

Southern Africa: a cradle of evolution

Martin Pickford*

Thanks to recent palaeontological surveys in the Miocene of southern Africa, it has become evident that, like the endemic plants of the Cape Floristic Region, there are numerous lineages of animals that originated in southern Africa during the Neogene. The spread of some of the plants and many hitherto endemic southern vertebrate lineages northwards into the tropics and beyond into Eurasia from Middle Miocene times onwards, has watered down the appreciation of endemism among the vertebrates, because several of the lineages that used to be endemic to southern Africa have subsequently become pan-African or even cosmopolitan. Among these are the ostrich, the Nile crocodile, pliohyracids, bovids and other groups, which previously were thought to have originated in the tropics or even in Eurasia. It is likely that the early onset of arid biotopes in the Namib arose well before they occurred anywhere else in Africa, and started a long period of adaptation to semi-arid, arid and hyper-arid conditions, well removed from similar biotopes in other parts of the world. The location of the Namib, in the south-western extremity of the continent, meant that it was far from the Eurasian landmass. This factor no doubt promoted a high degree of isolation of the Namibian gene pool from that of the latter region, and thus weakened the effects of the Eurasian gene pool on southern African faunas compared with its influence on northern and eastern African ones. At the same time faunas in north and central Africa, on the one hand, and in Eurasia, on the other, were participating in relatively free genetic flow on a much more regular basis throughout the Miocene. When other parts of Africa became arid in the Late Miocene and Plio-Pleistocene, several lineages that had originated in southern Africa spread northwards and occupied those areas, replacing some of the autochthonous lineages before they themselves could adapt to the changes.

Introduction

It has long been appreciated that the Cape Floral Region has a great diversity of endemic plants, so much so that, despite its relatively small area, it has often been classed as one of the six floral biogeographical realms of the world, indicating a long period of endemic evolution with restricted input of genes from outside. What is not so well known is that during the Neogene the subcontinent was likewise highly endemic in its vertebrate and invertebrate faunas, at least until well into the Miocene, with some lineages still being restricted to the region up to the present day.^{1,2}

There are several reasons for this general lack of appreciation of South Africa's role in producing autochthonous animal lineages. First, the Miocene faunas from the region were relatively poorly known, but recent work by the Namibia Palaeontology Expedition has radically improved parts of the fossil record.^{3,4} Second, the much better known fossil record of eastern Africa has tended to overshadow the poorer southern African one. Third, the influence of Eurasian vertebrates on African palaeofaunas throughout the Cainozoic was strong, and this

tended to sidetrack scientists into thinking that many lineages originated in that continental mass rather than in Africa, and in particular southern Africa. Fourth, many of the lineages that evolved in southern Africa have subsequently spread northwards into the tropics and beyond, their presence in the north has been misinterpreted as supporting an equatorial or northern origin for the group.

It is now increasingly evident that many lineages of animals have a longer history in southern Africa than anywhere else. Even though the ruminants and perissodactyls surely originated in Eurasia, once they reached Africa they diversified and produced several endemic lineages. Among these the Bovidae, Climacoceratidae, and Dicerotinae (and perhaps Tragulidae) seem to have evolved in southern Africa and then spread northwards to other parts of Africa and Eurasia. Other lineages with longer histories in the subcontinent than elsewhere include some freshwater and terrestrial molluscs, chelonians, crocodiles, some birds, and several mammalian lineages including carnivores, hyracoids and rodents.

This paper highlights the lineages that we now consider to have originated within southern Africa, and then spread northwards to the tropics and beyond, even into Eurasia. I also discuss some of the palaeoenvironmental and palaeoclimatic factors that possibly played a role in their evolution.

