

Plates, Climate and Hominoid Evolution

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Environment as the context for evolutionary change and diversification is explored here in the evolution of higher primates during the Neogene. We postulate that the climatic changes that resulted both globally and regionally, in the low and middle latitudes of the Old World, from the final breakup of Laurasia and Gondwana, which had begun much earlier in the Jurassic, influenced the radiation and extinction of Miocene hominoids. The convergence of Africa upon Europe and collision of India against Asia during the Miocene greatly reduced the Tethys Sea, thereby removing an important source of moisture and ameliorating maritime influence in southern Eurasia. Miocene open forest-woodland replaced Palaeogene closed forests. Similar vegetational change occurred in East Africa, but was due to local uplift and rifting in the Miocene rather than the tectonic events that were affecting Eurasia.

When Africa and Eurasia met, African Miocene hominoids moved into Europe and Asia, taking advantage of a new habitat — the open forest-woodland — that spread across the low and middle latitudes of the Old World. Continuing cooling of the northern hemisphere, compounded by the latest Miocene Messinian desiccation, caused the subsequent local extinction of Eurasian hominoids. By contrast, the East African hominoids experienced further thinning of the open forest-woodland that accompanied continued regional uplift, which thereby created the widespread savanna-mosaic into which their descendants, the hominids, moved. In this interpretation of Miocene hominoid evolution, we provide for the first time an integrated process-model by which tectonic, climatic, environmental, molecular and evolutionary phenomena are brought together. We also provide a broad framework that can be tested with further information at the global and regional levels.

Omgewing word in die geval van die evolusie van die hoër primate in die Neogeen as konteks vir evolusionêre verandering en diversifisering ondersoek. Daar word gepostuleer dat die wêreld- en streekveranderings vanweë die opbreking van Laurasië en Gondwana — wat veel vroeër tydens die Jura begin het — die uitspreiding en uitwissing van Mioseen-hominoïede beïnvloed het. Die konvergiering van Afrika en Europa en die uitkuiwing van Indië onder Asië uit tydens die Mioseen het die Tethys-see aansienlik verklein en daardeur 'n belangrike bron van vog en 'n matigende see-ïnvloed in Suider-Eurasië verwyder. Die oop woud-bosveld van die Mioseen het die Paleogeen se aaneengeslote woude vervang. Soortgelyke veranderings in die plantegroei het in Oos-Afrika voorgekom, maar was eerder die gevolg van die plaaslike Mioseen-opheffing en -skeuring as van tektoniese gebeure wat Eurasië beïnvloed het.

Toe Afrika en Eurasië bymekaar gekom het, het Mioseen-hominoïede van Afrika in Europa en Asië in-beweeg en 'n nuwe habitat — die oop woud-bosveld — benut wat oor die Ou Wêreld se lae en middelbreedtegrade gestrek het. Die voortgesette afkoeling van die Noordelike Halfrond, saam met die jongste Mioseen-Messiniaanse opdroging, het tot die daaropvolgende plaaslike uitwissing van die Eurasiëse hominoïede gelei. Hierteenoor het die Oos-Afrikaanse hominoïede verdere uitdunning van die oop woud-bosveld ervaar wat met voortgesette plaaslike opheffing gepaard gegaan het, waardeur die wyd verspreide savannemosaïek geskep is wat deur hul nakomelinge, die hominiede, binnegetrek is.

Met hierdie vertolking van die Mioseense hominoïed-evolusie word tektoniese, klimaats-, omgewings-, molekulêre en evolusionêre verskynsels die eerste keer saam verklaar. 'n Omvattende raamwerk word verskaf wat aan nadere inligting op wêreld- en plaaslike vlak getoets kan word.

Role of the environment in human origins

A popular image of the role of the environment in hominid origins is one depicting forests drying up and disappearing, thereby forcing the forest-living apes into the open savanna-mosaic.* Now more vulnerable away from their forest protection, these apes evolve into hominids.

Such scenarios, although seemingly simplistic and naive, emphasize the relationship between environmental change, morphological transformation, and origin of a new phyletic line. However, recent studies have recognized the importance of this interaction between organism and environment, and have focused on the environment as a context for understanding, for example, morphological and cultural change during human evolution;^{2,3} hominid origins and evolution;^{4,5} gracile and robust australopithecine adaptation;⁶ anthropoid evolution;⁷ and bovid evolution.⁸

By incorporating data from geology, palaeontology, biochemistry, comparative morphology and behaviour, we now add to this a palaeoecological perspective setting forth a broad hypothesis that relates events of hominoid evolution and the emergence of the hominids to changing global climate and habitats. Our purpose is to propose a unifying scenario that ties together many pieces of information from a diversity of disciplines that have looked at one or other facet of hominoid evolution. Our interpretation follows G. G. Simpson's⁹ concept of 'opportunism in evolution' whereby the behavioural and genetic potential of a species

*'Savanna-mosaic' follows the definition of Cox and others:¹ seasons are regulated by rainfall (100–150 cm/yr) rather than by temperature; it lies between the Tropics of Capricorn and Cancer; always very warm with long, dry season; plants often drought-resistant; variety of trees in discontinuous stands or clumps.

becomes realized when physical access permits entry into a new ecological opportunity. Thus the behavioural potential of a late Miocene/early Pliocene ape with physical access to the newly spreading savannas permitted exploitation of savanna-mosaic resources; this line became the hominids.

More specifically, for the period of the late Oligocene and Miocene epochs, between 25 and 5 million years ago, a number of studies have examined the palaeoecology of specific hominoid sites in Africa and Asia.¹⁰⁻¹⁵ It is generally agreed that from the Miocene onward, and possibly even earlier, world climates became cooler and more seasonal. The influence of these climatic factors on Miocene-Pliocene hominoid evolution has yet to be fully determined (see, for example, refs 2, 4 and 5).

Rather than enumerating and repeating the data from analyses of specific sites, we address more global questions in order to arrive at a more complete picture of the environment within which hominoid evolution should be viewed. We ask, for example, what global climatic factors account for environmental changes in the Old World tropics during the Miocene? What is the nature of the change? What were the habitats of the Miocene hominoids? Is there evidence for early hominids as a savanna-mosaic species? Did the hominid transition occur in Africa or Asia? What environmental conditions drove that transition in one place rather than another? Can this perspective clarify the sometimes ambiguous interpretations made on the local level of specific sites?

In addition to an expanding fossil record — more fossils from more sites — two other directions of inquiry have developed in the past two decades that are useful in addressing the above questions: plate tectonic theory, and molecular phylogenies with their estimated times of species' divergence. Plate tectonics provides a unifying framework for the earth sciences, much in the same way that Darwin's mechanism of natural selection contributed to the biological sciences. Seemingly unrelated phenomena, such as the distribution and composition of regional terrains, the locations and characteristics of earthquakes and volcanoes, the origin of mountain systems, and the structure of ocean basins are now explained by common tectonic mechanisms.

The molecular data for evolutionary studies grew out of the early immunological work of Nuttall and subsequent discoveries in molecular biology which began in the 1950s, first with the discovery of the structure of DNA and later by deciphering the genetic code. These data contribute to our understanding of evolutionary relationships that cannot always be derived from the morphology of fossils alone. Studies of the proteins and DNA of many species of plants and animals not only clarify the genetic relationships among species but also provide estimates of their dates of divergence from a common ancestor.

In this regard, two important findings bear on hominoid evolution: 1) morphological and molecular (at the level of DNA and proteins) changes do not necessarily occur at the same rate,^{16,17} making it precarious to rely on comparative morphology alone for estimating genetic relationships; and 2) the molecular data provide a means for establishing a set of branching points among related hominoid species as well as their approximate time of occurrence.¹⁸ Although some questions do remain on the molecular clock concept,¹⁶⁰ the preponderance of evidence from many protein, DNA and RNA sequences (summarized in ref. 161) support the idea that these molecules may be used as 'molecular clocks' with sequence differences roughly proportional to divergence times.¹⁶² Changes in DNA bases (point mutations) do not, of course, occur with the regularity of a metronome, but have been shown to occur with statistical regularity.¹⁶³⁻¹⁶⁵

These molecular findings are largely independent of the sometimes ambiguous and incomplete fossil record to which they must be compared. Molecular data therefore permit one to establish correlations between branching times and inferred environmental changes. In short, the molecular data suggest an absolute temporal framework within which functional and en-

vironmental inferences can be more securely placed and tested.

Once a tentative phylogeny is established based on molecular comparisons, the morphology of fossil bones and teeth, and their comparison with living forms, contribute to refining the details of a group's evolutionary history. Studies of fossil morphology cannot reveal climatic or ecological context directly, although it is possible to suggest habitat types through analogies with living species and the corresponding functional morphology. The new data from molecular biology, therefore, help establish times of origins of hominoids and hominids, whereas information on global tectonics and local geology help establish the environmental context. If there is a fit between the two kinds of data, it should be possible to establish links between organism and environment. What behavioural/technological responses ought to be postulated for hominoids which were newcomers to the savanna-mosaic? Are there environmental factors that might help us understand the rapid morphological transformation of the hominids into a new adaptive type?

In formulating our admittedly broad yet inclusive hypothesis, we must of course sacrifice agreement in every last detail. However, the heuristic benefits of a unifying hypothesis that draws together diverse pieces of evidence will presumably stimulate further research and force us to take a more critical look at current competing hypotheses. Finally, it should serve to re-emphasize the role of the environmental setting as a major driving force in hominoid evolution, just as in the evolution of other major groups of organisms.

In the remainder of this article, we first review the record of primate evolution during the latter half of the Cenozoic era, beginning with the appearance of the higher primates. Then, using the most recent evidence from stratigraphic and tectonic geology, we provide our interpretation of the environmental setting of the Old World tropics where this evolution occurred. We conclude by relating specific habitat changes in East Africa, Europe and South Asia to the origin, radiation and extinction of hominoids and hominids in the Miocene and Pliocene epochs.

