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环境变异及其对人类进化的作用*

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摘　要

长时期以来，早期人类进化被认为是对于从森林到开旷的栖息地（如林地、稀树草原、冰川地区）的定向变动的反应．但是人类进化时期中的长期古环境纪录却与这种简单的定向趋势加上继之而来的稳定的开旷栖息地的观念相矛盾．而深海岩芯、古植物和古湖泊的证据全都暗示着高度的和步伐不规则的环境波动．在人类进化时期的环境波动的程度比新生代的任何较早的时期为大．对自然选择提出的互相冲突的要求的适应可以提供比对简单定向趋势或稳定环境的适应更好的解释．南肯尼亚更新世的一个例子显示，环境变异可以如何影响物种的持续和变化．

关键词　人类进化，古生态，稀树草原假说，环境变异，哺乳动物进化，东非，奥罗格塞里

前　言

越来越多的古人类学家将他们的研究工作集中到人类进化的古生态学方面．这些研究人员利用化石纪录尽可能直接地探索人类祖先的情况和环境的情况．按照达尔文（1859，1871）建立的范例，外界条件直接有力地影响于有机体的适应战略和物种的起源与寿命．古人类学将这一范例应用于人类的祖先和有关的两足行走的生物．

本文的目的是阐述以下问题：什么是我们所知的人类起源的确切的环境条件？特别是，什么是我们所知的自然选择对人类所起的作用．

古人类学中的达尔文范例

在非洲、欧洲和西亚工作的科学家中，关于人类适应进化的流行观点可以归于两个部分．第一，定向的环境变化是人科起源与进化中涉及的超越一切的力量．新第三纪和第四纪的气候持续地在变凉、变干燥，并向着开旷带植被生态构造发展着．Vrba(1985，1992；Vrba 等，1989）曾提出，这种定向的趋势乃脉冲式地出现而不是持续地，逐渐地

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变化着。这些脉冲对应于物种的形成、绝灭，也对应于非洲稀树草原的人类和其它大型哺乳动物的适应变化。

流行观点的第二部分是由下述的进行性环境变动滋生出来的。人类变得适应于特定的开旷地区的栖息地，特别是热带和亚热带地区的开旷的林地和稀树草原，在某种情况下可能到温带的无树平原、草原和冰川地区。相当多的科学争论集中于早期人类的特定的环境背景（例如：森林、林地或草原）与特定的小生境（例如：狩猎、捡食剩尸或采集植物）。这些争论起源于一种假定，即人类有一个特定的祖先栖息地，也就是说，人类是在回应一种颇为特定的生态构造或一套适应的条件中发展着的。

就以非洲为基地的人类进化的最早时期而言，流行的范例可以归结如下：原始人类随着稀树草原的扩展而变得更多在地面生活。稀树草原栖息地有利于向更加依赖工具和肉食的方向的选择。至少有一支早期人类的进化链对这些选择压力作出了强烈的反应，在这一支人类中，地面生活，使用工具，肉食交互作用，有利于强烈地增大脑子（参见 Klein, 1989: 180−182; Wolpoff, 1980: 98−102; Pilbeam, 1972）。

这种解释（稀树草原假说）是达尔文（1871）首先提出来的，当时并没有人类化石证据、奥杜韦石器或早期的肉食。当然现在在非洲已出现丰富的这一类证据。按照这一范例，人类适应的主要事件和变化是由于从温暖湿润的环境向着凉爽、干燥并较开旷的栖息地的进行性的（即使是时有时无的）变化所促成的。当环境变化出现时，便对人类具有经常性的作用。指示环境趋势对适应变化的经常性作用的常用词"压力"或"迫使"都指示着自然选择的定向的影响。对自然选择的这种理解已广泛地为古人类学家所采纳。按照关于人类进化的通俗书籍所说，例如"由于选择而产生的变化的速率，每一世代往往是很小的，但是当这些变化在长时期中在同一方向进行着的情况下，小变化可以产生大的结果"(Wolpoff, 1980: 22)。

人们试图详细说明东非的早期工具制造者的栖息地或小生境，以此为例证来说明传统的范例。有几位研究人员最近把这种小生境描绘为靠近水边的多树的平原栖息地的一种拣食猛兽食剩物的适应（Blumenschine, 1987; Cavallo and Blumenschine, 1989）。关于特定的一套选择条件驱动着人类进化的假设，在行为生物学家的著作中也是很明显的。许多行为生物学家把现代人的行为归因于一种特殊的祖先环境的经常性的影响（Barkow *et al.*, 1992）。

然而上新世和更新世的环境资料却是与人类在其中生活的简单的、定向的趋势和稳定的生态构造相矛盾的。我将在此勾画出关于人类进化的一个稍有不同的观点，强调过去600万年内自然选择条件的变异性和地理区域气候和植被环境的多样性。

晚新生代的环境纪录

新生代趋势： 新生代的整个环境趋势首先表现为对流行的范例提供强有力的支持。例如深海岩芯的氧同位素数值指示着全球气候变凉和冰川增强，因为在这段时间中重氧(O−18）在增加（图1）。这种趋冷的趋势暗示着干旱的增重，从5000万年前到现代都能看到。

