
The Autocatalytic Nature of Hominid Evolution in African Plio-Pleistocene Environments

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Causal explanations of hominid evolution may be derived from a synthesis of paleontological data and evolutionary theory. Paleoecological perspectives gleaned from the fossil record may contribute the critical element of time depth for testing hypotheses derived from interdisciplinary research on contemporary evolutionary and ecological phenomena. The challenges for paleoecologists are to correctly interpret fossil data in light of the inherently incomplete nature of the fossil record and to reconcile long-term perspectives gained from interpretations of the past with what is known from the present. The theoretical perspective of autocatalytic evolution, viewing evolutionary change as a result of intraspecific changes independent of external events, may provide an appropriate yet counterintuitive solution to these challenges.

In this chapter I present a fundamental approach to mammalian paleoecology based on the notion of autocatalytic evolution. Such an approach appears to be consistent with theories derived from population genetics, the developmental basis of morphology, and mammalian ecology. The theoretical approach of autocatalysis is also consistent with emerging data and analyses of African fossil fauna, including the early hominids. A hypothetical model of hominid evolution can be developed from this basis, with implications for the evolutionary processes governing the origins of mammalian species in general. To build a theoretical model of the ecological causes and conditions of mammalian evolution, a number of basic premises must be borne in mind.

As an initial and most important premise, it is clear that the genetic basis of morphological and physiological novelties arise at random with respect to events in the external environment. In this sense, "random" does not imply that all possible mutations within a genome are equally likely but that environmental influences do not induce novel directional changes in that genome. Within an environmental context, natural selection then may act on those mutations in a directional fashion if the phenotypic consequences of the new allele somehow affect the relative fitness of an animal. Alternatively, alleles with selectively neutral effects may be subject to other forces of evolution such as genetic drift.

Novel phenotypes, when arising from genetic mutations or new combinations of alleles, will only be of selective value if they are consistent with the developmental and physiological processes of an organism. Thus there are inherent structural constraints limiting the range of possibilities that may have selective value. For example, a giraffe's neck cannot become longer without the proper anatomical and physiological mechanisms to control blood flow to the head (Mitchell & Skinner, 1993). Likewise, evolving features, such as the human head and face, must conform to the limits imposed by birth processes and antenatal conditions. Alternatively, changes in the geometry and physiology of developmental processes may lead to evolutionary opportunities (Thompson, 1942).

Central to the theory of autocatalytic evolution is a

further premise, perhaps less clear, that the most important part of a mammal's environment, with respect to natural selection, is its own species. At birth mammals must receive nurturing. This usually comes from the offspring's mother (to varying degrees), but often directly or indirectly from other conspecifics as well, and requires appropriate feeding morphology and behavior that may be unrelated to adult adaptations. Sometimes a newborn must compete with siblings for that nurturing, thus initiating a further mode of natural selection. Among social mammals, a developing individual must somehow fit into norms of behavior to benefit from existing mechanisms of group survival and to successfully find a mate. The relative importance of these factors may vary depending on the behavioral patterns of the mammal, but they are inevitably important to some degree in determining Darwinian fitness (which in mammals depends primarily on mating success).

Ecological factors of a mammal's selective environment are of less consequence than the intrinsic selective constraints, as represented by the heuristic diagram in figure 4-1. Each concentric circle represents the ever-widening sphere of existence for an animal subjected to natural selection. Taken from the point of view of the animal whose task it is to survive and reproduce, the progression of subsequent spheres is fairly straightforward. Each species would take a characteristic pathway from the center, out through the various levels of selective constraints and adaptive opportunities. Some of the phenotypic consequences of the pathway may then be reflected in the morphology of the fossils we find. Each ring is successively more peripheral to the genetic basis of a phenotype and

places less stringent constraints on the microevolution of the population.

Conversely, what is not so obvious is that the pathway from the outside-in, the effect of the environment on the genetic resources of organism, is not so easily determined. Starting from the broad sphere of a regional environmental context, potential ecological determinants of how an animal's morphology relates to that environment must accurately penetrate each successive layer of selective constraints before changes in the gene frequencies take place. The selective values of an animal's adaptations within a particular environment are largely buffered by the more immediate constraints within the more central rings. This is due not only to the intrinsic nature of genetically controlled development arising at random, but also to the greater importance of epigenetic effects on an animal's relation with the environment (e.g., adaptable behavior and physiology throughout varied temperature and rainfall regimes). Thus the relative effect of each ring will depend on the peculiarities of an animal's adaptations and adaptability within an environmental context.