Motors of faunal change

Global changes affecting the climate of Africa

Correlation of Miocene faunal turnover pulses with global geological and climatic events reveals some thought-provoking coincidences.⁵ For example, the principal faunal change at the end of the Early Miocene coincides in time with the expansion of the Antarctic ice cap to continental proportions.⁶ Prior to this, the ice cap was confined to mountain tops, but by about 17 Myr (Myr) it covered most of the continent (Fig. 1) and started to affect global climatic patterns to an ever greater extent. At this time there was no Arctic ice cap to counter the effects of the expanding Antarctic one, with the result that all the ecoclimatic belts of the world (such as the tropical, subtropical, and boreal) were displaced northwards and converged towards the North Pole. A consequence of the growth of the Antarctic Ice Cap was the shedding of vast quantities of cold water into the southern oceans, which flowed generally northwards as cold 'bottom water' until forced to upwell along the western coasts of the southern continents.³ Within southwestern Africa, a major result of the upwelling of cold waters along the coast was the onset of hyper-arid conditions in the Namib, extending as far north as the equator. The growth of the ice cap also forced the northwards shift of the tropical zone, which came to lie well north of the equator, and even extended into southern Europe, which, as a consequence, became home to many tropical and subtropical lineages of vertebrates, such as hominoids, giraffes, ostriches, aardvarks, hyraxes and many others. During the Middle Miocene, what is now the Sahara was clothed in tropical forest.

The establishment of the Namib Desert in southwestern Africa at the onset of the Middle Miocene created a variety of arid and semi-arid environments that had not occurred before, or were hitherto only poorly represented in the continent. After the end

*UMR 5143 du CNRS, Département Histoire de la Terre, 8, rue Buffon, 75005, Paris, and Collège de France, 11, place M. Berthelot, 75005, Paris, France.
E-mail: pickford@mnhn.fr

of the Early Miocene, a spectrum of environments existed in the southern half of the continent, ranging from hyper-arid desert on the one extreme to tropical forest on the other. Prior to this, the environments ranged mostly from tropical forest to woodland. Many plants and animals soon adapted to the new arid environments and, in a very real sense, the Namib Desert and its neighbouring arid and semi-arid regions can be thought of as a veritable 'centre of evolution' and the climatic changes that produced these environments as a 'motor of evolution'.

At the end of the Miocene, between 8 and 7 Myr, the ice fields in the northern hemisphere, such as the one on Greenland, began to increase in size (Fig. 1), eventually, by the end of the Pliocene, to form the Arctic ice cap. The effect of this boreal cooling trend was to force the ecoclimatic zones of the world back towards the south. Southern Europe ceased to be tropical and most of it became part of the boreal zone, with the result that many vertebrate lineages that were adapted to warm climates with wet season-dry season cycles disappeared from the continent, whereas vertebrates adapted to more boreal, cool climates and winter-summer seasonality colonized its mid-latitudes.

In East Africa, the effect of this Arctic expansion was dramatic, and led to the increasing aridification and more marked seasonality that occurred there from 8 Myr onwards, culminating in the rapid expansion of grasslands during the Pleistocene. Farther north in Africa, the main effect of the development of the Arctic ice cap was the onset of aridification in the Sahara, which was eventually to become the largest desert in the world. This history is supported by the fossil record, which reveals that tropical forest was growing in central Libya 16 Myr,⁷ but by 7 Myr the region was woodland to savanna,⁸ and by the Pleistocene it was hyper-arid.

In the meantime, southwest Africa had been desert from 17-16 Myr (Fig. 2), with arid conditions extending to north of the equator in Gabon, Congo and Uganda.^{3,4} Because southern Africa has been arid for so long, numerous lineages of plants, invertebrates and vertebrates have had ample time to adapt to arid and unstable environments. This pool of endemic evolutionary activity was largely isolated from the evolutionary action

