the organism. If this point moves such that the value of d decreases, then the environmental change is adaptively advantageous. Conversely, if d increases, then the change is maladaptive. Fisher noted that small-scale undirected (i.e., stochastic) changes in environmental parameters are equally likely to increase or decrease d , and thus are equally likely to be selectively deleterious or advantageous, respectively. In contrast, large-scale stochastic changes are more likely to be deleterious, because even if the position of the perfect adaptation moves in the direction of the organism, it can "overshoot" (Pianka, 1978: 84) such that the resulting d is greater than the initial d . However, advantageous large-scale change is still possible, and is more likely to occur in species with broad, rather than narrow, environmental tolerances (Pianka, 1978). The reason for this is that generalists can maintain adaptive viability at greater distances from the ideal point. As a result, specialists will tend to be found closer to this point, and their initial value of d will be small. Consequently, large perturbations in environmental parameters are more likely to induce overshoot. If the increased oscillations in temperature that began in the late Miocene can be viewed as stochastic, then Pianka's (1978) model may apply to early hominins.

Potts (1998a,b) has also proposed a model, termed Variability Selection, to explain the evolution of hominin versatility (Fig. 2). Potts (1998a,b) explains his model as follows. Consider a gene locus that represents an adaptation to a particular environmental variable (e.g., climate). Assume that two alleles each code for opposing specialist abilities (e.g., dry vs. wet habitat

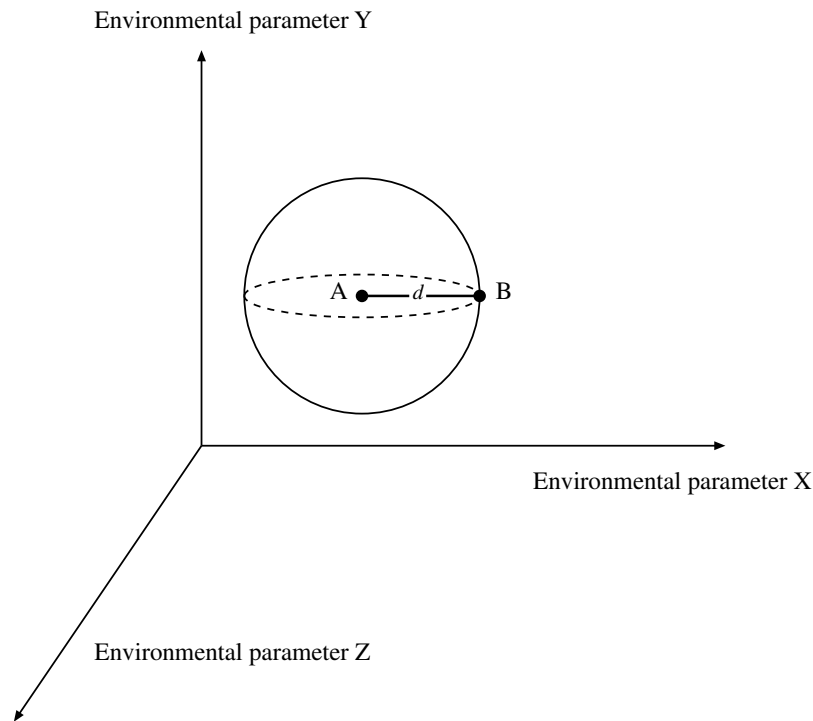


Fig. 1. Fisher's (Fisher, 1930, 1958) model of adaptation. The adaptation of an organism can be viewed as a point in a multidimensional space whose axes are environmental parameters. For simplicity, only three axes are shown. "A" is a point representing the ideal adaptation of a given organism. In reality, organisms are not perfectly adapted, but are located at a point "B" some distance " d " away from "A". "A" is the center of a sphere of radius " d ". As environmental parameters change, so does the position of "A". If "A" moves such that "B" is found within the sphere, then the environmental change is selectively advantageous to the organism because its adaptation is now closer to being ideal. Figure after Pianka (1978): 84.

specialist), and that a third confers a flexible adaptation so that the organism can cope with a range of environmental conditions (e.g., dry and wet habitats). Under conditions of strong environmental oscillation, the specialist allele will experience periods of high positive selection when their preferred habitat is present, but also high negative selection when that habitat disappears. Thus, the specialist alleles will suffer "boom" and "bust" cycles. In contrast, according to Potts (1998a,b), the flexible allele will always experience higher fitness than specialist alleles in their bust cycle. As environmental oscillations persist over time, the flexible allele will steadily increase its frequency in the population. Eventually, the specialist alleles will be eliminated in a bust cycle, and the flexible alleles will become fixed in the population.

The competing ecological hypotheses outlined above are difficult to evaluate. One critical factor is the relative importance of the overall cooling trend versus short-term climatic oscillation. Moreover, the two models dependent on environmental instability (Pianka, 1978; Potts, 1998a,b) differ with respect to the mechanism by which eurytopy evolves. In Pianka's (1978) model, generalists are favored because in each episode of environmental change, they are more likely to experience positive selection than specialists. In Potts' (1998a,b) model, there are always specialists that experience stronger positive selection than generalists. It is only after many recurrences of environmental change that generalists predominate. The testing of these ecological hypotheses will be an important avenue of future research in paleoanthropology.