Once these fundamentals of evolutionary theory are explored, the difficulties encountered by a paleoecologist become clear, as well as the difficulties with theories that posit environmental change as a major causal force in the evolutionary origin of species. Questions arise as to how much of a species' physiology and morphology, including that detected in fossils, is relevant in the context of broader environmental features such as climate, vegetation, competitors, and so on. If that environment then changes, and potentially adaptive features are arising at random, what

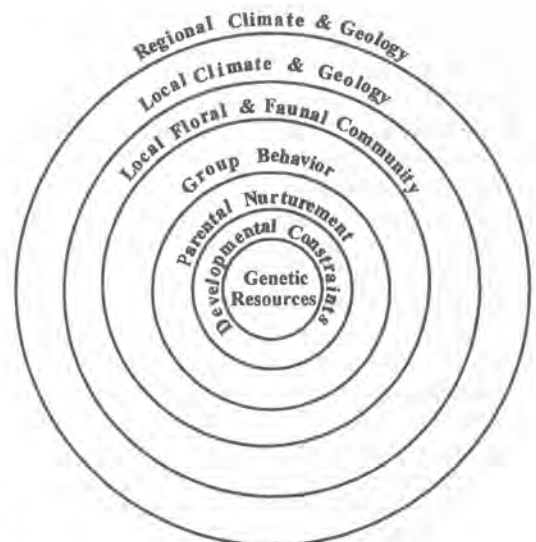


Figure 4-1. Schematic diagram of selective constraints on the genetic resources of a mammalian species population.

determines whether or not species have the genetic resources to adapt? Do some species have more genetic potential, making them more evolvable than others? Do adaptable species necessarily need to adapt morphologically to survive, or should they be treated differently in paleoecological studies from specially adapted animals? These questions may be answerable by an approach centering on the theory of autocatalytic evolution.

Autocatalytic Evolution

In the theory of autocatalytic evolution, most evolutionary change among mammals is catalyzed by the inherent nature of intraspecific variability (genes, morphology, and physiology), and not by changes in the external environment. Autocatalysis is responsible for origins of morphological novelties recognized by paleontologists as "species" characteristics as well as the origin of true "species"; in other words, it applies throughout microevolutionary and macroevolutionary levels. Thus evolution and perceived speciation would proceed with or without changes in climate or in the plant and animal community with which a species interacts.

Notions of autocatalysis depend on chance relations of evolving features with the successive rings of the selective milieu. "In this sense chance means that a variation having appeared, *chanced* to find a suitable environment" (T. H. Morgan, 1910:203; emphasis in original). Furthermore, genetically based phenotypic novelties do not necessarily become fixed in a population by natural selection alone, for the contribution of genetic drift could have the same effect on changing the character of a population. Due to these elements of chance, the timing of an evolutionary progression need not correspond to, or be catalyzed by, a

change in the external environment of the evolving lineage. Change in the broader selective environment may shape an evolutionary pattern and cause evolution to proceed in one direction rather than another, but is not necessary to initiate or sustain the process.

Cogent arguments for evolutionary autocatalysis among hominids have previously focused on the autocatalytic acceleration of increasing encephalization (Mayr, 1963; Bielicki, 1969; Holloway, 1972a; Godfrey & Jacobs, 1981; Tobias, 1981, 1994; Henneberg, 1987, 1992). Such a model is based in the mutual reinforcement of selective advantages between increased brain size and increased behavioral plasticity. The model of autocatalysis presented here, however, does not necessarily lead to an accelerating feedback loop. The loop is limited to that allowed by genes and morphology and thus could temporarily stall or completely halt at any time, depending on the availability of appropriate genetic resources on which the forces of evolution may act.

In models of autocatalysis, an evolving species derives evolutionary opportunity from a greater amount of variability within a successful lineage. This differs from models of environmental causation, in which the conservative forces of natural selection act during times of environmental change. When a species is under stress from a changing environment, natural selection works within the bounds of existing variation. Variation is thus limited by the selective process, whether the stress comes from climatic changes, as in the turnover-pulse hypothesis (Vrba, 1985a,e; 1988, 1993c), or from changes in the biotic community, as in the Red Queen hypothesis (Van Valen, 1973; Foley, 1984). If that variation is not sufficient to allow the species to adapt, then extinction is more likely than an evolutionary progression (Felsenstein, 1971; Foley, 1994).

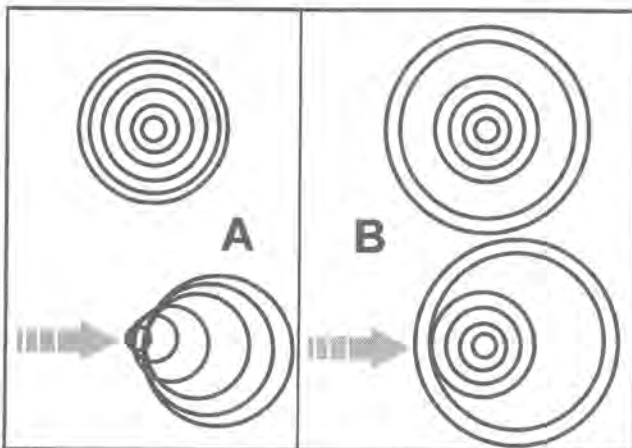


Figure 4-2. Environmental change effects (arrows) on highly adapted (A) versus adaptable (B) populations. Concentric circles represent selective constraints on the genetic resources of a population.