哺乳动物在新生代的纪录显示出食草动物颊齿体积的增加（例如偶蹄类和奇蹄类的高冠齿），食草动物各条进化世系上身体度量反复的增大和行动器官的特化（例如远侧段肢骨的延长）．所有这些都指示着越来越开旷的栖息地，特别是粗糙的、带砂砾的植物性食物和长距离的运动的重要性（Janis and Damuth, 1990）．因此化石纪录证实了整个环境变得干燥，稀树草原在扩展，显示出其对哺乳动物进化世系的冲击．

中新-上新世：然而，图 1 指示着人类进化的过去的 600 万年的这段时间中，氧同位素比例的综合变化或平均变化是循序渐进的，大约达到百万分之 1.5 到 2．但是对氧同位素资料进行更详细的考察便可看出，越来越多的温度和湿度的波动也是这一时期的特征．

按照 Stein 和 Sarnthein（1984）研究的海洋岩芯资料，氧同位素在接近中新世时变得更显著（图 2）．在 600 万与 460 万年之间出现了达到百万分之一的振荡．氧同位素曲线的这些变动被认为是反映了南极洲的冰川的进和退．这暗示着全球水文学条件在波动着，因为在极地的冰中水被反复地冻结和释放．

这也是墨西拿含盐度危机（Messinian salinity crisis）的时间，典型地被描绘为地中海盆地的干涸．这一干涸事件影响着环地中海大陆，包括非洲可以获得的湿气．这段时期的地中海地层序列实际上显示出一系列蒸发沉积物，指示着间杂着泛滥时期的盆地变干过程．这是一个干和湿波动的序列，而不是单纯的干旱事件或趋势．

这一时期非洲的陆地纪录目前还很稀缺．把见之于早期南方古猿的一系列不寻常的行动特征联系到应付各种环境（有茂密树木的栖息地和树木很少的栖息地）的能力，这是很有吸引力的事情．这一假说与学者们复原的早期南方古猿栖息地的多样性（由森林到很开旷的地区）是很一致的（例如 Leakey and Harris, 1987; Andrews, 1989; Johanson *et al.*, 1982; WoldeGabriel *et al.*, 1994）．

晚上新世：Vrba（1988）已经注意到大约 250 万年前非洲稀树草原扩展的主要事件．这个事件与向较凉和较干环境的全球变化相对应．按照 Vrba 的换新-脉动（turnover-pulse）观念，这段时间的标志是牛科和人科中旧种的绝灭和新种的起源．

不过图 3 显示，氧同位素值的宽幅变化而不是单向的变化也是这一时期的标志．在新生代中同位素波动第一次高达百万分之 1.5．的确最近的氧同位素资料指示这一宽幅的振荡开始于至少 280 万年前．Vrba 和她的同事们现在利用 280 万年作为假设的干旱事件的开始时间．不过我要建议，这一“事件”反映振荡幅宽的增加，就是说，在整个环境趋势的大的周期性反转的开始．

第四纪：将过去 250 万年中的复合同位素曲线（图 1）与详细曲线（图 4）进行比较，大的周期性发生的振荡构成了整个趋势．振荡牵涉到接近百万分之二的同位素变化的第一个新生代事件，在过去 50 万年中是明显的．

这一时期的最佳陆地纪录证实了气候波动是重要的．中国明显的黄土序列不仅证实冰期状态的来临，也证明风吹的粉砂的干燥而开旷的环境与土壤所代表的湿润的树木繁茂的环境之间的振荡．对中国中北部的黄土序列的研究指示着冷干草原和温暖森林栖息地之间的反复变化（Kukla, 1987）．

过去 100 万年的化石孢粉最佳纪录之一来自马其顿的 Tenaghi Philipon 泥煤沼泽（参看 Kukla, 1989）．沼泽的孢粉构成作为一种气候指标示之于图 5，代表着封闭的森林与无树草原之间的变异．

奥罗格塞里(Olorgesailie)地点（南肯尼亚裂谷）提供了非洲的环境变化，化石哺乳动物和早期人类石器的年代最精确的纪录之一（Isaac, 1977; Potts, 1989, 1994; Deino and Potts, 1990）．这个地点保存了一套从120万年前到49000年前的硅藻土湖床，古土壤和火山灰堆积的序列．古湖泊堆积的硅藻已被研究过（Owen and Renaut, 1981）．结合到我们新的 ^{40}Ar／^{39}Ar 年龄，硅藻和岩性学指示着湖泊面积和深度的大规模波动（图6）．这种变化有一部分是由于构造运动，但是也牵涉到干–湿周期所指示的气候不稳定性．

我们在奥罗格塞里的研究符合于过去100万年温带的可获得的最好的环境纪录，并指示着程度令人惊异的环境变异．Foley（1987）和其他人已注意到季节性的变异，但最大的变异大大超过季节性的范围．在时间长得多的时间框架中，奥罗格塞里景观中的水、植物和动物资源都牵涉到气候变动、构造活动和附近的火山喷发．人科中的工具制造者和其他生物都经历了地域和生态背景的这些变异，我认为，这些变异对于他们的进化历史有过强的影响．