Overview of primate evolution

As shown in Fig. 1, the molecular data indicate a divergence between platyrrhines (New World monkeys) and catarrhines (Old World monkeys, apes and hominids) some 35–37 Myr ago during the early Oligocene, and a subsequent catarrhine divergence into Old World monkey (cercopithecoid) and ape-human (hominoid) lines some 20–22 Myr ago.^{18,19} Among the hominoids, the gibbon/siamang line diverges from the others about 12 Myr ago, the orang-utan diverges about 10 Myr ago, and the hominid, chimpanzee and gorilla lines show a three-way divergence about 5 Myr ago (Fig. 2). All the molecular data taken together, including those on DNA, cannot demonstrate that the chimp and gorilla are more closely related to each other than either is to hominids.²⁰

Oligocene catarrhine primates

The earliest unequivocal fossil evidence for anthropoids ('higher' primates in contrast to prosimians, the 'lower' primates) comes from the Egyptian Faiyum Formation, dated between 25 and 35 Myr ago²¹ and yields essentially all of our knowledge of early anthropoids and early catarrhines.

The majority of Faiyum fossils are represented by four genera: *Parapithecus*, *Apidium*, *Propliopithecus* and *Aegyptopithecus*. The first two taxa are monkey-like and the last two ape-like, on the evidence of dental characteristics,^{22,23} although this does not necessarily mean that these two taxa are the direct ancestors of monkeys and apes, respectively. The Faiyum fossils, bracketed at 25–35 Myr ago, occur not very long after the platyrrhine-catarrhine split as indicated by the molecular evidence and some of them qualify as catarrhine. One of the genera could well be ancestral to both the hominoids and cercopithecoids, and reassessments of earlier and more recently discovered fossil

evidence have led Kay and others²⁴ to propose *Aegyptopithecus* as a candidate for this common ancestor.

Conclusions about body size, diet and locomotion of the Faiyum anthropoids are based upon analogies with living primates. For example, limb bones assigned to *Aegyptopithecus* suggest an overall body size similar to that of howler or spider monkeys, with other morphological features most similar to howler monkeys, an arboreal quadrupedal New World monkey.²⁴⁻²⁶ The molar teeth of *Aegyptopithecus* lack a bilophodont* pattern as do living New World cebid monkeys and apes, and Miocene hominoids.²⁴ The more specialized bilophodont molar anatomy of Old World

Molecular data are compatible with these interpretations of the fossil record.¹⁶⁷

Faiyum habitat of Oligocene primates

The Faiyum is about 95 km south-west of Cairo, below where the Nile River currently empties into the Mediterranean. The Faiyum deposits were laid down in a deltaic floodplain (ancestral Nile Delta?) and were part of an extensive coastal lowland, broken by meandering streams emptying northwards a short distance away into the Tethys Sea.³⁰ As discussed in more detail in the following section, the Tethys Sea was more extensive during the Oligocene, and the Red Sea had not yet formed. The climate was probably warmer and more humid than today, owing to the more equator-ward position of the Faiyum region and the maritime influence of the Tethys Sea.

Reconstructions of the palaeoecology suggest that the Oligocene Faiyum was open or lightly wooded country with gallery forests along the river and a somewhat cooler climate than in the Eocene.^{31,32} Kortlandt³³ reconstructs the vegetation as a sahelian type with shrub, bushland and small trees without tall or medium height forests. Kortlandt argues that the Oligocene primates, rather than being exclusively arboreally adapted, were also ground dwellers and foragers. Kortlandt's evidence and its interpretation have been examined in detail and questioned by Bown and others.³⁰ They extensively review the existing data, present much new information that covers the stratigraphy, invertebrate and vertebrate fossils, plant fossils — including fruits, leaves and pollen — and argue for the presence of well-developed forests. In contrast to Kortlandt, they conclude that large forests of tall trees existed in much of the Faiyum, that the flora resembled tropical to subtropical vegetation of modern Indo-Malaysian relatives, and that this flora was probably common to much of the Tethyan area in the Oligocene from western Europe to Indo-Malaysia. On the basis of palaeographic and palaeoclimatic evidence, and in the light of the proposed morphological-behavioural analogies between the arboreal, fruit-eating New World monkeys and Faiyum fossil primates, we also believe that for the Faiyum there existed a consistent pattern of a warmer and wetter, more forested environment than exists there today.

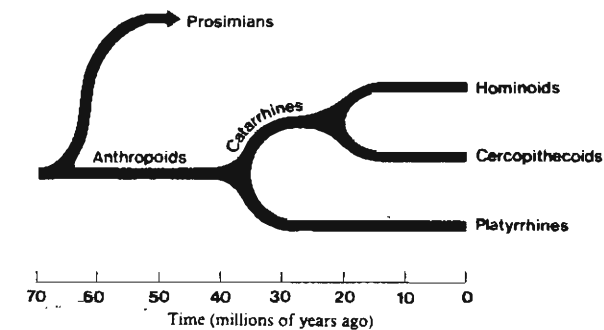


Fig. 1. Molecular phylogeny and times of divergence of major primate taxa (after ref. 18).

monkeys is presumably related to a shift away from the more primitive primate diet of pulpy fruits to one that includes more abrasive leaves and grasses.²⁸ New World cebid monkeys, like living apes, are predominantly fruit-eating and lack these specialized molars. Range of body sizes among the Faiyum anthropoids is estimated between 600 grams (*Apidium*) and 6000 grams (*Aegyptopithecus*).²⁹

In summary, dental, cranial and postcranial comparisons demonstrate that the closest living analogues of the Faiyum species occur among living New World cebids, which are diurnal, primarily fruit-eating, arboreal quadrupeds. Descriptions of every aspect of morphology indicate the Faiyum primates were anthropoid, and that some taxa were catarrhine at or near the ancestry of both apes and Old World monkeys. Many similarities shared by cebids and Faiyum primates indicate they may have been functional-ecologic equivalents and that the latter may still have retained some features shared with their recently diverged platyrrhine relatives.¹⁶⁶

*In the 'bilophodont' molar pattern, the molars have only four cusps, having lost the ancestral fifth cusp; the two cusp pairs are connected by crests and the crowns are high, or hypsodont.²⁷

Early and early middle Miocene (22 – 16 Myr ago): cercopithecoids and hominoids

Molecular data indicate that the separation of the catarrhine primates into the cercopithecoids and hominoids occurred about 20 – 22 Myr ago (Fig. 1). On the evidence of dentition, several fossil primate species are distinguished, and about this time a monkey lineage and an ape lineage existed.

The 'monkey' lineage includes at least two genera and several species. *Prohylobates* occurs at two North African fossil sites, Wadi Moghara in Egypt, perhaps 18 – 20 Myr ago, and Gebel Zelten in Libya, c. 16 Myr ago.^{34,35} The dentition shows only beginning specializations away from the ancestral condition: the fifth

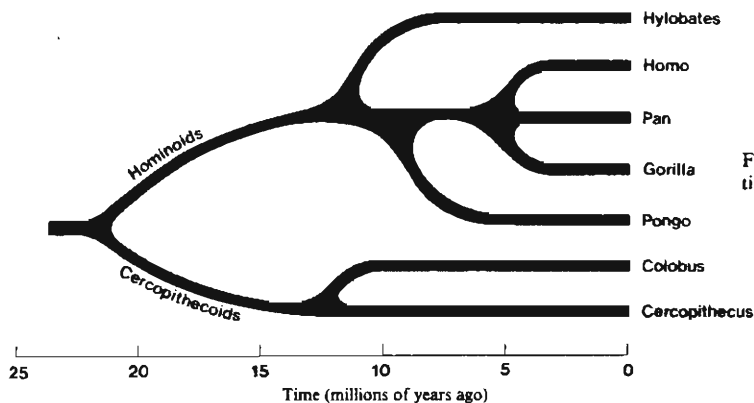


Fig. 2. Hominoid-cercopithecoid divergence and hominoid radiation based on molecular evidence (after ref. 18).

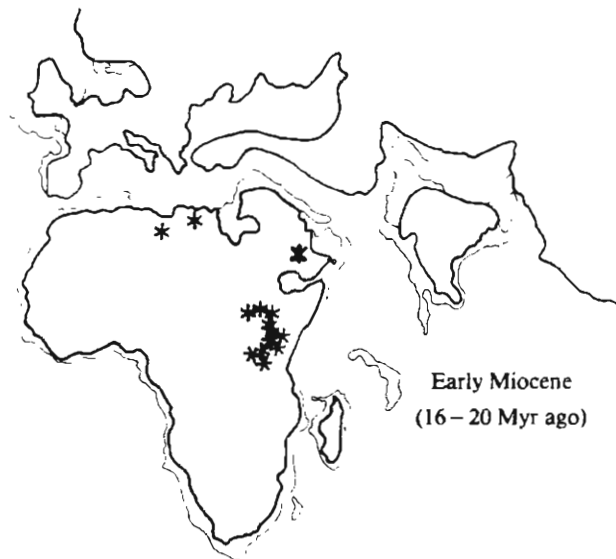


Fig. 3. Distribution of fossil sites containing cercopithecoids and hominoids from the early Miocene.

that engage in suspensory locomotion. But, unlike living apes, the hand and wrist joints were not well adapted to resist the forces of either brachiation or knuckle-walking.⁴⁷⁻⁵⁰ Thus, *Proconsul* is best described as an arboreal quadruped.

In summary, fossil evidence of the early Miocene and early middle Miocene in North and East Africa indicates three species of cercopithecoid monkeys. In the early Miocene there were eight to ten species of dryopithecids with thinly enamelled molar teeth and unique limb bones found in East African and Saudi Arabian sites. They had a range of body size comparable to that between small Old World monkeys and the large gorilla.⁴⁰ There is no evidence of hominoids or cercopithecoids outside of Africa for the early Miocene (Fig. 3).

Hominoid expansion in the middle Miocene

During the middle Miocene, hominoids increased in overall diversity, a new family of hominoids appeared, and hominoids expanded out of Africa into Europe and Asia (Fig. 4). The eight to ten species of early Miocene hominoids in Africa decreased to about four species in the middle Miocene.⁴⁰ These latter included species of *Proconsul* as well as a new hominoid species from Maboko, Kenya, called *Sivapithecus*.^{51,52} Other specimens of this latter hominoid found at Majiwa and Kaloma near Moboko in western Kenya are dated between 12 and 16 Myr ago.^{36,36} The Fort Ternan site in East Africa, between 12.5 and 14 Myr ago, also yields remains from this group of *Ramapithecus* (= *Kenyapithecus*) as well as several *Proconsul* species.⁴²

The Kaloma jaw and isolated teeth from Majiwa and Maboko indicate increased enamel thickness, a more robust and thicker mandibular body, and differential molar wear pattern, all features unlike those in *Proconsul*.³⁶ Although the *Ramapithecus/Sivapithecus* group* are generally thought of as a Eurasian radiation, they are found quite early in Africa.⁵⁷

The earliest occurrences of hominoids outside of Africa are in Europe (France, Austria and Czechoslovakia) at sites dated 15 – 16 Myr ago where dryopithecids are found.^{40,57} The oldest occurrence of ramapiths may be from Pasalar, western Turkey, perhaps as old

*There has been much discussion, revived lately, on the classification of this group. Some suggest that *Ramapithecus* may be subsumed under *Sivapithecus*,⁵³⁻⁵⁵ whereas others prefer to keep the genera separate.^{36,57} We refer to these fossils as ramapiths when discussing the group, because the exact taxonomic assignment of a specific fossil is not the issue here.