Difficulties with models of catalysis by environmental change can be illustrated by extrapolating the concentric circle analogy of morphological adaptation. In figure 4-2, two different types of mammalian reactions to the environment are represented. The first set (A) represents an animal that is ecologically specific with rings that are tightly bound. This would be a highly adapted animal with specific ecological requirements. Should the environment change, the outer circle impinges on various levels of morphological adaptation. The animal will only evolve if there is sufficient genetic variability already in place to allow it to shift with the environment; certainly this can happen, albeit rarely. However, should the environmental alterations severely stress the species, as in vicariance models (see Vrba, this volume), smaller selected populations with reduced variability (limiting evolvability) and possibly eventual extinction is the more likely outcome.

Effects of environmental change on ecologically adaptable animals (such as those with considerable behavioral and dietary plasticity) are represented by the second set of concentric circles (fig. 4-2B). Such mammals' relationships to the external environment are much less tightly constrained, so that a shift in the environment may not impinge upon their genetic variability at all. Environmental change would neither lead to morphological adaptation nor to the danger of extinction. I suggest that early hominids, indeed most mammals, fall into this category.

Natural selection in autocatalytic evolution, however, is initiated from the genetic and developmental source. It works from within, largely on the basis of selective advantages of niche expansion and population growth rather than selective pressure reducing and fragmenting populations. Any shift of the inner circle is possible, as long as it is consistent with the successive rings around it. Other options may be eliminated by natural selection. The selective advantages of any shift are more likely to be those dealing with changes in the inner circles, especially if reproductive success is accelerated. Sexual selection would be a good example, in which a species would evolve, perhaps dramatically (Fisher, 1958), regardless of fluctuations in the external environment. Any shift that gives a reproductive advantage to an animal carrying a novel variant would be favored by natural selection. Likewise, many variants could take hold due to genetic drift, as long as they are consistent with the developmental and ethological patterns of the species.

Continuous and potentially accelerating evolution is possible through autocatalysis. As features arise that allow niche expansion, and/or greater success at re-

production and survival, a population may grow. With a larger population, genetic variants are more likely to arise and, if they provide a reproductive advantage, to subsequently proliferate throughout the population. Initially a single populous, variable species would evolve and disperse. Subsequently, in some cases, divergent species could evolve through the process of centrifugal speciation.

Even extinction can be autocatalytic. McCann & Yodzis (1994) produced an ecosystem simulation in which top predators went suddenly and inexplicably extinct without any perturbation to the ecological system. Likewise, Lande (1994) has demonstrated that extinctions of small populations can ensue with the chance fixation of a mildly deleterious mutation, also in the absence of an environmental stimulus.

Autocatalytic evolution may be particularly relevant to the origins and spread of hominids. Here I present a hypothetical autocatalytic scenario and then support the model with paleoecological and morphological data, primarily from southern Africa. Although many aspects of the model are in need of further testing, the approach raises new questions about hominid evolution and the role of natural selection in an environmental context.

The Hominid Scenario

Narratives of autocatalytic evolution among hominids may begin with a hypothetical arboreal primate as the common ancestor of the lineages that ultimately led to *Australopithecus* and an ancestral form of *Pan*. The evolutionary process was initiated by a genetically controlled change in morphology which arose by chance (in the sense defined by Morgan, 1910). This morphological change allowed the arboreal primate to augment its locomotor and dietary behavior such that the early primates could exploit the resources on the ground as well as in the trees. There would have been a selective advantage in widening the formerly limited arboreal niche, especially if resource availability in the trees was limited either by competitors or saturation of the niche by expansion of the evolving population.

Derived features of the modified terrestrial locomotor and dietary morphology would have been preadapted to the exploitation of a niche outside of the forest. When further genetically induced modifications allowed locomotor and dietary behavior beyond that which was adapted to the former confines of morphology and environment, the primate could then exploit the savanna (where available). In at least one population the accumulating advantages of niche exploitation led to selection for bipedality and or-

thograde posture. Other populations, which by chance hit upon a different mode of morphology, led to the knuckle walking and brachiation still employed by *Pan*.