解释人科中的适应变化

对过去环境的直接研究并不指示有恒定的趋势．周期性的运动，资源的紧缩和扩大都必定引起自然选择强度和方向的变动，即在选择性的适应战略中的相对价值和益处是不同的．我认为，这些自然选择条件随着时间演变而发生的这些不同对于包括人在内的大型哺乳动物的更新世进化世系的成功有过较为重要的作用，其作用比任何单纯的栖息地类型或环境趋势为大．

自从中新世以来越来越大的环境波动对于生物体在追寻攸关其生存与生殖的食物和水资源方面提出了新的问题．一个基因库（或进化世系）的持久存在会在两个方面进行改进：1）较大的移动能力或扩布能力，使得该群体能跟得上栖息地的变动，2）在行为和生态交往方面提高才能，使得该群体在新的环境体制下能持续下去．

除人以外的大型哺乳动物也面对环境的波动．南肯尼亚裂谷的进化世系使人们能够知道它们的情况．奥罗格塞里早更新世的大约40%的大型哺乳动物种现已绝灭，在遭遇死亡的那些物种之间有着一个共同点．奥罗格塞里的更新世哺乳动物的特征是一套大体型的吃青草的动物，包括象、斑马、猪、河马和猴子（图7）．这些大型的吃草动物在南肯尼亚的早和中更新世在数量上占优势，甚至比牛类还多．绝灭了的斑马（*Equus oldowayensis*）比其现生的亲戚（*Equus grevyi*）要大，门齿列扩大，颊齿增大，用于咬断青草的尖端和咀嚼．绝灭了的象（*Elephas recki*）也具有特化的臼齿以咀嚼粗的、多纤维的草．所有占优势的食草动物的体型大小和牙齿的特化都有力地保证它们能以青草为食，但是所有这些物种都于60—33万年前之间在南肯尼亚裂谷绝灭了（Potts and Deino, 1995）．相比起来，这些门类的生存下来的亲戚则具有相对地多样化的食性或者能够作长距离迁徙以获取食物和水．

南肯尼亚裂谷中的这种有区别地绝灭和存活的型式意味着对于生死攸关的资源所发生的周期性变化发展出了增宽幅度反应的那些进化世系最后是有利的．绝灭了的进化世系是与整个变干旱的趋势和开旷的稀树草原植被（草）显然很相匹配的门类．这些物种在早更

新世是占优势的，但是到中更新世当环境波动再次增强时竞争能力便变得较小了．

东非的大型食草动物对更新世人类的进化变化提供了潜在的线索．流行的范例并不能很好地解释现代人适应的某些关键的方面，例如提高行为的灵活性和多样性，群体长途移动的能力和提高缓冲环境动乱的能力．现代人类生态学的这些特征似乎并不容易解释为对一种单纯定向的环境变化适应的结果．但是对环境变异的强调却提供了一种较为开明的解释．我提出那些适应于长期的环境变异而不只是能适应季节性栖息地多样变化的群体，是比那些仅适于单纯类型的环境的群体更有利的．换句话说，人类群体的成功最终取决于他们对自然选择长期状况的差异应付得怎么样．

结　论

1.在人类进化过程中重复出现的栖息地交替意味着并没有早期人类栖息地的简单的“最佳”环境复原．将早期人类的环境描绘为一种稳定的不变化的状态也是容易引起误解的．

2.栖息地和资源的波动可能驱动了自然选择 (Potts, 1994)．上新世和第四纪的环境纪录使我们集中注意力于选择条件的变异性．把生态变异性作为人类行为起源的极为重要的因素，我们可以对解释自然选择所起过的作用的方式作出意义重大的修正．我们可以不是简单地把它看作选择的“压力”或对特殊环境的适应，而是把它认为在时间长河中，不同地域中对栖息地和资源的变异性的一种反应．这一种看法与现有的认为自然选择有着简单一贯作用的范例是颇为不同的．

3.这一看法展宽了进行古人类学比较的范围．研究环境、动物群和人类行为的考古证据的学者们倾向于没有比较地研究不同的大陆．本文勾画出的新范例意味着，更合适的目的是建立在时间长河中人类群体生活和持久生存的条件的范围．比较包括人类整个地理范围的长时间的环境状况可以获知人类进化的生态条件．在亚洲、非洲和欧洲工作的科学家之间的合作研究可以使合适的比较研究得以完成．

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插 图 说 明

图 1 包含过去 7000 万年的深海岩芯中海底有孔虫的 ^{18}O 纪录的综合测量
图 2 DSDP 397 地点的 640—460 万年海底 ^{18}O 纪录
图 3 DSDP 552A 地点的 300—200 万年海底 ^{18}O 纪录
图 4 最近 250 万年海底 ^{18}O 纪录波动的复合纪录
图5 马其顿更新世(Tenaghi Phillipon泥煤沼泽)的更新世气候变迁，根据的是橡、松和全部孢粉计数的气候指数（CI)。高的指数指示森林，低的指数指示开旷草原
图6 根据硅藻和约100万年与50万年之间的岩相学所作的奥罗格塞里湖泊深度曲线。P,C.和 G 分别指示广泛分布的古土壤、碳酸盐和砂砾的地层位置，它们夹插于湖相沉积的层序中
图 7 中更新世东非占优势的大体型吃草的动物