- lower molar cusp had not yet been lost and crests or 'lophs' characteristic of cercopithecoids are still poorly developed.²²

The majority of African Miocene monkeys occur at several sites in the Lake Victoria region.^{35,36} The largest sample, attributable to *Victoriapithecus*, is from Maboko of early middle Miocene age, 15 – 16 Myr ago.^{14,37,38} Dentally this genus shows a well-developed, bilophodont molar pattern and thus is more specialized like the living Old World monkeys than is *Prohylobates*.²² Postcranial elements mostly derived from one species resemble macaques in its elbow joint, though one humerus and phalanx belonging to another species resembles modern *Colobus*.²²

The 'ape' (or more precisely, hominoid) lineage of the early Miocene (23 – 17 Myr ago) consists of two genera, *Proconsul* and *Limnopithecus* (family dryopithecid),* and at least six species from several sites in East Africa including Rusinga, Karungu, Songhor and Koru.^{40,42} Two other species have been found at Ad Dabitiyah, Saudi Arabia, about 15 – 17 Myr ago.⁴³

Their molar teeth have low crowns and relatively thin enamel with the typical hominoid Y-5 pattern on the lower molars. The anterior teeth differ from living apes in their smaller size, orientation, and manner of occlusion; the canine teeth are more conical, a more primitive trait than found in living apes.³⁴ The molar structure of early Miocene hominoids, including *Proconsul* and *Limnopithecus*, falls closest to the living hylobatids, gibbons and siamangs, and *Pan troglodytes*, the common chimpanzee.⁴⁴ Extrapolating from the known diets of these living apes, Kay concludes that *Proconsul* species probably had diets consisting largely of fruit, though the early Miocene hominoids seem to show less dietary diversity than living hominoids.

Postcranial elements of upper and lower limbs have been found in association with *Proconsul africanus* from Rusinga.⁴⁵ Although there are differing viewpoints on their interpretation, most investigators agree that *Proconsul* was unique and did not possess structural adaptations in the upper limb for hanging like modern apes; their similarities overall seem to be with African colobine monkeys and South American howler and spider monkeys.⁴⁶⁻⁴⁹ In particular, the elbow joint may have been capable of nearly full extension, comparable with living apes as well as with some monkeys

*Another group of primates, the pliopithecids, which include *Dendropithecus* and *Micropithecus*, have been considered hominoid but are now thought to be a primitive catarrhine group with dental similarities with *Aegyptopithecus* as well as *Pliopithecus*, a later European form.^{27,29,40} They have a monkey-like intermembral index²⁷ and the European *Pliopithecus* had a tail the length of living *Cercopithecus*.⁴¹

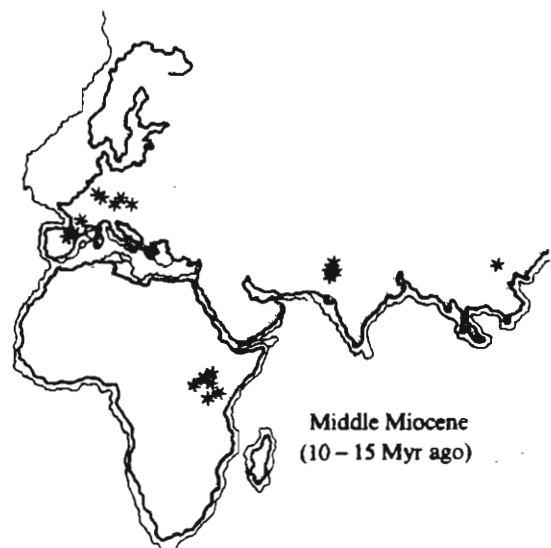


Fig. 4. Distribution of fossil sites containing hominoids from the middle Miocene.

as 15–16 Myr ago, and comprising two species of *Ramapithecus/Sivapithecus*.⁵⁸ In Asia, the hominoids do not date earlier than 13–14 Myr ago.⁵⁹ Thus, geographic expansion of hominoids explains the greater diversity in Eurasian species for this period of time: seven to nine species in Eurasia, including both dryopithecids and ramapiths, as well as four to five species of pliopithecids.⁴⁰

Isolated fossils from Africa and Europe for this time (mid-Miocene) include a series of postcranial remains in three distinct sizes reported from Pakistan.^{59,60} These remains indicate that more than one morphological pattern existed.⁶¹ Some features, such as the elbow, are similar to living African apes, and are advanced in comparison to early Miocene hominoids; but the overall pattern of the upper limb is unlike that of any living ape.⁶¹

Palaeoecological reconstructions of early Miocene environments in East Africa based on the non-hominoid fauna (mostly mammals) from specific sites, suggest an equatorial rain forest community that existed for six million years, from 23 to 17 Myr ago, with little apparent species turnover.⁶² Relict extant plants also suggest an African equatorial rain forest, extending to the Indian Ocean prior to the formation of the rift valleys and Africa's collision with Eurasia.⁶³ There is a faunal turnover about 16–17 Myr ago demonstrated from a number of sites, showing a shift from a closed forest habitat in the early Miocene (e.g. at Songhor and Rusinga) to an expanding open-forest, woodland in the middle Miocene (e.g. Fort Ternan).^{13,64,65}

The hominoids, which were numerous and found exclusively in East Africa during the early Miocene according to the existing fossil record, had by the middle Miocene expanded into Saudi Arabia (15–17 Myr ago), Eurasia, Indo-Pakistan and China.⁵⁷ Faunal lists from the middle and late Miocene sites in Eurasia that yield hominoid fossils appear to have been neither gallery forest nor dry grassland savanna. Pilbeam⁵⁹ notes that sedimentary and faunal analyses suggest the habitats in the Potwar region in Pakistan about 9 Myr ago were open and did not include large continuous rain forest.

In the late Miocene in Europe there are isolated teeth of *Dryopithecus* and no pliopithecids at all.⁴⁰ In Asia, *Ramapithecus* and *Sivapithecus* persist in the Siwaliks and in China to 7–8 Myr ago.^{66,67} In Africa the only evidence of hominoids consists of isolated molars from Lukeino, Kenya (6–7 Myr ago) and Ngororo, Kenya (10–12 Myr ago).⁶⁶ Only in the middle Pliocene, around 3.5 Myr ago, are hominoids again found in the African fossil record.⁶⁹

Because of the apparent regional changes in environment and consequent local shift in habitat type to a more open forest-woodland between early and middle Miocene times in Africa, and at the same time, the concomitant appearance of hominoids with thickly enamelled molars, Andrews and Evans⁷⁰ maintain that the ramapiths made the adaptive change from forest to non-forest habitats. In the late Miocene, however, accompanying the decrease in fossil hominoids, cercopithecoid diversity increased in both Africa and Eurasia, thus suggesting favourable conditions for monkey, but not ape, evolution in these areas.⁴⁰

We now turn to a more detailed discussion of environmental change on a global scale during the latter half of the Cenozoic, with particular emphasis on the last 20 million years.

Plate tectonics and environmental change

We first summarize the arguments and review the evidence for a significant cooling of the Earth's high and middle latitudes during the Cenozoic. Such cooling resulted from the final breakup of northern (Laurasia) and southern (Gondwana) supercontinents. We then examine the climatic changes that occurred in the low latitudes of the Old World during the Neogene. The Tethys Sea, which had separated the two supercontinents, diminished in size and in its influence on climate, as Africa and India moved north and impinged on southern Eurasia. Mountain-building in the Mediterranean and

Himalayan regions, as part of this tectonic activity, accentuated climatic change, globally and regionally, from warm and humid to cool and dry. During this same time (the Neogene), East Africa was rifted and uplifted, which reduced the rainfall and increased its seasonality. We argue that these global and regional tectonic events influenced climate and, consequently, the vegetation patterns. As a result of the new vegetation distribution, Miocene hominoids radiated out of Africa into the widespread open forest-woodland habitats of the Old World; later, as the climate deteriorated further, they were sharply restricted in their geographic distribution. These interactions of plates, climate, vegetation, and hominoid evolution are shown schematically in Fig. 5.

Cenozoic cooling

The older palaeobotanical literature, together with more recent studies of microfossils, isotopes and sedimentology of deep-sea cores, indicate that the temperature regimes of the Earth's high and middle latitudes have declined sharply during the Cenozoic, particularly during the last 20 million years.^{71,72} In particular, there is general consensus that the Arctic and Antarctic regions have undergone dramatic changes in climate from mild and humid in the Eocene to cold and dry in the Holocene.

Chilling of the South Pole in post-Mesozoic times resulted from the continued breakup of Gondwana that had begun earlier in the Jurassic (175 Myr ago). This led to the initial separation of the Antarctic continent from Australia in the late Eocene (38 Myr ago) and from South America by mid-Oligocene times (30 Myr ago), and eventually permitted the full-scale development of the circum-Antarctic Current, or Westwind Drift, by mid-Miocene times (15 Myr ago).^{72,73,74} Prior to the separation of Antarctica, the south polar seas were influenced by the gyral systems of the Atlantic, Indian and Pacific Oceans such that warm, equatorial surface waters mixed to some degree with colder, south polar seas, thereby ameliorating the south polar climate.⁷² The isolation of the Southern Ocean by late Oligocene times (25–30 Myr ago), however, led to the refrigeration of Antarctica and subsequent formation of the Antarctic continental ice-sheet by at least the late Miocene (10 Myr ago), although sea ice and local glaciers were present before them.⁷⁵

Antarctic bottom water circulation also developed at this time, so that the cold and oxygen-rich waters that formed near the surface in the Southern Ocean sank and moved equatorward in the Atlantic, Indian and Pacific Oceans. Thus these circulation patterns formed the deep boundary currents on the western margins of the ocean basins.⁷⁶ The sinking polar waters were ultimately replaced by warmer surface waters from lower latitudes, but this meridional heat transfer was less effective in warming the Southern Ocean than the earlier surface gyres.