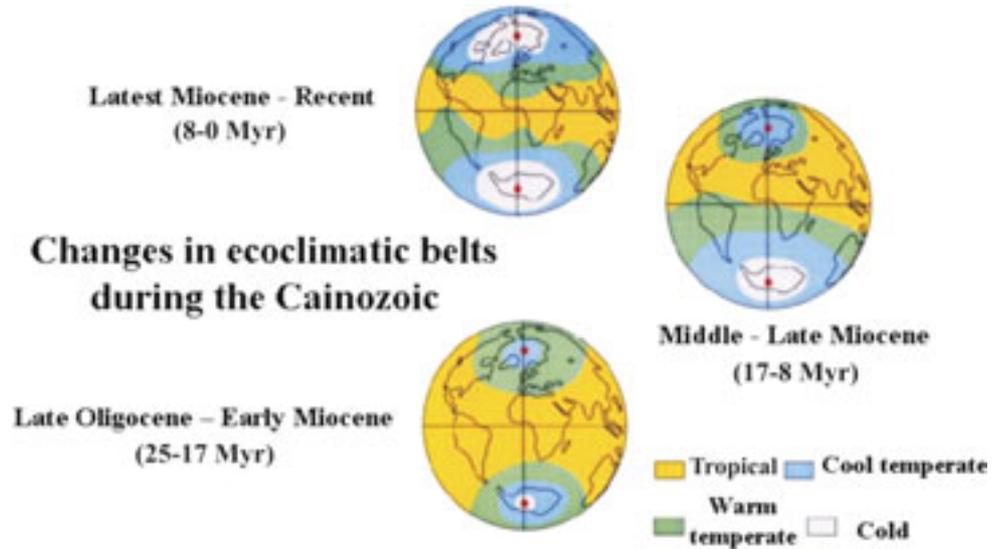


Fig. 1. Ecoclimatic belts of the world and polar ice cap development. During the Miocene the growth of the polar ice caps (first the Antarctic and then the Arctic several million years later) displaced the ecoclimatic belts northwards and then southwards. As a consequence of expansion of the Antarctic ice cap, mid-latitude Eurasia became tropical for several million years until growth of the Arctic ice cap forced the tropical zone back towards the equator. These biogeographical changes had great consequences for African mammals, those from East Africa in particular.

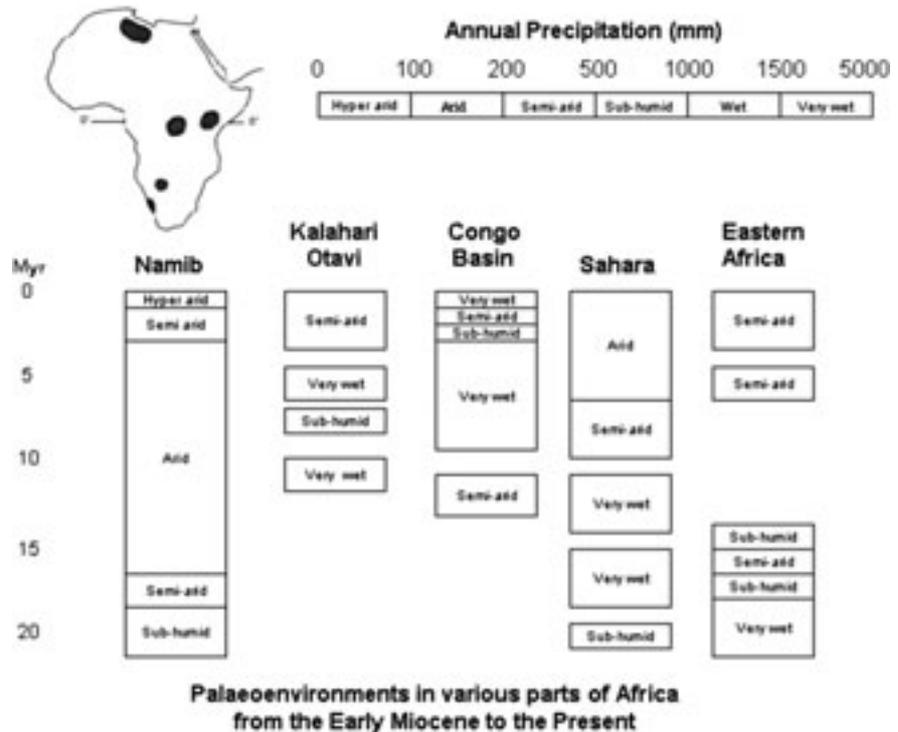


Fig. 2. Summary of palaeoenvironmental and palaeoclimatic evidence from various parts of Africa during the Miocene. Note that southwestern Africa has enjoyed arid to semi-arid conditions for at least 17 million years, whereas arid environments did not occur in eastern Africa and the region of the Sahara until much later in the Miocene (c. 8-7 Myr or even later). Mammals and plants of southern Africa thus had much more time to adapt to unstable, arid environments than any of the tropical or north African lineages.

that was taking place in Eurasia and north Africa, and it was to have far reaching consequences for African faunas. As eastern equatorial Africa became more and more arid during the Late Miocene, the environment became suitable for plants of southern African origin such as *Protea*, *Aloe* and possibly *Acacia*, as well as southern invertebrate and vertebrate lineages that were already adapted to such conditions, with the result that they simply expanded into the newly available niches to which they were accustomed. This wholesale occupation of equatorial niches by southern lineages left no time for the autochthonous

ones to adapt, with the result that most of them went extinct. Among the vertebrates now known to have colonized East Africa from the south are the ostrich, the Nile crocodile, percrocutids (hyaenid-like carnivores), the black rhinoceros, bovids of various kinds, climacoceratids (extinct African ruminants with branched horns), and pliohyracine and procaviid hyraxes, among others.