(岳 冰 译)

ENVIRONMENTAL VARIABILITY AND ITS EFFECT ON HOMINID EVOLUTION

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Abstract

Early hominids have long been considered to have evolved in response to a directional shift from forested to open habitats (e.g., woodland, savanna grassland, glaciated terrain). Long–term paleoenvironmental records during the span of hominid evolution, however, contradict the idea of a simple directional trend followed by open–habitat stability. Rather, evidence from deep ocean cores, paleovegetation, and paleolakes all suggest a high degree and erratic pace of environmental fluctuation. The degree of fluctuation was higher during the period of hominid evolution than any earlier time during the Cenozoic. Thus adaptation to disparity, or to the conflicting demands posed by natural selection, may provide a better explanation of hominid evolu-

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tion than adaptation to a single directional trend or stable environment. An example from the Pleistocene of southern Kenya illustrates how species survival and change may have been affected by environmental variability.

Key words　Hominid evolution, Paleoecology, Savanna hypothesis, Environmental variability, East Africa, Olorgesailie, Mammalian evolution

Introduction

An increasing number of paleoanthropologists have focused their research on the paleoecological dimension of human evolution. These researchers use the fossil record to investigate as directly as possible the conditions, or environmental contexts, of human ancestry. According to the paradigm established by Darwin (1859, 1871), external conditions have direct impact on the adaptive strategies of organisms and the origin and longevity of species. Paleoanthropology is the application of this paradigm to human ancestors and related bipeds.

The purpose of this paper is to address the question: What exactly do we know about the environmental conditions of human origins? In particular, what do we know about the effects of natural selection on the hominids?

The Darwinian Paradigm in Paleoanthropology

Among scientists working in Africa, Europe, and western Asia, the prevailing view about hominid adaptive evolution can be defined in two parts. First, directional environmental change was the overarching force involved in the origin and evolution of the Hominidae. Climatic cooling, drying, and the development of open vegetation biomes were persistent during the late Neogene and Quaternary. Vrba (1985, 1992; Vrba *et al.* 1989) has proposed that this directional trend occurred in pulses rather than by continuous, gradual change. The pulses corresponded with periods of speciation, extinction, and adaptive change in hominids and other large mammals of the African savanna.

A second element of the prevailing view stems from this progressive environmental shift: Hominids became adapted to specific open–country habitats, particularly open woodland and savanna in the tropical and subtropical latitudes, and eventually steppe, prairie, and glacial terrain in temperate latitudes. Considerable scientific debate has focused on the specific environmental setting (e.g., forest, woodland, or grassland) and specific niche (e.g., hunting, scavenging, or plant gathering) of early hominids. This debate arises from an assumption that hominids had a specific ancestral habitat – i.e., that hominids evolved in response to a rather specific biome or set of adaptive conditions.

For the oldest period of hominid evolution, based in Africa, the prevailing paradigm can be summarized as follows: With the spread of savanna, proto–hominids became more terrestrial. The savanna habitat selected for much greater reliance on both tools and meat. At least one early hominid lineage responded strongly to these selective pressures, and in this lineage, ground living, tool use, and meat eating interacted to favor a dramatic increase in brain size (see Klein 1989: 180–182; Wolpoff 1980: 98–102; Pilbeam 1972).

This interpretation – the savanna hypothesis – was first developed by Darwin (1871) even before there was any fossil evidence of hominids, Oldowan stone tools, or early meat eating. There is now, of course, an abundance of such evidence from Africa. According to this paradigm, major events and changes in hominid adaptation were precipitated by the progressive (if sporadic) change from warm, moist environments to cool, dry, and more open habitats. When environmental change did occur, it had a consistent effect on the hominids. The directional influence of natural selection is indicated by the often–used terms "pressure" or "forcing", which indicate the consistent effect of the environmental trend on adaptive change. This understanding of natural selection is widely adopted by paleoanthropologists. According to a popular text on hominid evolution, for example: "The rate of change due to selection is ususally very small each generation, but small changes can have great results when they proceed in the same direction for long periods of time" (Wolpoff, 1980: 22).

The traditional paradigm is illustrated by attempts to define the specific habitat or niche of early toolmakers in East Africa. Several researchers have recently depicted this niche as a scavenging adaptation situated in a wooded savanna habitat near water (Blumenschine 1987; Cavallo and Blumenschine 1989). The assumption that hominid evolution was driven by a specific set of selective conditions is also evident in the writings of behavioral biologists, many of whom ascribe current human behaviors to the consistent influence of an specific ancestral environment (Barkow *et al.* 1992).

Pliocene and Pleistocene environmental data, however, contradict the ideas of a single, directional trend and stable open biome where hominids lived. A somewhat different view of hominid evolution may be outlined here, emphasizing the diversity of geographic locales, climates, and vegetational settings, and variability in the conditions of natural selection over the past 6 million years.

Late Cenozoic Environmental Records

Cenozoic trend: The overall environmental trend of the Cenozoic appears, at first, to provide strong support for the prevailing paradigm. Oxygen isotope values from deep-ocean cores, for instance, indicate global climatic cooling and increased glacial ice as the abundance of heavy oxygen (O–18) increased over time (Fig. 1). This cooling trend implies increased aridity, and can be seen from 50 Ma to the present.