Consequences of bipedality included freed hands, which has often been considered to provide potential selective advantages (Darwin, 1871). Bipedality also may have freed the cerebrum for further expansion. Orthograde posture set the initial conditions for cerebral expansion, as it occurred among hominids. The developmental requisites of orthograde posture included a considerable degree of basicranial flexion (Gould, 1977b; Ross & Ravosa, 1993). Developmental flexion at the base of brain resulted in greater developmental arching of the cerebral peripheries, consequently expanding the cerebral neocortex. A slightly expanded brain was thus an indirect morphological consequence of bipedal locomotion. This brain allowed even greater adaptability through behavioral plasticity, and the autocatalysis of hominid brain evolution began accelerating. (This notion elicits the intriguing possibility that the primary selective advantage of orthograde posture was in cerebral expansion rather than in the bipedal mode of locomotion.) The development of omnivory, eventually including the consumption of meat, allowed the reduction of the face and further expansion of the brain (Ross & Henneberg, 1995); the same opportunity was not afforded to the robust lineages(s).

Hominid morphological evolution, with one feature leading to another, was catalyzed by the advantages and increased variability allowed by niche expansion and population growth rather than by environmental change. It is true that had the environment not changed, and savanna had not become available, the process may have taken a different direction, but such processes would not have been halted. In other words, the direction of evolution may be guided by the environment, but the impetus for change is autocatalyzed independently of environmental events.

Fossil Evidence Regarding the Ecological Correlates of Hominid Evolution

Autocatalytic models of hominid evolution yield predictions distinct from those of environmental forcing and/or environmentally induced vicariance. Given the random nature of the process, evolutionary events (as recognized paleontologically by changes in skeletal morphology) should be random with respect to the timing of climatic and environmental change. I have argued elsewhere that, at least from the southern African perspective, species origins among all mammals

may have occurred randomly with respect to time (McKee, 1995). Analyses by Bishop (1993, this volume) Reed (1995, 1996), and Behrensmeier et al. (1997) also show no evidence of an increased pace of evolution or turnover at times of climatic change.

Origins of bipedality and associated hominid features would not necessarily be related to climatic shifts in the autocatalytic model. This prediction is difficult to assess, given the lack of confirmed fossil data bearing on the origins of bipedality. But if *Ardipithecus (Australopithecus) ramidus* (T. D. White et al., 1994, 1995) does turn out to be a biped (or even an incipient biped), and the environmental reconstructions (Wolde Gabriel et al., 1994) are correct, then the origins of bipedality would have appeared in a wooded environment and would not be associated with major ecological shifts in climate or terrestrial biota.

Southern African data appear to support a further prediction of the autocatalytic model that early hominids should have exploited a variety of environments. By the time *Australopithecus africanus* emerges in the fossil record of southern Africa, sometime around 3 m.y. (and perhaps earlier), the hominid lineage had achieved complete habitual bipedality, albeit with vestiges of arboreal adaptations. Evidence suggests that the environments surrounding the caves in which these hominids were deposited were quite diverse, ranging from subtropical forest at Makapansgat to a more xeric environment at Taung.

Makapansgat

Makapansgat, the oldest of the established *A. africanus* cave sites (McKee, 1996a), has been characterized by Rayner et al. (1993) as being surrounded by subtropical forest at the time of deposition, largely on the basis of pollen analysis (Cadman & Rayner, 1989) and geomorphology. Although the palynological analysis may be dubious due to the inclusion of modern exotics in the sample sediments, the fauna of Members 3 and 4 (McKee et al., 1995; Reed, 1995) are certainly consistent with a forested environment (table 4-1). Makapansgat has the greatest number of bovids, which were probably primary browsers, and the highest biodiversity of any Transvaal Pliocene cave site. The presence in the sample of numerous grazers, as well as *Acinonyx jubatus* (cheetah, currently known to prefer open habitats), however, suggest that a mosaic environment may have characterized the general area. Nevertheless, Makapansgat appears to be the wettest and most densely vegetated area at the time of deposition as compared to any other southern African Pliocene-Pleistocene site.

Table 4-1. Mammals identified from Makapansgat Members 3 and 4 (MAK3, MAK4), Taung Hrdlička and Dart deposits (TAUH, TAUD), Sterkfontein Member 4 (STS4), and current extant species in southern Africa (EXTA).