A counter-current of dispersal came from the north, with several vertebrates managing to colonize tropical Africa from the northern arid zones (southern Eurasia), including the white rhinoceros (*Ceratotherium*), giraffes, and several carnivores [true hyaenas, dogs, wolverines (*Plesiogulo*), the bear *Agriotherium*], suines (*Potamochoerus*), porcupines (*Hystrix*), and hares (leporids), among others. Thus, as the climate in East Africa became more and more arid from Late Miocene times onwards, its faunas were influenced by immigration pressures from two directions, southern Africa and southwestern Eurasia. The result was that many endemic vertebrate lineages disappeared from its fossil record (the crocodiles *Euthecodon*, *Tomistoma*, *Crocodylus cataphractus*, *Rimasuchus*), archaic rhinos (*Kenyatherium*, *Brachypotherium*) or became much reduced in frequency (chalicotheres (*Ancylotherium*)) palaeotragine giraffids, bundont gomphotheres (*Tetralophodon*, *Anancus*) tragulids (chevrotains) and others, at the same time that intruding taxa became more prevalent.

Thus two of the major Neogene African faunal turnover events appear to be directly linked to the development of the polar ice caps, first the Antarctic one about 17–16 Myr, and secondly the Arctic one about 8–7 Myr.

Animal groups of probable southern African origin

Hydrobiidae

By far the oldest known specimens of the freshwater snail, *Tomichia*, occur in the Sperrgebiet, Namibia. The genus is unknown from any of the Miocene sites in East Africa, and even today it is represented only at a few localities outside southern Africa. It thus appears that the lineage originated in southern Africa, and that it spread northwards recently but has never secured a foothold in the tropics or beyond.

Acavidae

The terrestrial gastropod family Acavidae is endemic to southern Africa and Madagascar. The presence of the extant genera *Dorcasia* and *Trigonephrus* in Early Miocene deposits in the region attest to the fact that the family has an extremely long southern African pedigree. Its absence from other parts of Africa, including the well-known Miocene molluscan assemblages of East Africa,⁹ indicate that the family never became pan-African or cosmopolitan. The presence of Acavidae in Madagascar supports notion of a southern palaeoposition of this land mass prior to its move to its present location.

Pelomedusidae

The freshwater turtle genus *Pelomedusa* has been found at Langental, Namibia, many millions of years earlier than its earliest record in equatorial and northern Africa. Whatever the ultimate origin of the genus, during the Early Miocene it seems to have been restricted to southern Africa; in the rest of Africa it appeared during the Pliocene or Pleistocene.

Testudinidae

The land tortoise *Namibchersus*¹⁰ is a member of a group known as the small African endemics, which today include *Chersina*, *Psammobates*, *Homopus* and *Kinixys*. Apart from *Kinixys*, which is

known from the Early Miocene of Kenya,¹¹ all the others are endemic to southern Africa. The presence of *Namibchersus* in the early Miocene of the subcontinent indicates that the group probably evolved there.

Crocodylidae

The crocodile from Arrisdrift (c. 17.5 Myr), *Crocodylus garipeensis*¹² is morphologically much closer to the extant Nile crocodile, *C. niloticus* than is the species *C. lloydi*. The Nile crocodile was previously thought to have evolved from the latter species during the Pliocene,¹³ but *C. lloydi* has recently been placed in its own genus, *Rimasuchus*,¹⁴ thereby distancing it from the ancestry of the Nile crocodile. *Crocodylus niloticus* makes its appearance in East Africa during the late Miocene (Lothagam, c. 7 Myr¹⁴) and it is common in Pliocene and Pleistocene deposits. Its main adaptation is to rivers and lakes, many of which are unstable and not surrounded by tropical forest. Crocodylian faunas in Early, Middle and Late Miocene deposits of tropical Africa are dominated by *Rimasuchus* and *Euthecodon*, but also contain *Tomistoma*, *Osteolaemus*¹⁵ and *Crocodylus cataphractus*. All these forms appear to have been dependent on stable, freshwater lakes and rivers, and it was when such environments deteriorated in East Africa that these crocodiles became rare and eventually disappeared, and the Nile crocodile took over. *Osteolaemus* and *C. cataphractus* survive today in freshwater bodies of equatorial Africa, where the Nile crocodile is absent.