The mammalian Cenozoic record shows an increase in herbivore cheek–tooth volume (e.g., hypsodonty in artiodactyls and perissodactyls), repetitive increases in body size in various herbivore lineages, and locomotor specializations (e.g., lengthening of distal limb bones) – all of which indicate progressively more open habitats, particularly the importance of a coarse, gritty plant diet and long–distance movement (Janis and Damuth 1990). Thus the fossil record cor-

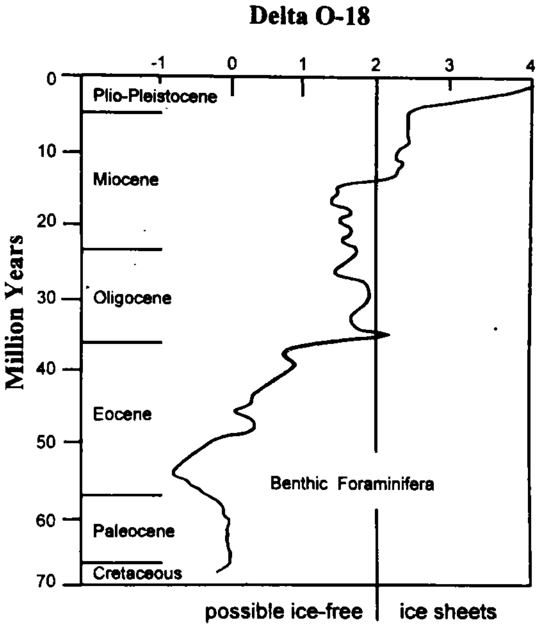

Figure 1. Composite measurements of delta ^{18}O of benthic foraminifera from deep ocean cores spanning the past 70 million years (Raymo and Ruddiman 1992)

roborates the overall environmental drying and spread of savanna, and demonstrates its impact on mammalian lineages.

Mio–Pliocene: Consider, however, the past 6 million years during which hominids evolved. Figure 1 indicates that the composite, or average, change in the oxygen isotope ratio during this time was progressive, approximately 1.5 to 2 parts per mil. Yet a more detailed look at the oxygen isotope data suggests that this time period was also characterized by increased fluctuation in temperature and moisture.

According to ocean–core data studied by Stein and Sarnthein (1984), fluctuation in oxygen isotopes became more marked near the end of the Miocene (Fig. 2). Repeated oscillations of up to 1.0 parts per mil occurred between 6.0 and 4.6 Ma. These shifts in the oxygen isotope curve are thought to reflect glacial advances and retreats in Antarctica, which imply that global hydrological conditions were fluctuating, as water repeatedly became locked up and released in polar ice.

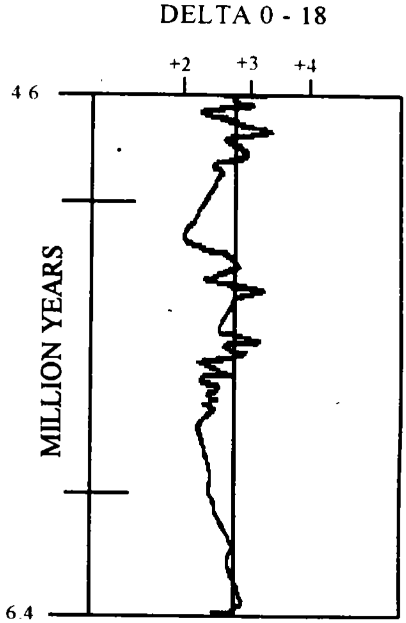

Figure 2. Benthic delta ^{18}O spanning 6.4 to 4.6 Ma, from DSDP site 397(Stein and Sarnthein 1984)

This was also the time of the Messinian salinity crisis, typically portrayed as a drying up of the Mediterranean basin. This drying episode affected the moisture available to circum–Mediterranean continents, including Africa. The Mediterranean sequence of this period actually shows a series of evaporite deposits, indicating drying interspersed with periods of flooding of the basin. A sequence of dry–wet fluctuations occurred, not a single aridity event or trend.

Terrestrial records in Africa are currently quite scarce for this time period. It is tempting nonetheless to link the unusual array of locomotor characteristics seen in the early australopithecines to an ability to cope with variable environments – habitats with dense stands of trees and habitats with very few. This hypothesis agrees well with the diversity of reconstructed habitats of early *Australopithecus* – from forested to quite open (e.g., Leakey and Harris 1987; Andrews 1989; Johanson *et al.* 1982; WoldeGabriel *et al.*1994).

Late Pliocene: Vrba (1988) has drawn attention to a major episode of savanna expansion in Africa about 2.5 Ma. This corresponds with a global change to a cooler, drier environment.