The isolation and refrigeration of the south polar region today has resulted in average air temperatures ranging from 27°C at the equator to –50°C at the South Pole. Today this temperature difference is about three times greater than what it had been in the late Mesozoic, when it was 27°C at the equator and at least several degrees above zero at the poles.⁷⁷

Similar polar refrigeration occurred in the northern hemisphere during the Neogene, but for somewhat different reasons. According to one theory, the northward movement of the fragmented Laurasian land masses during the Cenozoic resulted in increased albedo, or surface reflection, of incoming solar radiation in high latitudes.⁷⁷ Increased surface reflection reduces the amount of solar heat absorbed by the Earth's surface (for a given latitude) and consequently, the amount re-radiated into the overlying atmosphere as sensible heat. On average, land surfaces absorb about one-third less solar radiation than the sea (at the same latitude). Therefore, a significant increase in land area in the north polar region during the Cenozoic resulted in a sharp decrease in average annual temperature there.⁷⁷

The temperature gradient from the equator to the North Pole

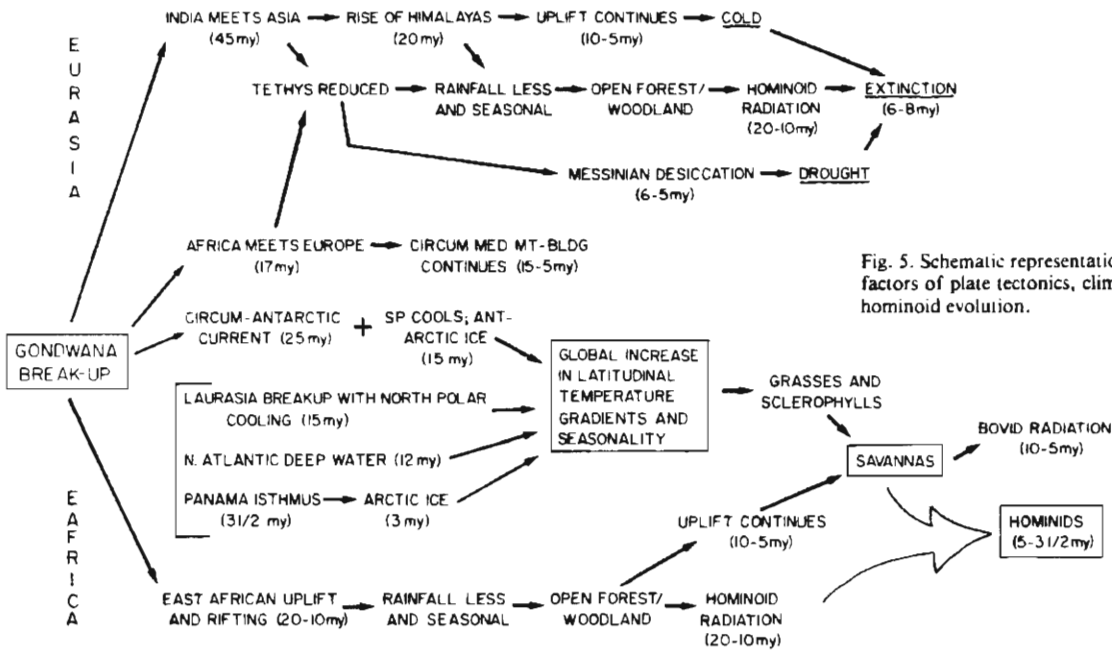


Fig. 5. Schematic representation of the interacting factors of plate tectonics, climate, vegetation and hominoid evolution.

almost doubled from 22°C in the Mesozoic (27°C at the equator and 5°C at the pole) to 42°C today (27°C at the equator and -15°C at the pole). Experimental models of Palaeogene gyral circulation in the Pacific Ocean indicate that warm surface waters mixed with the ancestral arctic seas, thereby making the high latitudes of the northern hemisphere rather temperate.⁷⁸ For example, fossil vertebrates and plants from Ellesmere Island (at more than 78°N) indicate a relatively mild climate in the Eocene.⁷⁹

Later, with the continuing breakup of Laurasia, the Greenland and Norwegian seas opened and allowed southward flow of cold deep-water into the Atlantic; this occurred by at least 12 Myr ago.¹⁰⁵ Although there is evidence for local glaciation at high latitudes in the northern hemisphere by mid-Miocene times (10-15 Myr ago), major ice sheets did not form until the Pliocene (c. 3 Myr ago) when the rise of the Panamanian Isthmus possibly altered the circulation of the Arctic sea.^{73 78 80}

Thus, polar chilling — first in the Antarctic, later in the Arctic — led to overall sharper latitudinal global temperature gradients in the Neogene.^{71, 81, 82} What, then, might we infer about their climatic impact?

The Earth's equatorial regions receive more solar radiation than the poles. There is, therefore, heat flux from the equator to the poles, with the atmosphere accounting for about two-thirds of the energy transfer and the oceans about one-third.⁷¹ In general, the greater the latitudinal imbalance of heat, the more vigorous the heat transfer across the latitudes. Thus, we conclude there was greater seasonality of climate and more storm activity in the middle latitudes as the equator-to-pole temperature gradients increased during the Neogene. For example, the severity of the northern hemisphere winter today is mostly controlled by the formation over land of large, cold polar air masses that sink and spread southward into the middle latitudes. If the average north polar temperature has dropped some 20°C since the end of the Mesozoic, we would expect colder mid-latitude winters in the northern hemisphere. Storm activity, too, in the mid-latitudes would be greater because of the larger temperature contrast between these cold polar fronts and the warmer (and wetter) air masses of the middle latitudes when they converge.^{71 83}

Reduction of the Tethys Sea

In addition to global cooling in the middle and high latitudes during the Neogene, the gradual diminution of the Tethys Sea affected

the climate of the low latitudes of the Old World. As Africa and India converged northward upon southern Eurasia, the disappearance of the Tethys Sea in South Asia and its shrinking in the circum-Mediterranean area resulted in drier and cooler conditions, as regional climate became less maritime and more continental. For example, as noted earlier, the Faiyum region during the Oligocene was apparently warmer and wetter than today.

The breakup of Gondwana in the Mesozoic led to the eventual convergence of Africa upon Europe towards the end of the early Miocene (17 Myr ago). The total latitudinal displacement of Africa during the Cenozoic was about 15° northward, about half occurring since the early Miocene.⁸⁴ This convergence culminated in circum-Mediterranean mountain-building that had begun earlier in the Mesozoic as the African and European continents approached each other.⁸⁵⁻⁸⁷ The positioning of Africa against Europe at this time (17 Myr ago) permitted intercontinental faunal exchange in the northwest via the Iberian Peninsula, in the north via Sicily and Italy, and in the northeast via the Arabian peninsula, with endemic African mammalian genera declining from about 74% in the early Miocene to some 50% in the late Miocene.⁸⁸ It is about this time that the geographic expansion of Miocene hominoids from Africa begins.

The Indian subcontinent, having separated from the northern edge of Gondwana, reached the southern edge of the Asian continent by the middle Eocene (45 Myr ago), judged by the first presence of Asian mammals in India at that time.⁸⁹ However, it was not until the end of the early Miocene that the northward thrusting of the Indian Plate against Asia led to the start of the vertical uplift of the Himalayas.^{90, 91} The great wedge of mid-Miocene to Holocene sediments in the Indus and Ganges plains and in the Siwalik Hills records the rise and erosion of these mountains. Thus, although India and Asia had made contact earlier, it was not until later thrusting that the Himalayas began to rise vertically. Initially after collision, marine and lowland coastal sediments accumulated.⁹¹ Absolute ages for the transition from marine and coastal sediments to coarser non-marine sediments range from 17 Myr ago along the Himalayan Front in Kashmir to 12 Myr ago in the Kutch, western India, some 1300 km to the south, indicating a southward-building, sedimentary wedge as the Himalayas subsequently rose and coarse sediments spread southward. We can therefore date the disappearance of the eastern Tethys Sea as occurring during the middle Miocene (16-12 Myr ago), after its initial

reduction in the preceding Eocene when there was first contact between the Indian and Asian Plates.

Palaeobotanical evidence supports this conclusion.⁹² Fossil plants of the Tibetan region and of India are distinct from each other during the early Eocene (the Cathaysian flora and the Gondwana flora, respectively). After the early Eocene, the floras of the two regions became more alike. Moreover, the timing and extent of the Himalayan uplift can be inferred from the character of the floras, which indicates altitudes of 1500 m in the early Miocene in central Tibet, 3100 m by the Pliocene, and 3500 m by the late Pleistocene.⁹² The great height of the Himalayas and Tibetan Plateau today apparently was achieved in recent geological times, with perhaps as much as 3000 m of uplift being added in the last 500 000 years.⁹³

Estimates of the proportions of land and sea in the Tethyan region have been made by Barron and others.⁹⁴ They calculate a reduction in the area of the Tethyan Sea of some 10 million square kilometres from early Miocene times to the present. This corresponds to an increase in land surface area approximately equal to the size of Canada.

What climatic changes might we infer, given this significant reduction in the area of the Tethys Sea in the middle Miocene, some 10–15 Myr ago, in the low and middle latitudes of the Old World? First, there would be a significant increase in albedo.^{94*} With less absorption of incoming solar radiation on the newly emergent land surface, there would be less heat available to be re-radiated back into the local atmosphere. Hence, there would be an overall cooling in this region.

Second, owing to the lower heat capacity of the land compared with the sea, any seasonal temperature variations would not have narrowed. Third, the reduced area of the Tethys Sea would remove an important source of local atmospheric water vapour that could be precipitated as rainfall. Thus, as the sea diminished in area, we might expect the surrounding lands to become drier, as in Greece, Turkey, and Indo-Pakistan. Fourth, given the reduction of surface evaporation and precipitation, the latent heat made available by local evaporation could not be released as sensible heat with local re-precipitation. Therefore, the cooling that resulted from increased albedo would be reinforced. Regional cooling would also produce less regional evaporation and precipitation, and consequently a drier climate overall.