The presence of unstable lakes, rivers and other water bodies in the vicinity of the Namib Desert ever since the Early Miocene, long before they developed in tropical Africa, means that southern African crocodiles had a lengthy span to time in which to adapt to such conditions. Having adapted, these crocodiles were well suited to the unstable waterbodies that subsequently developed in East Africa during the Late Miocene. They merely moved in before any of the pre-existing local crocodile lineages could adapt. East African crocodylian diversity diminished during the Pliocene and Pleistocene, leaving the Nile crocodile the only surviving lineage.

Struthionidae

Several post-cranial fossils from Elisabethfeld, Namibia, belong to a struthionid ostrich which is substantially smaller than the extant species, *Struthio camelus*, but the skeletal anatomy of which is only slightly different from it.¹⁶ These specimens are far older than the next oldest known ostrich material from the Middle Miocene of Kenya [Nyakach (14 Myr), Fort Ternan (13 Myr)]¹⁷ and later deposits in Eurasia, and indicate that the family probably evolved in the southern parts of Africa.

Macroscelidea (Myohyracidae and Rhynchocyoninae)

The abundance of fossils and the higher diversity of hypsodont macroscelidids in the early Miocene of southern Africa compared with East Africa, suggest that the group originated in the former region. However, the genus *Myohyrax* managed to colonize tropical East Africa quite early, and is to some extent coeval with its South African record. The genus *Protypotheroides* is unknown outside southern Africa.

Miorhynchocyon is represented in both East and South Africa, and it is currently not possible to determine where it originated.

Tenrecidae

The genus *Protenrec* is present in the Early Miocene of both eastern and southern Africa, and with currently available data it is not possible to be precise about where the family developed.

Lagomorpha

Austrolagomys is surely the descendent of an immigrant lineage from Eurasia, most likely originally Asia, where lagomorph history is long, dating well back into the Eocene. Its presence in both East and South Africa during the Early Miocene indicates that it was widespread over the continent at the time.

Rodentia

Out of the abundant lineages of rodents represented in the Sperrgebiet, several have never been found elsewhere. These include two genera of hypsodont Pedetidae, *Parapedetes* and an undescribed new genus, and the brachy-hypsodont (one side of the tooth brachyodont, the other side hypsodont) genera *Pomonomys* and *Neosciuromys*. There are also abundant bathyergids in the Early Miocene of southern Africa, but fossils of this group are also known from East African basal Miocene deposits. The absence of the family in northern Africa and Eurasia suggests that it evolved in the southern half of the continent. Other rodent genera were apparently widespread, also being present in East African deposits. They include the brachy-hypsodont forms such as *Diamantomys* and *Bathyergoides*, as well as bundont kinds such as *Protarsomys* and *Sciuridae*, the latter family being rare in Namibian Early Miocene deposits. A puzzle is the recent recovery of *Ctenodactylidae* in the northern Sperrgebiet, a family that was hitherto known only from Eurasia and north Africa.

Creodonta and Carnivora

As is usual among carnivores, their distribution tends to be cosmopolitan, and apart from one species confined to the Sperrgebiet the rest are not exceptional. *Metapterodon* and an amphicyonid from the Sperrgebiet are close to species known from East Africa. A new genus and species of ultra-sectorial creodont has been found only in Namibia and may represent an endemic lineage.