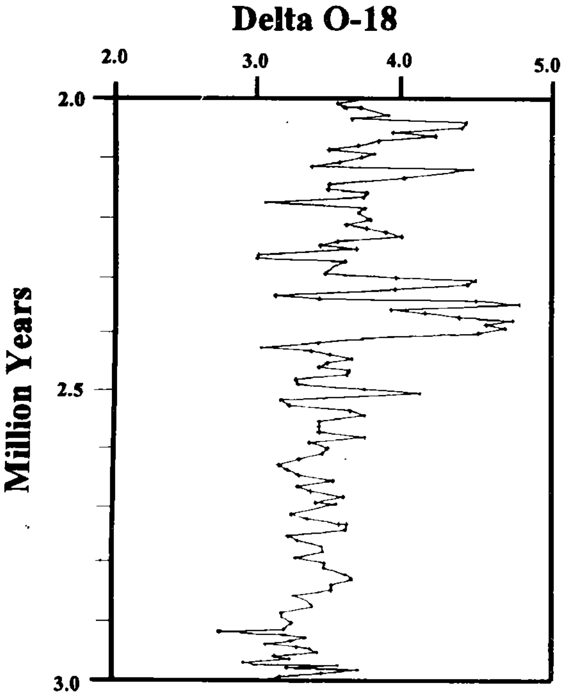

Figure 3. Benthic delta ^{18}O spanning 3.0 to 2.0 Ma, from DSDP site 552A (Shackleton *et al.* 1984)

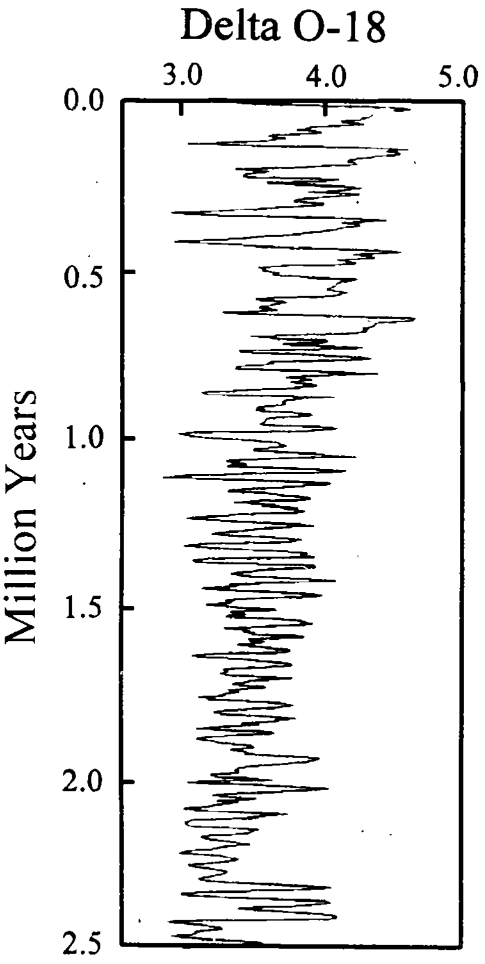

Figure 4. Composite record of benthic delta ^{18}O fluctuations spanning the last 2.5 million years (see Crowley and North 1991: 113)

According to Vrba's turnover—pulse idea, this time was marked by extinctions and new species origins in the bovids and the hominids.

Figure 3 shows, however, that this period was also marked by widened variance in oxygen isotope values rather than by a single directional shift. For the first time in the Cenozoic, the isotopic fluctuation reached as much as 1.5 parts per mil. Indeed, the latest oxygen isotope data indicate that this wide oscillation began at least 2.8 Ma. Vrba and colleagues are now using 2.8 million as the start of the supposed drying episode. I would suggest, however, that this "event" reflects a rise in the *amplitude* of oscillation, i.e., the onset of large, periodic reversals in the overall environmental trend.

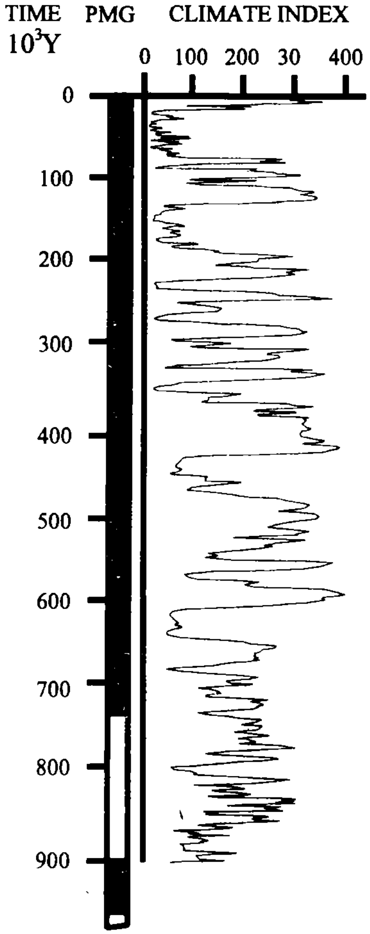

Figure 5.　Plestocene climatic variation in Macedonia (Tenaghi Phillipon peat bog) based on a climate index (CI) of oak, pine, and total tree pollen counts. A high CI indicates forest, a low CI indicates open steppe. Compiled by Kukla (1989) based on work of Wijnstra and colleagues (see references in Kukla 1989)

Quaternary: Compare the composite isotope curve (Fig. 1) with the detailed curve (Fig. 4) for the past 2.5 million years. The overall trend is made up of large, recurrent fluctuations. Oscillation involved the first Cenozoic episodes of isotopic change of nearly 2 parts per mil, evident over the last 500,000 years.