The Tethys Sea straddled the line of latitude 30°N, where the descending branch of the atmospheric Hadley cell creates subtropical high pressure areas that generate long periods of clear, dry weather⁹⁴ because the descending air masses become warm and thereby hold more water vapour. Such high pressure areas, like the Summer Pacific High off the coast of southern and central California, are effective in blocking or diverting seasonal, westward-moving storms.

In short, reduction of the Tethys Sea during the middle Miocene would have resulted in an overall drier and cooler climate in the northern low latitudes of the Old World. We also conclude that rainfall and temperature would have become more seasonally variable. This would have had an important impact on the vegetation. As summarized by Axelrod,⁹⁵ Neogene forests retreated across the mid-latitudes in the Old World with a corresponding spread of more open patterns of vegetation that included grasses, forbs (a number of which are xerophytic and cactoid), and the sclerophylls (small, hard-leaved scrubby plants); thus, the vegetation adapted to drier, cooler or more seasonal climates. More specifically, with respect to the Tethyan region, Axelrod⁹⁵ states that during 'the Miocene and later, forests and savannas in western India-Pakistan retreated eastward as dry climate expanded, enabling invasion by elements of the subhumid to arid . . . floras'. The palaeobotanical

*Barron and others⁹⁴ argue that Cenozoic global cooling was due to just such changes in land and sea areas, especially in the tropics, and the resulting differences in albedo, rather than changes in the distribution of continents by latitude as proposed by Donn and Shaw.⁷⁷

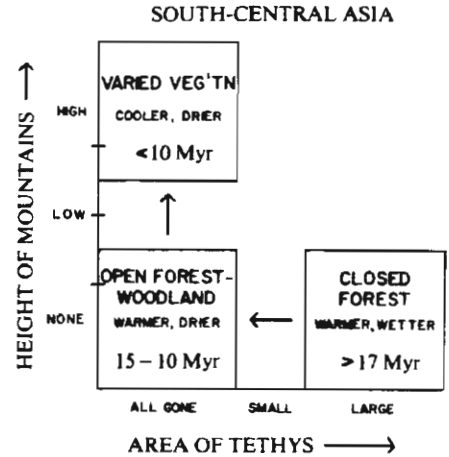


Fig. 6. Schematic relationship of the contraction of the Tethys Sea and the rise of the Himalaya Mountains, showing their effect on climate and vegetation.

evidence cited by Hsü⁹² and Nandi⁹⁶ also supports the interpretation that vegetation adapted to drier and/or cooler conditions became dominant in the Himalayan region during the Miocene and Pliocene.

Finally, computer-modelling of the South Asian monsoon circulation by Hahn and Manabe⁹⁷ demonstrates that the July position of the intertropical convergence zone (ITCZ) and associated rainfall does *not* depend on the presence of the Himalayan Mountains. This suggests that the annual migration of the ITCZ within the Tropics of Capricorn and Cancer influenced seasonal rainfall in the low latitudes straddling the equator then as now. These results indicate that the Himalayas themselves are not the cause of seasonal rainfall.

In summary, we conclude that in the early Miocene (before 19 Myr ago) the presence of the Tethys Sea and absence of the Himalayas generated a warm and humid climate in the circum-Tethys (southern Eurasia and northern Africa) that supported a subtropical vegetation, presumably like the closed, canopied forests with broad evergreen trees found today in the Congo Basin and Indo-Malaysian region. During the middle Miocene (10–15 Myr ago), after the contraction of the Tethys Sea and while the Himalayas were still of relatively low altitude, south-central Asia became significantly drier, somewhat cooler and certainly more seasonal. In response, the forests became more open woodlands so that tree cover was less continuous and intervening grass more widespread (see Fig. 6). Because a similar, but less drastic, reduction of the Tethys Sea in the west was also occurring in the circum-Mediterranean due to mountain-building, we further conclude that similar climatic and vegetational changes took place there as well in the middle Miocene.

East African rifting and uplift

East Africa, like southern Eurasia, also experienced pronounced uplift during the Neogene. At least by the end of the early Miocene (17 Myr ago) the African Plate had separated from the rest of fragmented Gondwana and settled into place against southern Europe.⁸⁵ The East African Swell — one of several broad elevated areas on the African continent — appears to have been, and continues to be, a region of vertical uplift that overlies a rising convection current, or plume, in the mantle below; as the region rose, tensional faults or rifts created down-dropped, north-south basins and ridges.⁹⁸ Upwarping began in the late Oligocene, but major uplift and rifting started only in the middle to late Miocene and has continued into the Quaternary.^{99–101}

Evidence from East African terrestrial mammals reflects these tectonic events. As noted earlier, the dominant mammalian communities shifted from equatorial rain forests to savanna-mosaic

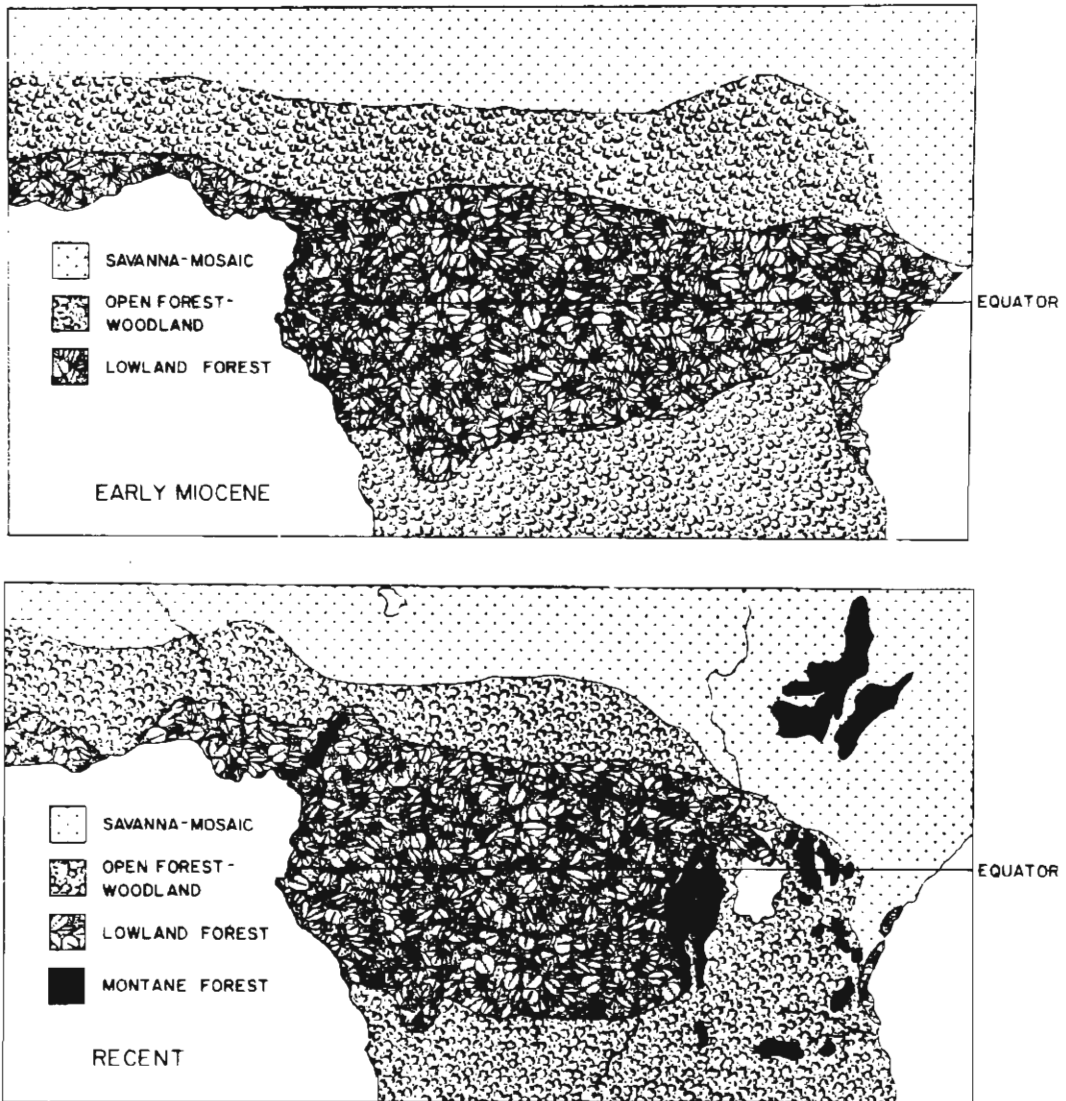


Fig. 7. Changes in vegetation patterns in Central Africa as a result of rifting and uplift in the middle Miocene (after ref. 63).

during the Neogene.⁶³ These workers infer that mid-Miocene uplift and rifting generated a rain shadow on the eastern third of the African continent. We further infer that moist air masses, originating over the Gulf of Guinea, continued to bring precipitation to the Congo Basin but did not penetrate much beyond the Western Rift as they had in the early Miocene. Annual rainfall today on the western side of the Western Rift is 180 cm but less than 100 cm on the eastern side.¹⁰²

The northeast and southeast trade winds that reach the eastern coast of Africa today are poor in moisture. The January northeast trades have a relatively short fetch over the Arabian Sea and hence do not acquire much moisture; the July southeast trades, although moisture laden when they meet the coast, diverge so broadly that local precipitation is fairly light.¹⁰² When rain does fall in East Africa, it is strongly seasonal, coinciding with the meridional migration of the ITCZ.¹⁰² The tropical savanna-mosaic vegetation of East Africa today (Fig. 7) reflects this seasonality of diminished rainfall in that dominant grasses, herbs and trees are heat-adapted and drought-resistant.¹

Environmental change and its influence on hominoid evolution

The Oligocene and Miocene sites in North and East Africa represent only a small fraction of the areas where primates may have liv-

ed, and the missing evidence may hold the key for understanding their evolution. Given the present data, however, we can focus on three issues where the environment may be a critical factor in accounting for the origin, radiation and extinction of hominoids (Fig. 8). These are: 1) the question of the adaptation of the ramapiths and their relationship to present-day hominoids; 2) the extinction of hominoids in Europe and the Near East and their restriction to South East Asia; and 3) the spread of the savanna-mosaic and its impact on the origin of hominoids.

The dilemma of Ramapithecus

The case of *Ramapithecus* and its place in hominoid evolution is an example of conflicting interpretations — whether it represents an adaptive shift that is on its way to the hominid line, whether it converges in adaptation with orang-utans and hominids, or whether it is on the line leading to orang-utans. Knowledge of the environment in the middle and late Miocene might help decide among these alternatives.