Tubulidentata

The aardvark, *Orycteropus*, has a long fossil record in both eastern and southern Africa.^{18,19} The Early Miocene forms were all considerably smaller than the extant *O. afer*, and there was a trend towards increase in size through the Miocene, not only in East Africa, but also in South Africa. The earliest known fossils of the extant species occur at Langebaanweg, South Africa, at a time when East African aardvarks such as *Orycteropus guilielmi* from Lothagam, Kenya, were smaller than it. It is possible that the *O. afer* originated in southern Africa and then spread northwards to East Africa by the Middle Pliocene. The presence of extinct species of aardvarks in Late Miocene and Pliocene deposits of Europe and Asia complicates the issue, but available fossils indicate that all the Eurasian forms were somewhat different from *O. afer*, not only in size, but also in some details of morphology. The Langebaanweg fossils are morphometrically indistinguishable from the extant species, and they thus make a more convincing candidate for its ancestry than any of the Eurasian lineages.

Hyracoidea

The genus *Prohyrax* is the earliest known representative of its family, the Pliohyracidae, and has been reliably reported only from Namibia.²⁰⁻²² Its late Middle Miocene descendent *Parapliohyrax* is known from South Africa, Namibia, Kenya, Morocco and Tunisia, while the Late Miocene of Europe and Asia has yielded several genera of the family (*Pliohyrax*, *Sogdohyrax*, *Kvabebihyrax*, *Postschizotherium*, *Hengduanshanhyrax*). The Pliohyracidae showed a strong tendency to increase in size

with the passage of geological time, and thus represent a good example of Depéret's rule. In East African Early Miocene deposits, the only hyracoids known are Titanohyracidae, a family that is better represented in the Early Oligocene of Egypt. There can be little doubt that the Pliohyracidae originated in southern Africa, and only spread northwards after several million years of residence in the south.

The origins of the extant hyracoid family, Procaviidae, are unknown, but the earliest fossils of this group have been found in Namibia (Berg Aukas)²³ and Kenya (Nakali).²⁴ Of these, Berg Aukas (c. 10 Myr) is slightly earlier than Nakali (c. 9.5 Myr). Fossils of this family are rare, but from the Late Miocene onwards they are known from both East and South Africa. Today procaviids occur as far north as Syria in the Middle East, but they have not been found as fossils anywhere in northern Africa or Eurasia. This suggests that the family originated in the sub-Saharan part of the continent, although we cannot exclude the possibility that the group evolved in the tropics as opposed to the south.

Proboscidea

The Sperrgebiet sites are poor in proboscidean remains, so little can be said about them, except to record that the genus *Eozygodon* was present there almost as early as its earliest record in East Africa. A second proboscidean of gomphotherian grade is present in the Namibian Early Miocene deposits, but it is too fragmentary to yield any useful information. The poor fossil record of proboscideans in the northern Sperrgebiet could be due to taphonomic factors, but it could also be the result of ecological ones, the region being appreciably drier than contemporaneous sites in tropical Africa. Proboscideans from the Orange River Valley are better known, and the genera *Progomphotherium* and *Afromastodon* are defined there. Of these, *Progomphotherium* has been recorded only as far north as Uganda, which suggests that it may be a lineage that originated in the south. *Afromastodon* is a widespread genus that has also been recorded in Egypt, Libya and Tunisia, but not so far from Eurasia.

Rhinocerotidae

The only firmly identified rhinocerotid in the Early Miocene of the northern Sperrgebiet is *Brachypotherium heinzlini*. East African deposits of similar age possess five genera of rhinos, suggesting that the Namibian ones were peripheral to the main centre of evolution of the family. Initially, of course, the Rhinocerotidae colonized Africa from Eurasia some time in the Late Oligocene, and it is quite possible that most of the genera had already differentiated there before entering Africa. The only exception appears to be the hypsodont lineage, *Ougandatherium*, the earliest known iranotheriine.²⁵

The genus *Diceros*, the black rhino, is recorded earliest in the Orange River Valley at Arrisdrift²⁶ (c. 17–17.5 Myr). Its next oldest record is in the Late Miocene of Tunisia and East Africa, indicating that it was resident in southern Africa for several million years before spreading northwards.

Suiformes

Anthrotheriidae are rare in southern African Early Miocene deposits, suggesting that the subcontinent was peripheral to the main range of the family, which is highly diverse in North African and East African deposits of the same age. The only genus definitely identified in the south is *Brachyodus*, represented by a large species, *B. depereti*, best represented in Egypt, while a closely related, but slightly smaller species, *B. aequatorialis*,

occurs in East Africa.