The best terrestrial records from this time period corroborate the importance of climatic fluctuation. The remarkable loess sequence of China documents not just the advent of glacial conditions, but also the oscillation between dry, open environments of wind–blown silt and moist, wooded environments, represented by soils. Study of the loess sequence in north–central China indicates a repetitive change between cold steppe and warm forest habitats (e.g., Kukla 1987).

One of the best records of fossil pollen for the past 1.0 m.y. comes from the Tenaghi Phillipon peat bog in Macedonia (see Kukla 1989). Change in the pollen composition of the bog are shown in Figure 5 as a climate index, representing variation between closed forest and treeless steppe.

The Olorgesailie locality (southern Kenya rift valley) provides one of the most precisely–dated records in Africa of environmental change, fossil mammals, and early human artifacts (Isaac 1977; Potts 1989, 1994; Deino and Potts 1990). This locality preserves a sequence of diatomite lake beds, paleosols, and volcanic ash deposits from 1.2 to 0.049 Ma. Diatoms from the ancient lake deposits have been studied (Owen and Renaut 1981). Combined with our new $^{40}Ar/^{39}Ar$ dates, the diatoms and lithologies indicate large–scale fluctuations in lake size and depth (Fig. 6). Tectonic activity was responsible for some of this variability, but moist–dry cycles indicative of climatic instability were also involved.

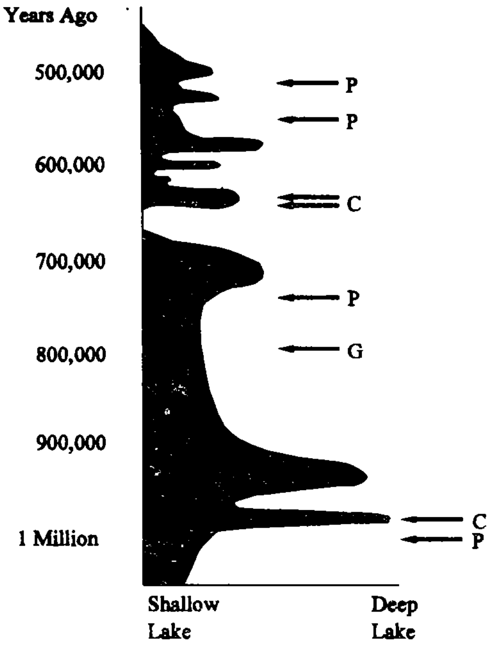

Figure 6. Olorgesailie lake depth curve based on diatoms (Owen and Renaut 1981) and lithologies, between ca. 1.0 and 0.5 Ma (Deino and Potts 1990). P, C, and G indicate the stratigraphic position of widespread paleosols, carbonates, and gravels, which interrupt the sequence of lake deposits

Our research at Olorgesailie is in accord with the best environmental records available from the temperate latitudes over the past 1 m.y., and indicates a surprising degree of environmental variability. Attention has been paid by Foley(1987) and others to seasonal variability, but the largest variations greatly exceeded the seasonal range. Climatic shifts, tectonic activity, and nearly volcanic eruptions were involved in altering the water, plant, and animal resources on the Olorgesailie landscape over a much longer time frame. These variations in terrain and ecological setting were experienced by hominid toolmakers and other organisms, and, I suggest, had an strong influence on their evolutionary history.

Explaining Adaptive Change in Hominids

Direct investigation of past environments does not indicate a consistent trend. Periodic movement, contraction, and expansion of resources must have caused shifts in the strength and direction of natural selection – i.e., in the relative costs and benefits of alternative adaptive strategies. I suggest that these *disparities* in the conditions of natural selection over time had a more important effect on the success of Pleistocene lineages of large mammals, including hominids, than did any single type of habitat or environment trend.

Increased environmental fluctuation since the Miocene presented new problems to organisms with regard to tracking food and water resources pertinent to survival and reproductive success. The persistence of a gene pools (or lineages) would have been promoted in two ways: (1) greater mobility or dispersal capabilities, enabling populations to track the movement of habitats, and (2) increased versatility in behavior and ecological interaction, enabling populations to endure new environmental regimes.

Large mammals besides hominids also faced environmental fluctuation. Pleistocene lineages of the southern Kenya rift valley provide insight into how they fared. About 40% of the large mammal species from the early Pleistocene of Olorgesailie are now extinct, and there is a similarity among those which met their demise. The Pleistocene fauna of Olorgesailie was typified by a suite of large–bodied grazing specialists, including elephants, zebras, pigs, hippopotamus, and monkeys (Fig. 7). These large grazers were numerically dominant during the early and middle Pleistocene of southern Kenya, even more abundant than the bovids. Compared with its living relative (*Equus grevyi*), the extinct zebra *Equus oldowayensis* was larger and had an expanded incisor row and enlarged cheek teeth used in cropping and processing grass. The extinct elephant *Elephas recki* also possessed specialized molars for dealing with coarse, fibrous grass. The size and dental specializations of all of the dominant herbivores are indicative of a strong commitment to a grazing diet, yet each of these species became extinct in the southern Kenya rift between 600 and 330 ka (Potts and Deino 1995). By comparison, the surviving relatives in each of these taxonomic groups possess a relatively diverse dietary strategy or the ability to migrate long distances to obtain food or water.