After Simons^{103 104} proposed *Ramapithecus* as a hominid and ancestral to *Australopithecus*, Pilbeam and Simons,¹⁰⁶ on the basis of dental evidence, argued 'that profound behavioural, dietary and locomotor changes had already occurred among species of *Ramapithecus*' (p. 244). Its thickly enamelled molars and small canines supposedly aligned *Ramapithecus* with the earliest

hominids and indicated their shared dental adaptations for grinding, in contrast with the African apes, which have molars with thinner enamel. The issue of thick versus thin enamel became the reason for supposing an early divergence of the great ape and hominid lines, a conclusion which conflicted with the molecular evidence. Debate on the hominid status of *Ramapithecus* has focused on dental and molecular evidence (see, for example, refs 107–112).

The palaeoecology of the middle Miocene was also an important part of the debate. The change from a closed forest habitat in the early Miocene to one of open forest-woodland in the middle Miocene became a basis for arguing that the emergent ramapiths were more ground-dwelling in locomotion and in feeding than were early Miocene hominoids.^{70,113} For example, Andrews¹¹⁴ concluded that *Ramapithecus* 'must have been at least partly terrestrial because of discontinuities in the woodland canopy and because of greater seasonal variation in the supply of fruit'. Assuming ancestry from *Ramapithecus* to *Australopithecus*, it was suggestive to view *Ramapithecus*' ecology and behaviour as intermediate between those of the fully arboreal hominoids of the early Miocene and the fully ground-dwelling australopithecines of the Pliocene. Thus, inferences about ramapith behaviour based upon palaeoecology were influenced by what was known for the australopithecines. However, if *Ramapithecus* is not a hominid, and if the separation of apes and humans is as recent as 5 Myr ago, it is necessary to re-evaluate such inferences.

Evidence for the hominid status of the ramapiths has been extensively reviewed.^{55,115} Two current interpretations are in conflict: that the ramapiths are on the hominid line⁵⁴ or else that they are on the line leading to orang-utans.^{116–118} The basis for these interpretations relies on dental, gnathic and cranial features, and palaeoecology is no longer treated as central. Kay⁵⁴ interprets the massive jaws and great enamel thickness of the molar teeth of *Ramapithecus* as shared derived features with *Australopithecus*, and argues that 'ramapithecines are ideal ancestors of *Australopithecus* and *Homo*'. By contrast, Andrews, Cronin and Pilbeam view the thick molar enamel of the ramapiths as a feature shared with orang-utans, implying an ancestor-descendant rela-

tionship; these authors note many similarities between the skulls of orang-utans and newly discovered skulls from Pakistan and China.^{116–118}

Obviously the dentition is not conclusive for determining phylogeny if it can be invoked for either interpretation. Furthermore, dental features may suggest dietary adaptation, and convergence rather than ancestry may therefore determine them. Molar enamel thickness implies fruit-eating rather than foliage-eating.¹¹⁹ In particular, among living anthropoid species having the thickest enamel — the New World *Cebus* monkey and the orang-utan — their diet includes fruits, seeds and nuts with such hard coverings that extracting them requires teeth which can resist occlusal stress created by powerful vertical compression.¹¹⁹ By analogy with these living species, Kay¹¹⁹ suggests that the ramapiths ate significant amounts of hard nuts or seeds enclosed in tough pods. The thick enamel therefore does not by itself imply ground-dwelling or arboreal habits, as presumably a diet of such hard-shelled foods could be obtained either on the ground or in the trees.

The postcranial evidence of the ramapiths is also not conclusive in defining ancestry or adaptation. As mentioned earlier, the very few limb bones attributed to this group resemble neither orang-utan nor bipedal hominids.⁵⁹

The molecular data connect hominid origins with those of chimpanzee and gorilla and are not compatible with the ramapiths being only on the hominid line.¹²⁰ These data throw doubt on thick molar enamel indicating phylogeny, as chimpanzees and gorillas have thin molar enamel. The conclusion that *Ramapithecus* is an ancestral orang-utan is compatible with the molecular evidence.¹¹⁶

The *Ramapithecus* dilemma intensifies when we consider palaeoecology. Previously it was argued that *Ramapithecus* adapted to living on the ground after the breakup of the equatorial rain forest; now the same creature is cast as the ancestor of the most arboreal of the great apes. We reject the hypothesis of the hominid ancestor on molecular grounds and question the orang-utan ancestor hypothesis on palaeoecologic grounds. We suggest instead that the common ancestor of all the great apes and hominids descended from the ramapiths, with the orang-utans branching off about 10 Myr ago, perhaps from an Asian species, which soon

Fossil Hominoids in Old World Neogene

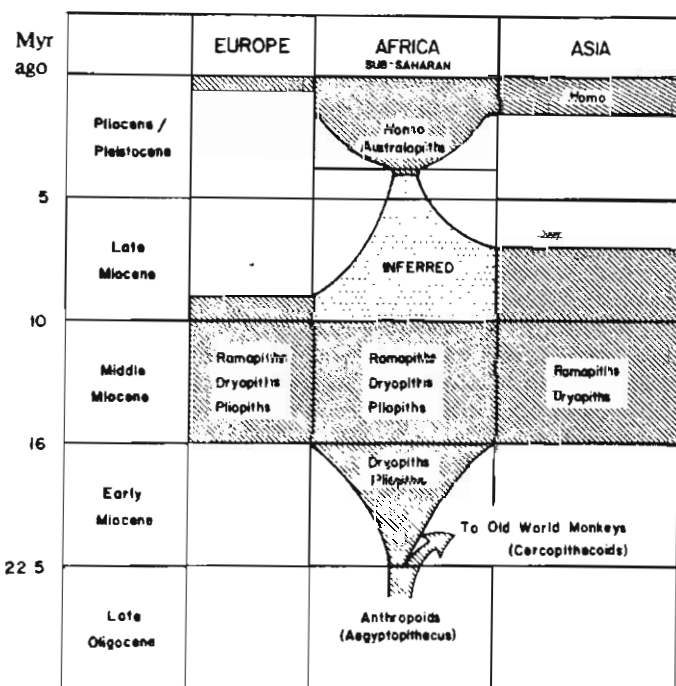


Fig. 8. Origins and radiation of fossil hominoids.

became restricted to South East Asia; the African hominoids branched off from a later African ramapith species.* Reduction of enamel thickness from ancestor to descendant chimpanzee and gorilla can be explained by dietary changes, whereas its retention in *Australopithecus* could also be dietary and perhaps a 'pre-adaptation' in the ancestral ape group for hominids to process food with a tough covering or from the ground.

Ramapiths have tended to be regarded as Asian but there is evidence for their appearance 15–16 Myr ago from Maboko and Kaloma in Kenya. Rather than regarding them as evolving in Asia or Europe and spreading to Africa, it is just as likely that because of their success in the newly developed open forest-woodland habitat in Africa, the ramapiths spread from there and became particularly successful in Asia and less so in western Europe. More specifically, we postulate that with the fragmentation of the closed forests, new adaptive opportunities opened up for apes that could also feed on ground foods and move on the surface. The closest living analogues may be the African apes which feed both in the trees and on the ground, travel mostly on the flat, yet retain in the upper limb (shoulder and elbow joints) the ability to hang and climb. (We do not, however, postulate that *Ramapithecus* was a knuckle-walker like living African apes.) In spite of cranial and dental similarities between one species of ramapith and living orang-utans, we question the phylogenetic connection; if the postcranial skeleton ever comes to light, we would not expect it to resemble the modern orang-utan, given the palaeoecological context in which the dental and cranial fossil remains are found in Pākisan. The dental and cranial resemblances between ramapiths and living orang-utans may be accounted for by convergence, whereas the limb bones are critical for interpreting the locomotor adaptation in the palaeoecological setting.

Late Miocene restriction of Eurasian hominoids

The hominoids which appeared in Europe about 16 Myr ago did not survive beyond the late Miocene.^{40 56} In Asia, the record differs somewhat with the earliest hominoids* occurring there about 12–13 Myr ago and persisting until 7 Myr ago in Pakistan^{12,66} and 8 Myr ago in China.⁶⁷ What can we infer about late Miocene environments in southern Eurasia that might explain the restriction of hominoids during the late Miocene to their present-day tropical distribution in South East Asia?

We assume that the moderate-sized Miocene hominoids, like modern apes, were ecologically limited by warm temperatures and availability of water. We further conclude that the late Miocene increase in continentality (seasonal cooling and increased aridity) brought about the extinction of Eurasian hominoids.

As noted previously, there is evidence for significant cooling of the northern hemisphere during the Cenozoic with annual mean temperatures falling below freezing about 12–13 Myr ago. Initial ice formation in North America began shortly after this, around 10 Myr ago, and widespread continental glaciation by at least 3 Myr ago.^{71,77 122}

Today in the northern hemisphere, because of the dominant influence of the huge Asian land mass, high pressure systems of extremely cold air develop in winter in its east-central region, giving an average January temperature of some -20 to -40°C .^{102 123} However, owing to the high, east-west barrier of the Himalayas and Tibetan Plateau, there is restricted meridional circulation of this very cold air. Hence, much of South Asia today is insulated from the southward flow of cold air masses in winter.¹²³ If we postulate a cooling trend in the northern hemisphere during the Cenozoic,

*This suggestion is similar in some respects to the hypothesis advanced by Greenfield,¹²¹ though he provides a different supporting argument from the one presented here.

**Gigantopithecus*, which did not appear until about 9 Myr ago, is a significantly larger fossil hominoid that did survive and persist in China into the Pleistocene.⁵⁹

leading to significant glacial ice formation near the end of the epoch, and if we also postulate a relatively recent uplift of the Himalayas to their present elevation, we might further conclude that cold air masses at least occasionally penetrated southern Asia during late Miocene times. These probably limited the northward distribution of Miocene hominoids.

We are not claiming that late Miocene faunas of the kind found in the Siwaliks are cold-adapted. Rather we believe they will be found to exclude those taxa that would be limited by periodic winter cold. Interestingly, *Gigantopithecus*, the hominoid which persists after late Miocene times in South Asia, is more than twice the size of most of the middle Miocene fossil hominoids at an estimated 68 kg.⁵⁹ Such a large-bodied primate might well be adapted to a cooler climate: in Africa today adult gorillas weigh over 90 kg and live in areas where temperatures are often near freezing.¹³⁰ The cooling of the northern hemisphere was probably also the reason that southern European catarrhines (dryopithecids and pliopithecids), like their South Asian relatives, became locally extinct.