	MAK3	MAK4	TAUH	TAUD	STS4	EXTA
Artiodactyla						
Bovidae						
<i>Antidorcas bondi</i>					•	
<i>Antidorcas recki</i>					•	
<i>Cephalophus parvus</i>				•		
<i>Gazella gracilior</i>	•					
<i>Gazella vanhoepeni</i>	•					
<i>Hippotragini gen et sp nov</i>	•					
<i>Hippotragus equinus</i>					•	•
<i>Hippotragus cookei</i>	•				•	
<i>Makapania broomi</i>	•	•			•	
<i>Oreotragus oreotragus</i>	•	•	•	•	•	•
<i>Parmularius sp nov</i>	•					
<i>Parmularius braini</i>	•					
<i>Redunca darti</i>	•	•				
<i>Syncerus acoelotus</i>			•		•	
<i>Tragelaphus angasii</i>	•		•		•	•
<i>Tragelaphus pricei</i>	•					
<i>Wellsiana torticornuta</i>	•					
Suidae						
<i>Notochoerus scotti</i>	•	•	•			
<i>Potamochoeroides shawi</i>	•	•			•	
Hippopotamidae						
<i>Hippopotamus amphibius</i>	•					•
Proboscidea						
Elephantidae						
<i>Anancus kenyensis</i>		•				
<i>Elephas recki</i>					•	
Perissodactyla						
Rhinocerotidae						
<i>Ceratotherium simum</i>	•					•
<i>Diceros bicornis</i>	•					•
Equidae						
<i>Hipparion libycum</i>	•					
Chalicotheriidae						
<i>Ancylotherium hennigi</i>	•					
Primates						
Cercopithecidae						
<i>Cercopithecoides williamsi</i>	•	•	•		•	
<i>Papio izodi</i>	•		•		•	
<i>Parapapio broomi</i>	•	•		•	•	
<i>Parapapio whitei</i>	•	•			•	
<i>Parapapio jonesi</i>	•	•			•	
<i>Parapapio antiquus</i>	•		•			
<i>Theropithecus darti</i>	•	•				
Hominidae						
<i>Australopithecus africanus</i>	•	•		•	•	
Carnivora						
Canidae						
<i>Canis mesomelas</i>	•	•	•		•	•
<i>Vulpes chama</i>	•	•				•

(continued)

Table 4-1. (continued)

	MAK3	MAK4	TAUH	TAUD	STS4	EXTA
Carnivora (continued)						
Felidae						
<i>Acinonyx jubatus</i>	•				•	
<i>Dinofelis barlowi</i>	•			•		
<i>Felis issiodorensis</i>	•					
<i>Felis libyca</i>	•					
<i>Felis serval</i>	•					•
<i>Homotherium crenatidens</i>					•	
<i>Homotherium nestianus</i>					•	
<i>Megantereon cultridens</i>					•	
<i>Panthera leo</i>					•	•
<i>Panthera pardus</i>	•		•		•	•
<i>Sivatherium maurisium</i>	•					
Hyaenidae						
<i>Chasmaporthetes silberbergi</i>					•	
<i>Chasmaporthetes nitidula</i>					•	
<i>Crocuta crocuta</i>		•			•	•
<i>Hyaena brunnea</i>					•	•
<i>Hyaena hyaena</i>	•	•				
<i>Pachycrocuta bellax</i>	•				•	
Viverridae						
<i>Cynictis penicillata</i>	•	•				•
Hyracoidea						
Procaviidae						
<i>Gigantohyrax maguirei</i>	•	•				
<i>Procavia antiqua</i>	•	•	•	•	•	
<i>Procavia transvaalensis</i>			•			
Tubulidentata						
Orycteropodidae						
<i>Orycteropus afer</i>	•					•
Insectivora						
Soricidae						
<i>Crocidura taungensis</i>			•			
<i>Crocidura bicolor</i>			•			•
<i>Diplomesodon fossorius</i>		•				
<i>Myosorex robinsoni</i>	•				•	
<i>Myosorex varius</i>		•				•
<i>Suncus varilla</i>	•	•	•		•	•
<i>Suncus infinitesimus</i>		•			•	•
Vespertilionidae						
<i>Eptesicus bottae</i>		•				
<i>Eptesicus hottentotus</i>		•				•
Chrysochloridae						
<i>Amblysomus hamiltoni</i>		•				
<i>Calcochloris hamiltoni</i>		•				
<i>Chlorotalpa spelea</i>					•	
Rodentia						
Batherigidae						
<i>Cryptomys hottentotus</i>		•				•
<i>Cryptomys robertsi</i>	•		•		•	
<i>Gypsorhynchus darti</i>			•	•		
<i>Gypsorhynchus makapania</i>	•					
<i>Gypsorhynchus minor</i>			•			

(continued)

Table 4-1. (continued)

	MAK3	MAK4	TAUH	TAUD	STS4	EXTA
Rodentia (continued)						
Cricetidae						
<i>Mystromys antiquus</i>	•		•		•	
<i>Mystromys hausleitneri</i>		•				
<i>Proodontomys cookei</i>	•	•	•		•	
<i>Stenodontomys darti</i>		•				
<i>Desmodillus auriculatus</i>			•		•	
Gliridae						
<i>Graphiurus monardi</i>					•	
Hystricidae						
<i>Hystrix africaeaustralis</i>	•		•		•	•
<i>Hystrix makapanensis</i>	•					
<i>Xenohystrix crassidens</i>	•					
Macroscelididae						
<i>Elephantulus antiquus</i>	•	•	•		•	
<i>Elephantulus brachyrhynchus</i>		•				•
<i>Macroscelides proboscideus</i>	•		•			•
Muridae						
<i>Acomys cahirinus</i>	•		•			•
<i>Aethomys chrysophilus</i>		•				•
<i>Aethomys namaquensis</i>		•			•	•
<i>Dasymys</i> sp. nov.			•			
<i>Dendromus mesomelas</i>					•	•
<i>Malacothrix typica</i>			•			•
<i>Mastomys natalensis</i>	•		•		•	•
<i>Otomys gracilis</i>	•	•	•		•	•
<i>Otomys sloggetti</i>		•				•
<i>Prototomys campbelli</i>			•			
<i>Tatera brantsii</i>			•		•	•
<i>Thallomys debruynei</i>			•			
Pedetidae						
<i>Pedetes gracilis</i>				•		
Petromyidae						
<i>Petromus minor</i>			•			
Chiroptera						
Rhinolophidae						
<i>Rhinolophus clivosus</i>		•				•
<i>Rhinolophus darlingi</i>		•	•		•	•