Kenyapotamine hippos have been found in Kenya and Tunisia, ranging in age from about 16 to 9 Myr. True hippos appear abruptly in the East African fossil record about 7 Myr, and they are also known from similar-aged deposits in North Africa, Spain, the Arabian peninsula and the Indian subcontinent. However, it is unlikely that true hippos originated in tropical Africa, northern Africa or Eurasia, as the Late Miocene fossil records of these areas are devoid of any hint of their immediate precursors. Thus the origins of hippopotamines are 'hidden', but it is as likely that they originated in southern Africa as elsewhere.

Suidae are unknown in African Early Oligocene deposits but are common from Early Miocene times onwards. The family is a Eurasian one that colonized Africa late in the Oligocene or during the Basal Miocene, but once it arrived in Africa it soon radiated into different forms. Those from Early Miocene deposits of southern Africa belong to the subfamily Kubanochoerinae, which originated in Africa after suids had colonized the continent. The smallest and earliest known species is *Nguruwe namibensis*, which is slightly smaller than *Nguruwe kijivium*, best known from East African Early Miocene localities as well as Arrisdrift, Namibia. This species is close in morphology and size to *Aureliachoerus* from Europe, which may be the original suid group that colonized Africa. At present it cannot be determined whether the kubanochoeres evolved within South Africa and then spread to East Africa, or whether they were more widespread from the start.

The abrupt appearance of hypsodont, polycuspidate suids such as *Notochoerus* and *Metridiochoerus* in the Basal Pliocene of East Africa has usually been interpreted in terms of autochthonous evolution, yet it is more likely that they originated in southern Africa and spread northwards as open, arid environments developed there. We can eliminate north Africa and Eurasia from the equation, as these suid lineages appeared later there than in East Africa. The subfamily Suinae originated in Eurasia, where they are known from Late Miocene (c. 9–10 Myr) times onwards, their earliest record in Africa being middle Pliocene (c. 4.5 Myr). The wart hog, *Phacochoerus*, in contrast, is an African endemic which appears abruptly in East African deposits of Middle to Late Pleistocene age, with no signs of transition from *Metridiochoerus*, its likely ancestor. The most primitive and oldest known phacochoeres are from Kromdraai, Swartkrans Brown Breccia, Bolt's Farm and other sites in Gauteng, South Africa,²⁷ suggesting that the genus originated in the south, and subsequently spread to equatorial regions as fully evolved wart hogs.

Sanitheriidae are a family of poorly known suoids with peculiar features in the dentition, cranium and post-cranium. Their earliest records are in the Early Miocene of East and southern Africa, from where they spread northwards into Europe and Asia during the Middle Miocene (MN 5), following several million years of independent evolution in Africa. Although sanitheres are suoids, the group from which they originated is unknown, with various authors proposing relationships to suids, anthracotheres and palaeochoerids. The family appears to have originated in the southern half of Africa from an unknown suoid ancestral group that itself originally invaded the continent from Eurasia sometime during the Oligocene.

Ruminants

Ruminants are unknown in the Early Oligocene and older deposits of Africa, but are common and quite diverse in the Early Miocene and later deposits of East and South Africa. The

superfamily must have entered the continent from Eurasia sometime during the Late Oligocene or Early Miocene. After having arrived in the continent, the various lineages (at least two and perhaps more, represented by Tragulidae and Pecora) diversified and endemic groups soon emerged. Among these were the tragulid *Dorcatherium*, which eventually repopulated Europe and perhaps Asia after residing in Africa for several million years. Another family that originated in Africa, more specifically in southern Africa, was the Bovidae, of which by far the earliest known representative in the world is *Namibiomyx* from the basal Early Miocene of the northern Sperrgebiet. This genus very likely gave rise to *Namacerus*, which possessed horns. It was after developing horns that the family eventually spread northwards after surviving in the south for several million years, first to tropical Africa and then to Eurasia, where similar forms have been called *Eotragus*. The extinct Climacoceratidae appeared for the first time in the Early Miocene of southern Africa (*Sperrgebietomyx*, *Propalaeoryx*, *Orangemyx*) and subsequently spread to East and North Africa during the Middle Miocene, where the family is represented by the genera *Climacoceras* and possibly *Prolibytherium*, respectively. This family is unknown outside Africa.