The last Miocene Messinian desiccation (some 6 Myr ago) would have accentuated these climatic effects of increased continentality by removing the moderating influence of the remaining western portion of the Tethys Sea. There would thus have been a regional increase in general aridity. (In contrast, the Mediterranean Sea today is a source of moisture-laden, low pressure air masses that not only bring rainfall to the surrounding area, but also often travel even farther east into Asia.^{102 123}) During the Messinian desiccation these lows would have been much drier than usual and so both local and more easterly precipitation would have been correspondingly less. There is palaeosol evidence for just such increased aridity in the Siwalik stratigraphic sequence at 6 Myr ago, for a 'drying trend... resulting in more seasonally arid conditions and a more open vegetative physiography in late Siwalik time'.¹²

Up to eleven desiccation events have been recorded in the Upper Evaporite of the latest Messinian section in the Mediterranean region.¹²⁴ Such events suggest multiple glacial lowerings of sea level, although this has not been established with certainty.¹²⁵ However, if there were multiple glaciations at the end of the Miocene to cause such changes in sea level, the climatic consequences would be twofold. First, there would have been a cooling of as much as 10 to 15°C over wide areas of the Eurasian land mass; computer models have postulated a 20% decrease in precipitation in July at such times.^{126 127} Second, large falls in sea level, whatever their cause (glacial, tectonic or geoidal), would have sharply lowered water-tables and also promoted aridity.¹²⁸⁻¹²⁹

We therefore conclude that late Miocene climate was cool and dry enough to account for the disappearance of hominoids in Europe, and to confine them to the tropical areas of South West Asia.

Hominid origins in East Africa in the late Miocene and Pliocene

In both popular and scientific literature the origin of the hominids has long been associated with a savanna-mosaic habitat. However, the question remains: What precisely characterized the interaction between hominid origins and environment? Does the environment have a role in 'shaping a species'? We argue that hominids radiated into the savanna-mosaic because that habitat was becoming widely available. Nor was the hominid radiation an isolated one. Other species, notably pigs and bovines, were similarly colonizing this habitat at the end of the Miocene.¹³¹⁻¹³³ We further argue that the species ancestral to hominids was an ape, specifically an African ape. The anatomical and behavioural characteristics of the earliest hominids reflect adaptations to a savanna-mosaic, as opposed to a forest or even an open forest-woodland environment.

Scattered fossil localities in Kenya at Ngororo (10–12 Myr ago), Lukeino (6–7 Myr ago) and Kanapoi and Lothagam (4–6 Myr ago) have yielded isolated teeth and fragmentary limb bones of an as yet undetermined hominoid or hominid species. (See ref. 5 for a comprehensive compilation.) Numerous hominid fossils appear in

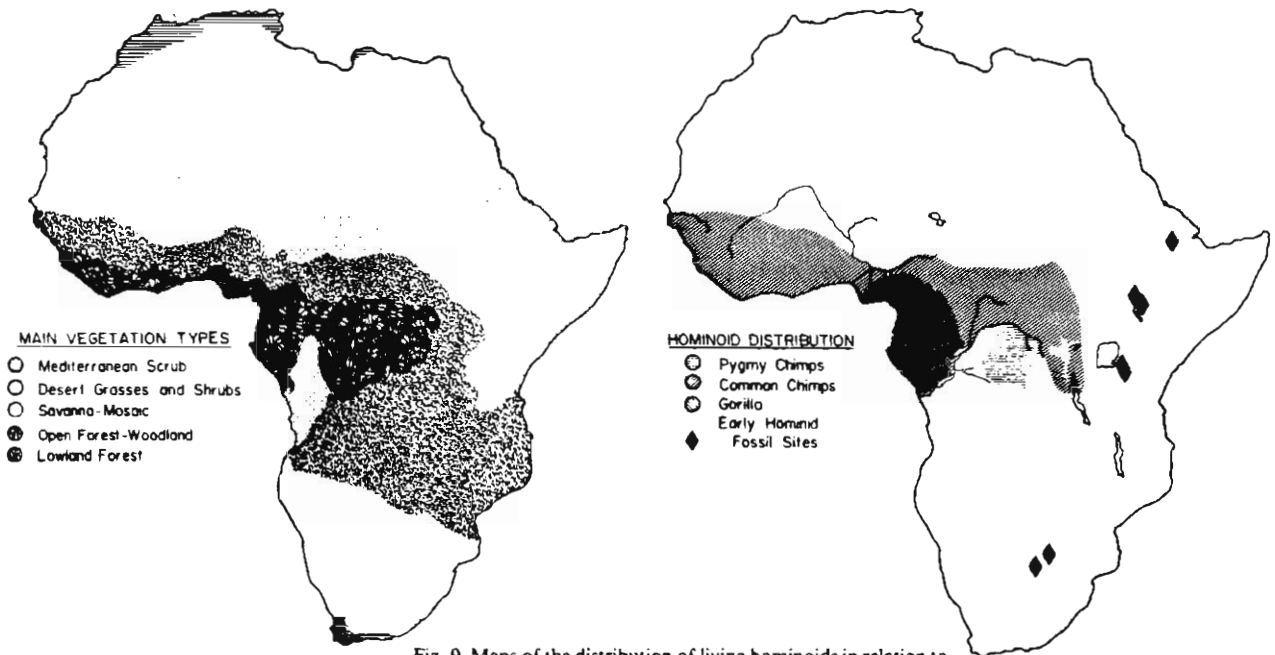


Fig. 9. Maps of the distribution of living hominoids in relation to fossil hominid sites and the main vegetation types in Africa to suggest the radiation of hominids into the savanna-mosaic.

deposits of Pliocene age, the earliest from Laetoli in Tanzania about 3.6 Myr ago, later from Hadar in Ethiopia about 3 Myr ago.¹³⁴ Hominids from Sterkfontein in South Africa may be as old as 3 Myr.⁶⁹

The climatic changes we have noted for the middle Miocene must have set the stage for subsequent closed-forest fragmentation, lowered and seasonal precipitation, and seasonal cooling. The savanna-mosaic habitat with its marked seasonality of rainfall became widespread in eastern and southern Africa by the end of the Miocene as well as in southern Eurasia.

As Simpson⁹ has emphasized, evolutionary novelty depends upon genetic and behavioural potential, ecologic opportunities, and physical access to the new environment. Molecular data (Fig. 2) imply that the origin of hominids is not a separate event from that of chimpanzees and gorillas; these species differ by only one percent of their genetic material.^{16,18} Such similarity suggests not only a genetic basis for at least some of the observed behavioural similarities among these species, but also that in the transition from the African ape ancestor to the hominid only a small amount of genetic change occurred. The similarities in behaviour and morphology of modern humans and African apes strongly supports the idea that behavioural potential in the hominid ancestor (which would also be the ancestor of chimpanzees and gorillas¹²⁰) was more like modern chimpanzees or gorillas than any other living primate. More particularly, chimpanzees rather than gorillas are compelling as a morphological and behavioural model from which to derive hominids.¹³⁵⁻¹³⁷

The maps in Fig. 9 suggest a radiation of African hominoids into several habitats (deduced from vegetation zones), with early hominids expanding out into the savanna-mosaic, and chimpanzees and gorillas exploiting resources in the lowland and montane forests and open forest-woodland areas. What resources of food and space on the savanna-mosaic might have been available to the emerging hominids? How might they have gained access to these new ecological opportunities? To answer these questions we look to living human groups that exploit savanna-mosaic resources, modern gatherer-hunter groups in Africa,¹³⁸⁻¹⁴¹ and chimpanzees that take advantage of savannas in part of their geographic range.^{142,143}

The savanna-mosaic is not simply a broad expanse of uninterrupted grassland but consists of patchy vegetation comprising trees,

shrubs and tall grass. Seasonal rainfall affects plant production so that it too varies in abundance, throughout the year, and thus influences movements of larger mammals, including hominids, that depend upon its availability.¹⁴⁴ Savanna species by being mobile can compensate for fluctuating availability of food and water, especially in the dry season, either by being nomadic or by migrating to new areas.¹⁴⁴ Savanna-mosaic plant and animal species that form a subsistence base for hunter-gatherers may be widely scattered, available locally and seasonally. These people must continually move throughout the year and over larger or smaller home ranges, perhaps as extensive as several hundred square kilometres.

In adapting to the savanna-mosaic and the dry season, plants have acquired tough outer covers around the fruit (e.g. melons and mongongo nuts¹³⁹) or have developed underground (e.g. roots and tubers¹³⁸⁻¹⁴¹). Social groups tend to be larger during the wet season when water is abundant and nearby food sources are ample for feeding larger numbers for a limited time.¹⁴¹ During the dry season, the ≠Kade San — who may represent an extreme development of the savanna-mosaic adaptation — rely more on water from roots and tubers than on standing sources, and their subsistence base for two months at this time is tubers.¹⁴⁰ To exploit savanna-mosaic plant resources, these gathering and hunting groups rely on implements to recover roots and tubers, for extracting nutmeats from protective coverings, for preparing food, for carrying water while foraging and food, such as berries, once collected.

The challenges of the savanna-mosaic — perhaps ones that the early hominids faced — are further illustrated by recent studies of chimpanzees at Mt Assirik.^{142,143} The Mt Assirik region in Senegal enjoys highly seasonal temperatures and rainfall, and consists of gallery forest (3%), woodland (37%), bamboo and grassland (32%), and short grass plateau (28%). Although most chimpanzees live in forest or woodland habitats, those on Mt Assirik exploit the savanna-mosaic. During the wet season these animals colonize the open grasslands, in the early dry season they eat several types of seeds in the woodland areas, and in the dry season (January to March) they are confined to the gallery forest.

In contrast to human groups that live in the savanna-mosaic, the Mt Assirik chimpanzees travel freely only during the wet season when water and food are abundant and air temperatures tolerable. During the dry season, and especially at the close when temperatures are high and water is limited, the chimpanzees are

restricted to areas served by shade and water, namely the gallery forest. Here food is limited, and competition prevails among both chimpanzees and other primates for food and sleeping sites. The Mt Assirik chimpanzees have the largest home ranges reported thus far for their kind; yet they do not show the year-round mobility characteristic of savanna-mosaic mammals, or of their human counterparts, the hunter-gatherers.