References list can be found in McKee et al. (1995), updated by Reed (1995) and Watson & Plug (1995).

Sterkfontein

Analyses of Sterkfontein Member 4 suggest a Pliocene environment that was at least partially wooded, as compared to later sites in the Blaaubank river valley. This is evident from analysis of the Bovidae (Vrba, 1975; 1976; 1980b), which reveals a large number of buck adapted to dense vegetation (particularly *Makapania broomi* and cf. *Hippotragus cookei*) as compared to greater proportions of alcelaphini and antilopini at later Pleistocene sites. Notwithstanding the

possible differences in taphonomic agents that may have influenced these proportions (McKee, 1991; McKee et al., 1995), the faunal assemblage of Sterkfontein Member 4 is distinctive enough to reveal that at least local environmental changes to increased savanna in the Transvaal postdated the deposition of Member 4 and thus postdated a bipedal and slightly encephalized *Australopithecus africanus*. Yet the faunal diversity and composition appears to indicate an environment less rich than that of Pliocene Makapansgat.

Taung

Depictions of the Pliocene environment at Taung are a bit more difficult to interpret due to the destruction of most of the *A. africanus* type site by quarrying. After seven years of excavation and research at the site (McKee & Tobias, 1994), some conclusions can be drawn with a measure of caution. Most of the fauna known from Taung comes from deposits of the Hrdlička pinnacle and are unlikely to be associated directly with the hominid fossil, perhaps being separated by as much as 200,000 yr. The hominid was probably derived from a deposit temporally and spatially associated with the remaining Dart deposits (McKee, 1993a,b; McKee & Tobias, 1994). There are clear taphonomic differences between the Dart and Hrdlička deposits to compound the possible effects of the temporal separation, but knowledge gained from comparisons of the deposits at least suggest a paleoecological similarity.

Excavations of Hrdlička deposits have yielded a fauna dominated by cercopithecids, particularly *Parapapio antiquus* and *Papio izodi*, neither of which reveals a particular habitat affinity. The few bovid fossils recovered consist of mainly medium-sized alcelaphines that are unidentifiable to species level, but which tend to indicate the presence of extensive savanna grassland. The presence of the genus *Syncerus*, a probable primary grazer, would support a grassland reconstruction of Taung at the time of deposition.

Hrdlička deposit excavations have yielded two browsers, *Oreotragus oreotragus* (sensu Watson & Plug, 1995), a klipspringer, and *Tragelaphus angasii*, the nyala. Habitat requirements of both of these modern species would be consistent with Taung being surrounded by considerable savanna, as long as there was sufficient plant growth (Skinner & Smithers, 1990). The klipspringer prefers rocky outcrops, which certainly would have been provided by the tufa accretions at the edge of the Ghaap escarpment, not unlike Taung today. The nyala is known to be a mixed feeder that prefers thickets in dry, savanna woodland. The springs at the edge of the escarpment which apparently fed the tufa accretions would have been sufficient to promote localized thickets, as they do in certain areas along the Ghaap escarpment today, literally at the margin of the Kalahari desert.

Observations of the rodent fossils from southern African by Denys (1992a) also show the Taung fauna to be distinct from Transvaal sites representing the Plio-Pleistocene. The rodent evidence supports the notion of a relatively more arid environment at Taung.

Mammalian fossil evidence thus points to the probability of a savanna or perhaps savanna wood-

land, with small, localized oases supporting somewhat more dense brush, characterizing Taung at the time of deposition in the caves of the Hrdlička deposits. The Dart deposits and hominid-associated breccias reported by Broom (1934) do not have sufficient faunal remains to make a comparable reconstruction (table 4-1). It is tempting to extrapolate the environmental reconstruction of the Hrdlička deposits to the Dart deposits, albeit with considerable circumspection. For example, caution may come from the presence in the Dart deposits of an extinct member of *Cephalophus*, for the modern species of the genus is limited to forest habitats; other closely related members of the subfamily cephalophinae, however, such as *Sylvicapra grimmia*, occur in savanna woodland or grassland (Skinner & Smithers, 1990). (Note that *Sylvicapra* has been identified from the loose breccia over the Dart deposits, and is probably associated with them, but due to the disturbed context it has been omitted from the faunal list.)