The pattern of differential extinction and survival in the southern Kenya rift suggests that those lineages that evolved a broadened response to periodic change in critical resources were eventually favored. The lineages that became extinct were ones apparently well matched to the overall drying trend and open savanna vegetation (grasses). These species dominated early in the Pleistocene, but became less competitive in mid–Pleistocene contexts when environmental fluctuation again intensified.

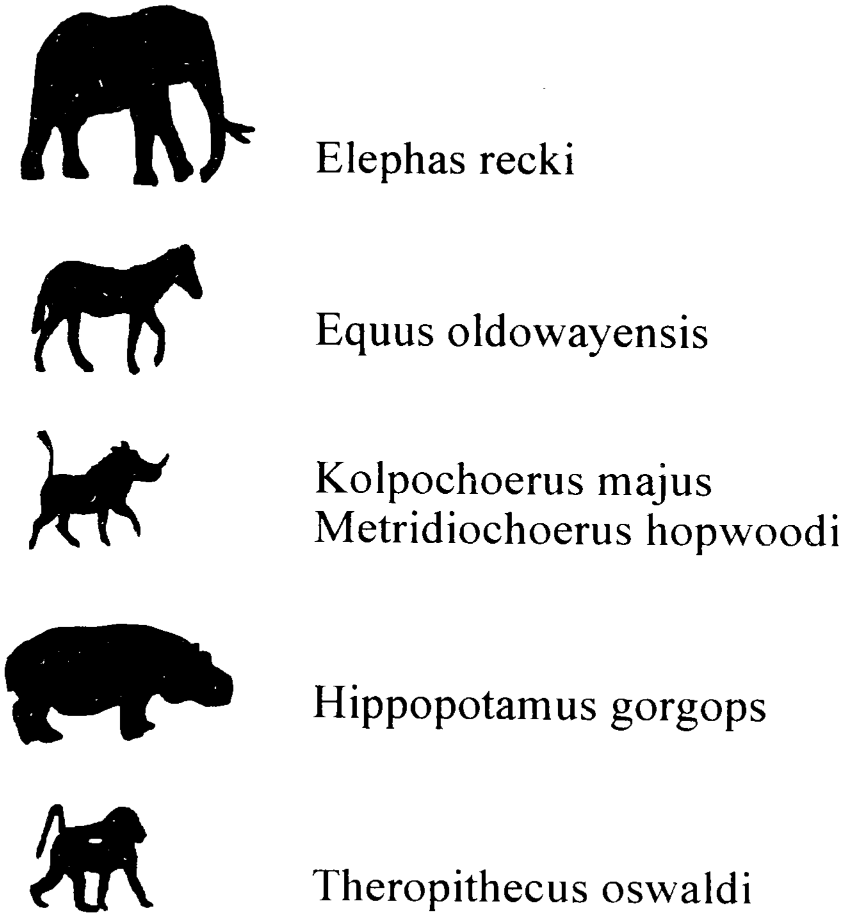

Figure 7. The dominant large–bodied grazing herbivores of East Africa during the Middle Pleistocene

The large herbivores of East Africa offer a potential clue about evolutionary change in Pleistocene hominids. The prevailing paradigm does not explain very well certain key aspects of modern human adaptation, such as increased behavioral flexibility and diversity, long–distance mobility of populations, and increased ability to buffer environmental disturbances. These features of modern human ecology do not seem to be easily explained as a result of adaptation to a single directional environmental change. An emphasis on environmental variability, however, provides a more enlightening explanation. I propose that populations adapted to long–term environmental variability, not just seasonal habitat diversity, were favored over those preferring a single type of environment. In other words, the success of hominid populations ultimately depended on how well they coped with disparities in the long–term conditions of natural selection.

Conclusion

1. Repeated habitat alteration during hominid evolution suggests that there is no single "best" environmental analogue or reconstruction of early hominid habitat. It is also misleading to portray the environment of early hominids as a stable, unvarying state.

2. Fluctuations in habitats and resources may have driven natural selection (Potts 1994). Pliocene and Quaternary environmental records lead us to focus on **variability** in selective conditions. By adopting ecological variability as a critical factor in the origin of hominid behaviors, we may significantly revise the way natural selection is construed to have operated. We may think of it not simply as selection "pressure" or as adaptation to a particular environment, but rather as a response to habitat and resource variability from place to place and over time. This outlook is rather different from the existing paradigm of a single consistent effect of natural selection.

3. This outlook widens the scope of paleoanthropological comparison. Researchers studying environments, fauna, and archeological evidence of hominid behavior have tended to work on separate continents without much comparison. The new paradigm outlined here implies that the more appropriate aim is to establish the range of conditions under which hominid populations lived and persisted over time. The ecological conditions of hominid evolution can be learned by comparing long sequences of environments encompassing the entire geographic range of hominids. Collaborative research among scientists working in Asia, Africa, and Europe will enable the appropriate comparisons to be made.

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