We know that chimpanzees use sticks and grass stems for extracting insects from mounds and hills, rocks for pounding open hard-shelled fruits, and crumpled leaves as sponges to obtain water in the hollows of trees.¹⁴⁵⁻¹⁴⁷ Sometimes they dig for underground foods,¹⁴⁸ and catch small animals to eat.¹⁶⁹ We believe that these similarities in behaviour between humans and chimpanzees reflect a shared genetic, motor and sensory organization (as related to hand-eye coordination in tool-making and using, for example).

The potential for bipedal locomotion is present in all the apes as part of their adaptation to climbing and hanging in trees. Fleagle and others ask: Why did humans but not other climbers become bipeds, when this would have been a 'natural' evolutionary option?¹⁴⁹ This question implies to us that physical environment is a central determinant of bipedalism. However, the mobility of the upper limbs of apes makes these limbs unsuited for bearing compressive forces. In chimpanzees the hind limbs must bear most of the body weight during quadrupedal locomotion.¹⁵⁰ For this reason Reynolds suggested that should a chimpanzee-like animal become fully committed to ground-dwelling, it would have little morphological choice but to become bipedal.¹⁵⁰ We argue that ground-dwelling in the context of the savanna-mosaic was critical for the development of bipedalism. In the Pliocene savanna-mosaic environment of the earliest hominids there were fewer trees, and resources were widely distributed, particularly during the dry season. Mobility therefore became a key to survival. The carrying of food and water was a necessity. Such demands for bipedal behaviour combined with the morphological constraints of an ape remaining quadrupedal would have contributed to the emergence of full bipedalism.

The Mt Assirik study points out the limitations placed on foraging activities and ranges of chimpanzees as a result of heat stress. African apes possess eccrine sweat glands, but these glands do not respond to heat stress.¹⁵¹ Humans are unique among primates in the functioning of their eccrine sweat glands,¹⁵¹ which thereby provide a mechanism not only for tolerating high temperatures, but more important, for performing muscular work under these conditions. When humans sweat, they need to replenish their internal water frequently.¹⁵² For the young with their higher metabolism, water needs are even greater. These physiological constraints and the importance of regular water intake will have influenced how early hominids dealt with their environment.

Technological developments will have accompanied the translocation of the early hominids from open forest-woodland to the expanding savanna-mosaic. Reliance on tools would have been essential for obtaining, extracting and preparing plant foods. And the early hominids may have used containers for carrying water (perhaps initially inside a melon or root) and for collecting food items, especially the smaller berries and seeds, and the occasional lizard and larval grub.

The anatomy of the early hominids developed for more effective exploitation of the savanna-mosaic. They have megadont molars, well worn and thickly enamelled, which are suggestive of a diet requiring grinding and crushing.⁶ Fossil hand bones, though retaining some ape-like characteristics, show changes in the wrist and fingers suited for tool manipulation,¹⁵³ although there is no direct evidence for the tools themselves until well after the hominids appear.

Changes in the locomotor system for accommodating bipedalism can be observed in the hominid ilium and knee joint from Hadar and Sterkfontein.¹⁵⁴ However, a number of morphological features in the hip joint and ischium, ankle and foot, body build and limb

length demonstrate that these early hominids had not yet developed a modern *Homo sapiens* bipedal pattern.^{137 155 156} With their mobile ankle joint and curved digits, *Australopithecus* and early *Homo* may have been capable of climbing trees¹⁵⁷⁻¹⁵⁹ (as youngsters do today without those anatomical aids), although it is unlikely that early hominids would have relied heavily on trees for food and sleeping in the savanna-mosaic — such reliance would have limited their mobility and their new adaptability to exploiting resources.

In summary, the Mt Assirik chimpanzees, having a limited ability to exploit savanna-mosaic resources, help us to imagine how the transformation from an ape with chimpanzee-like morphology and behaviour could have taken place. The early hominids are thus viewed here as an opportunistic species which began to exploit scattered, seasonal and clumped resources, especially plant foods and water, and which required a large home range and frequent long distance travel. This growing repertoire of skills would not have required much attendant genetic change.

Summary and conclusions

In this article we provide a broad framework encompassing tectonics, climate and environment in which to view hominoid evolution in the Neogene. We discuss in particular the following points:

1) The breakup of Laurasia in the Cenozoic led to increasing albedo in the north polar region that in turn produced a doubling of the difference in temperature between equator and pole. The Cenozoic fragmentation of Gondwana isolated the Antarctic continent and saw the development of the circum-Antarctic current such that the equator-to-pole temperature gradient almost tripled.

2) These substantial increases in global temperature gradients resulted in greater seasonality of climate — especially temperature and rainfall — in the middle latitudes during the Miocene and in widespread glaciation in high latitudes during the Plio-Pleistocene.

3) Africa's convergence with Europe, and India's collision against Asia, during the Miocene reduced the Tethys Sea and thus removed in the Old World an important source of atmospheric moisture and an ameliorating maritime influence in the low latitudes. This contraction of the Tethys Sea reinforced regionally the global increases in climatic seasonality.

4) Mantle convection and hot spot activity produced domes and rifting in East Africa during the Miocene-Pliocene, creating an increasing rain shadow between the wet Congo Basin and the rising East African plateau.

5) Reduction of the Tethys Sea and uplift in East Africa led to widespread open forest-woodland habitats in the Neogene that had been predominantly closed forests in the Palaeogene. Descendants of late Oligocene-early Miocene closed forest, arboreal anthropoids in Africa spread into this new habitat across southern Eurasia from Europe to China, migrating by means of new inter-continental land connections that had been established by the end of the early Miocene.

6) The mid-Miocene hominoid radiation was characterized by changes in diet and locomotion, with less dependence on an arboreal, fruit-eating way of life to one that included a greater variety of vegetation found on the ground or in trees with a much patchier distribution, that made at least part-time ground-dwelling feasible.

7) Continued cooling of the northern hemisphere and desiccation of the Mediterranean region in the late Miocene brought periodic cold and drought to southern Eurasia such that the hominoids there became extinct by the early Pliocene.

8) Although late Miocene hominoids in East Africa were insulated from this cold and drought, they were affected by the continuing uplift and rifting of the late Miocene-early Pliocene, which further thinned out the open forest-woodland, creating the widespread savanna-mosaic into which their descendants, the bipedal hominids, moved.

9) Skeletal evidence of Miocene hominoids and Pliocene hominids, as well as the geostatigraphy of the sediments in which

these fossils are found, suggest there was an overall shift in habitat, diet, and form of locomotion during the Neogene among these fossil apes, from arboreal fruit-eaters to ground-dwelling omnivores.

10) The origin of hominids is not an isolated evolutionary event, but rather is part of the overall radiation of African hominoids; nor is it an unusual ecological occurrence. The hominids are only one of several mammalian groups that include the pigs and bovids that were able to exploit the savanna-mosaic habitat that had become widespread by the end of the Miocene.

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Research Letter

Rapid Screening Procedure for Detection of Plasmids in *Campylobacter*

Organisms of the genus *Campylobacter* are recognised as a common cause of human enteritis worldwide¹⁻³ and are also implicated in other clinical conditions such as urinary infection and post-transfusional septicaemia.⁴ These findings have been due primarily to improved methods of isolation of this organism.^{5,6} Antibiotic resistance in *Campylobacter* has been reported^{4,6,7} and it has recently been suggested that tetracycline resistance in *C. jejuni* is mediated by a 38×10^6 dalton plasmid originating from a common source.⁶ *Campylobacter jejuni* from a variety of geographic sources have been shown to contain plasmids ranging in molecular mass from 5×10^6 d to 77×10^6 d. No correlation has been found between the presence of these plasmids and multiple antibiotic resistance in *C. jejuni*.⁵

Plasmid isolation techniques requiring dye-buoyant density gradient centrifugation for the screening of clinical isolates are expensive and time consuming. Techniques which permit the detection of plasmids directly on agarose gels^{8,9} sometimes present problems. These include the inadequate removal of chromosomal DNA and residual RNA which prevents the visualization of small plasmids. In certain cases poor cell lysis results in reduced plasmid yields. Unlike *Escherichia coli*, bacteria of the genus *Campylobacter* are difficult to lyse adequately to ensure the reproducible recovery of plasmids. This may be related to the difficulty of obtaining suitably dense exponential phase cultures for lysis. As a preliminary to the determination of the functions of *Campylobacter* plasmids we have

developed a rapid screening procedure for the detection and isolation of plasmid DNA from these organisms. This method utilizes a modification of certain steps from a plasmid extraction procedure¹⁰ and has been used to screen 121 strains of *Campylobacter* from a variety of clinical sources.

Plasmid extraction was performed on exponential phase cultures growing in 15 ml of Manclark and Pickett medium¹¹ containing $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$ (20 mg/ml), sodium pyruvate (500 mg/ml) and sodium disulphite (250 mg/ml).² Growth was under microaerophilic conditions at 37°C for between 42 and 45 hours. Cells were harvested by centrifugation at 4°C and the pellet was resuspended in 1 ml buffer [50 mM Tris (hydroxymethyl)-aminomethane, pH 8.0 and 2 mM sodium EDTA]. Proteinase K was added to a final concentration of 100 µg/ml and the cells lysed by adding 3 ml lysing solution (50 mM Tris and 5% SDS). The pH of the lysing solution was adjusted to 12.0 by adding 10 M NaOH and monitored using a glass electrode. After incubation at 37°C for 15 min, the solution was heated to 70°C for 30 min in a water-bath. After the heat treatment the lysate was extracted with unbuffered phenol/chloroform (1:1 volume ratio) and centrifuged to separate the phases. The clear aqueous phase contained the plasmid DNA.¹⁰ This phase was then transferred to a polypropylene tube. Samples (80 µl) were withdrawn and mixed in a 1.5 ml Eppendorf tube with 10 µl of 0.25% bromophenol blue in 20% Ficoll. Agarose gel electrophoresis was performed as previously described¹² except that we used a horizontal apparatus with a submerged gel. Gels were stained with 10 µg/ml ethidium bromide for 30 min at room temperature and photographed over a shortwave UV source on Ilford FP4 film through a Kodak Wratten 22 Orange filter.