Investigations of geological evidence from the limestone tufa in which the caves formed (McKee, 1993b), however, provide more compelling evidence for associating the environmental reconstruction of the Hrdlička deposits with those of the Dart deposits. Both are within the Thabaseek tufa; most of this tufa is consistently thinly laminated, having been formed largely by algal and moss concentrations of lime, much like the tufa forming at Taung today. There is no significant erosional valley either upstream or downstream from the Thabaseek tufa that would suggest a former river flow, so it appears as though the tufa formed from spring water emerging near the edge of the Ghaap escarpment. The nearby Oxland tufa accretion, however, which formed after the Thabaseek tufa, is quite distinct in its composition, geological association, and fossil inclusions, leading me to postulate that the tufa itself is indicative of the general environmental setting. The Oxland tufa has consistent inclusion of fossil branches and leaves, much like the tufas forming today in the wetter, subtropical montane forest environments of the eastern Transvaal. The Oxland tufa is associated with deep erosional valleys (including one that cut through the Thabaseek tufa; Peabody, 1954) and clearly formed from a substantial river. The fossils in the caves of the Oxland tufa (McKee, 1994), best represented by Equus Cave (Klein et al., 1991), yield fauna that certainly indicate a considerably wetter environment with more bush cover than exists today. The consistency of associations between tufa type and environment, past and present, imply that the nature of tufa can be used as part of an environmental reconstruction. Had the environment been substantially different between the times of deposition of the

Hrdlička and Dart deposits, then the difference should be revealed by distinct tufa types. But there is no difference, implying that relatively dry conditions prevailed during the formation of the Dart and Hrdlička deposits.

Southern African Environments and the Evolution of Hominids and Other Mammals

Now the best evidence from the Pliocene gives the appearance of a gradient of environments from Taung to Sterkfontein to Makapansgat. This is comparable to the gradient that exists today, but all of the sites would have been shifted toward somewhat warmer and wetter environments than those that currently characterize these areas. More than three decades of research have confirmed what Dart (1964:52) noted:

"The distribution of South African sites from Taung to Makapansgat and the climatic variation to which these sites were subjected geologically during their occupation by australopithecines show that the South African types had adapted themselves to almost, if not quite, as wide a range of climatic, soil and vegetational variation as modern mankind faces outside the arctic circle."

It would thus appear that *A. africanus* used and perhaps regularly inhabited a range of habitats. Our ancestor was probably therefore a generalist rather than a specialist, adaptable rather than adapted. The morphological variability of what is currently considered to be *A. africanus* is consistent with this notion. At Makapansgat and Sterkfontein there is enough variation in craniofacial morphology to elicit proposals of the presence of more than one species (Aguirre, 1970; Clarke, 1985); alternatively, the robust elements noted in some *A. africanus* specimens and the tremendous variability in the growing sample from Sterkfontein may attest to the variability of an evolving lineage without highly specialized facial adaptations. Likewise, whereas all *Australopithecus* fossils are undeniably orthograde and bipedal to a large degree, there are substantial vestiges of arboreal adaptations, particularly in the upper limb (Berger, 1994) and pelvis (Broom & Robinson, 1950).

Diverse habitat ranges are not limited to hominids. Removing the anthropocentric bias of this analysis, the same generalized level of adaptation should be true for *Oreotragus oreotragus*, *Tragelaphus angasii*, *Canis mesomelas*, *Cercopithecoides williamsi*, *Parapapio broomi*, *Panthera pardus*, *Procapra antiqua*, as well as six species of rodent, a bat, and a shrew, all

of which appear at Taung, Sterkfontein, and Makapansgat (table 4-1). Half of those species still exist in southern Africa today, suggesting that past environmental contingencies of evolutionary change seem to be irrelevant to this adaptable group.

Eastern African paleoecological data from *A. afarensis* sites demonstrate a broad habitat range for the hominid species (T. D. White et al., 1993). Together with the southern African data, the fossil record now appears to support the notion of a generalized adaptability and a wide niche for even the earliest known hominids. Thus one aspect of the scenario presented earlier, that of niche expansion, garners some support. In an autocatalytic model, this would propel further novelty as long as the genetic and phenotypic variability was available, and indeed the hominid fossil remains indicate such variability.