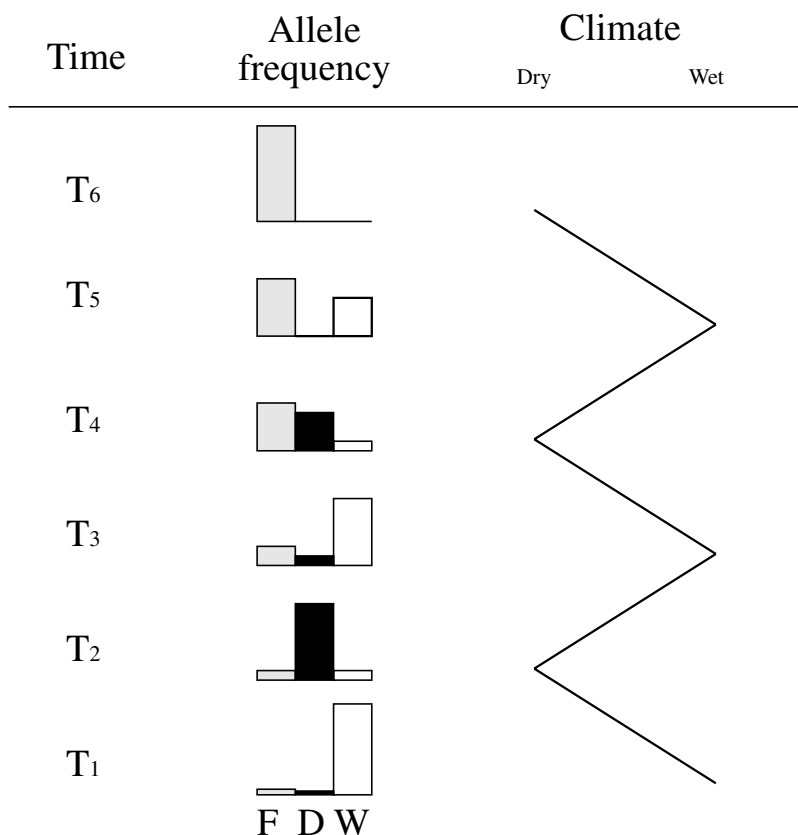


Fig. 2. Variability selection. Over six time intervals, the climate oscillates between wet and dry. Allele “D” is specialized for dry climates. Allele “W” is specialized for wet climates. Allele “F” is flexible in that it confers an ability to tolerate both climates, although not as well as “D” in a dry climate or “W” in a wet climate. As climate oscillates, the specialist alleles each experience alternating periods of strong negative and positive selection. The flexible allele always experiences modest positive selection relative to at least one of the specialist alleles. Thus, the allele frequency of “F” steadily increases, while those of “D” and “W” periodically increase and decrease dramatically. Eventually, the specialist alleles are eliminated during periods of strong negative selection. Figure modified after Potts (1998b).

Conclusion

For nearly fifty years paleoanthropology has operated within the paradigm that major adaptive differences between the *Homo* and *Paranthropus* lineages were responsible for the survival of the former, and the demise of the latter. In this paradigm the explanation for the contrasting fates of the two lineages is that the adaptive strategies they adopted in response to a shift to a drier climate and a more xeric habitat in Africa between 3 and 2 Ma constrained how they responded to a subsequent climatic shift between 1.5 and 1 Ma. This scenario suggests that the specialized masticatory

morphology of *Paranthropus* so reduced that lineage’s dietary options that, in the absence of culture, it was prevented from adapting to the different foods available in the newer habitats. In contrast, the more eclectic diet of *Homo*, combined with the latter’s technical expertise, were crucial components of feedback loops that enabled *Homo* to harness technology in its search for new sources of nutrition.

To our knowledge this is the first study to use a range of criteria to test the diet/climate hypothesis. Eleven criteria, ranging from attempts to reconstruct diet to assessments of species durations, were applied to the available data. The results

were not consistent with a simple *Paranthropus* stenotope and *Homo*/eurytope dichotomy.

These results suggest that the contrasting responses of the two lineages to episodes of climate change between 3 and 1 Ma are still unexplained. Evidence of modest sized increases in the size of the brain in *Paranthropus* between 2 and 1 Ma ago, and evidence that it may well have been able to use simple stone tools, certainly potentially blur the adaptive distinction between *Homo* and *Paranthropus*. We suggest that researchers have been misled by assuming that derived morphology always equates with a specialized adaptation.

Previously, researchers have drawn attention to the paradox of the modern human adaptation (e.g., Kaplan et al., 2000). In some senses (e.g., range of habitat) human adaptation is broad, but in others (e.g., life history, population age profile, a diet lacking or minimizing high-resistance objects) it is specialized. Certainly, without technology many aspects of the phenotype of members of the genus *Homo sensu stricto* are stenotopic. Culture must have played a decisive role in converting the morphologically stenotopic early *Homo* into a functional eurytope.

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