Virtual coincidence of environmental changes with the emergence of the genus *Homo* in southern Africa requires careful consideration. First, the morphology of *Homo* seems to be limited to a few changes in the face and a slight increase in cranial capacity, none of which is inconsistent with a gradual change from *A. africanus* given the high degree of morphological continuity, at least in craniofacial morphology (McKee, 1989). Second, taphonomic considerations and the geographical isolation of Transvaal sites obscure the reconstructions of subcontinental environmental change in southern Africa, and may make them appear more profound than they really were (McKee, 1991). Finally, when considering all of the fauna, the first and last appearances of species around that time cannot be differentiated from that expected by chance under a model of stochastically regular turnover (McKee 1995, 1996b). Only after about 1.8 m.y., following Swartkrans Member 1 and following the establishment of *Homo* in southern Africa, is there any unusual faunal change, and even this is not distinguishable from chance.

Origins of the genus of *Homo* in an apparently changing environment cannot be clearly distinguished as being anything more than mere coincidence. *Homo habilis* (sensu lato) at this stage appears in both eastern and southern Africa, seeming to indicate a proliferation of a successful lineage rather than a forced adaptation. In East Africa, the delineation of an event, as opposed to a continuous autocatalytic process, is dubious given the apparent gradual changes of ecological parameters (Cerling, 1992a; Bishop, 1993; Kingston et al., 1994; Denton, this volume). Only the East African bovids seem to show an evolutionary pulse (Vrba, 1985c), and this appears much later in southern Africa, following the introduction of *Homo*; the bovid scenario could thus be characterized as an

autocatalytic adaptive radiation rather than an environmentally induced event of vicariant speciations.

Discussion

Legitimate tests of autocatalytic evolution are difficult to formulate, as with models of climatic determination of the timing and pace of evolutionary origin of species, due to the limits of the fossil record. To support one model or the other, one must distinguish the effects of chance from true cause and effect, given a multiplicity of evolutionary forces. Although the chance nature of autocatalysis appears to have the edge in current analyses of fossil data, the apparent trends do not prove autocatalytic evolution; the African fossil record is as yet too incomplete. Thus the fossil record must be complemented with an appeal to known mechanisms of evolution.

Underlying models of either autocatalysis or climatic causation are the same genetic prerequisites, and these necessarily rely on chance origins of appropriate adaptive features. In summary, the selective forces in the two models differ in that climatic forcing depends on selective pressures decreasing variability, whereas under autocatalysis selective advantages are favored in highly variable populations. The selective advantage in the autocatalytic model comes with the advantages of niche expansion rather than reliance on what could have been untimely forcing. Environmental change, for specifically adapted mammals, is often more likely to lead to extinction than evolution, largely due to unlikelihood of the appropriate genetic basis for new phenotypes existing when the population of a species is reduced by environmental stress. For ecologically generalized mammals (and the evidence suggest that early hominids were just that), environmental change would have a negligible effect in initiating or sustaining evolutionary change.

The mechanisms and concepts of autocatalytic evolution are rooted in microevolutionary theory, but paleontologists usually try to observe them at a macroevolutionary level. Perceived macroevolution must be reconcilable with known microevolutionary mechanisms. Part of the problem with this reconciliation is the focus on species for perceptions of macroevolution. Paleontological "species" are notoriously difficult to define and recognize, for they are transient entities at best at any moment of geological time. The mosaic nature of hominid morphological evolution (McHenry, 1994a) makes species definitions particularly difficult. But perhaps species questions should be the last, not the first, part of fossil

analysis. To understand the ecological relevance of evolving lineages such as hominids, we must ask the right questions about the fossil data.

In the context of autocatalytic evolution, hominids may provide an example of an evolving lineage that poses legitimate research questions. A primary question in autocatalytic evolution would concern correlations of morphological features, such as orthograde posture, basicranial flexion, and encephalization. The tempo and mode of the evolution of features, not species, can then be assessed.

One must first find a means of identifying evolving features that may have affected the fitness of the evolving animals before addressing paleoecological questions. This is more difficult than it may appear, for directional trends do not always imply that natural selection has directly influenced traits. The confounding effects of other evolutionary forces (e.g., McKee, 1984) and what Vrba (1983) has termed the "effect hypothesis" limit the adaptive nature of many traits. The objective is not to fit traits to an environment, as is often done, but to discern the potential effects of traits within an environmental milieu. Once potentially selective significant features are recognized, then each of the levels of selection outlined in figure 4-1 must be considered. Thus only a few evolving features will be ecologically relevant, although certain features, such as encephalization, may act upon fitness at more than one level.

New paleoecological questions arise from the analysis of ecologically relevant morphologies. The key question is whether a trait or trait set is specifically adapted to an environment, and this is testable by circumspectly comparing paleoenvironmental clues from sites in which the animals possessing those traits are found. By then looking at lineages of related animals, one can approach questions of adaptiveness versus adaptability, evolved versus evolvable traits, and autocatalyzed versus environmentally induced evolution. We may even find unexpected general trends across species, such as one of increased adaptability in the evolution of mammals. Principles of the causes and consequences of evolution can then be gleaned within an environmental framework.

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