At the end of the Late Miocene and during the Pliocene, several tribes of bovids appeared abruptly in East Africa, suggesting that they evolved elsewhere and spread to East Africa as conditions there changed to become suitable for them. Lineages that may have originated in southern Africa and subsequently spread northwards include the springbok, impalas, wildebeest, alcelaphines, and reduncines, although there is uncertainty about some of these tribes. Gentry^{28,29} recorded the oldest African reduncine dentitions from Lukeino (6 Myr) and Mpesida (6.3 Myr) and wrote that they were similar to material from the Siwaliks (Pakistan). It could be that the group originated outside Africa, or spread from some other part of Africa to East Africa and Eurasia. However, reduncines have been reported from deposits about 9.5 Myr in Kenya, which would make them the oldest known in the world. Although the genus *Damalacra*²⁸ represents the oldest known alcelaphine, Gentry³⁰ considered it likely that some of the Fort Ternan and Ngorora bovids, thought at the time to be caprines, may have been ancestral to the Alcelaphini. The oldest evidence of the genus *Connochaetes* is from the Turkana basin, *C. gentryi*.³¹ The poor temporal resolution in the hominid-bearing cave deposits of South Africa makes it difficult to assess wildebeest origins.

Other bovid lineages that appeared in East Africa during the Late Miocene and Pliocene may well have evolved locally, such as the neotragines and tragelaphines, or probably spread southwards from Eurasia (bovines, caprines, ovibovines, antilopines, gazelles, hippotragines).

From Table 1, it is clear that the influence of Eurasian faunas on those of East Africa was pervasive, and more marked than that of southern African faunas. Yet, considering the relative dimensions of southern Africa and Eurasia, the imbalance is perfectly understandable. For its size, South Africa produced a goodly proportion of lineages that eventually colonized the equatorial regions of the continent, some of them after living for millions of years in the south. Several of the mammalian lineages with 'hidden' origins may also have originated in the southern parts of the continent, in particular bovid tribes that were adapted to open, arid, unstable environments, but until suitably aged fossiliferous deposits of Middle and Late Miocene age are found in South Africa, we will continue to remain in the dark about them.

Table 1. Appearance of selected vertebrate lineages in East Africa during the Miocene and Plio-Pleistocene.**1. From southern Africa**

Lineage	Record of ancestral lineage in southern Africa	Earliest record in East Africa	References
Nile crocodile	<i>Crocodylus gariepensis</i> , 17.5 Myr	<i>Crocodylus niloticus</i> , c. 7 Myr	14, 15
Struthionids	<i>Struthio coppensi</i> , 21 Myr	<i>Struthio</i> sp., c. 14 Myr	16, 17
Percrocutids	<i>Africanictis hyaenoides</i> , 17.5 Myr	<i>Percrocuta tobieni</i> , c. 13 Myr	32, 33
<i>Orycteropus afer</i>	<i>Orycteropus afer</i> , Langebaanweg c. 5 Myr	<i>Orycteropus afer</i> , Pliocene	18
Pliohipyridae	<i>Prohyrax tertarius</i> , 21 Myr, <i>Prohyrax hendeyi</i> , 17.5 Myr	<i>Parapliohipyax ngororaensis</i> , 12.5 Myr	20, 21, 34
Procaviidae	<i>Heterohyrax auricampensis</i> , c. 10 Myr	Procaviid at Nakali, c. 9.5 Myr	23, 24
Black rhinoceros	<i>Diceros australis</i> , 17.5 Myr	<i>Diceros bicornis</i> , c. 7 Myr (earlier records are known from N. Africa and Europe, c. 10 Myr)	26
Suidae	<i>Phacochoerus</i> , Mid-Pleistocene	<i>Phacochoerus</i> , Mid-Late Pleistocene	27
Climacoceratidae	<i>Spergebetomerx wardi</i> , 21 Myr	<i>Climacoceras africanus</i> , 16 Myr	36, 37
Bovidae	<i>Namibiomerx</i> , 21 Myr, <i>Namacerus</i> , 17.5 Myr	<i>Eotragus</i> , <i>Nyanzamerx</i> , 16 Myr	36, 38, 39
Alcelaphini	<i>Damalacra</i> , Late Miocene	<i>Damalacra</i> , 7 Myr	28

2. From Eurasia

Lineage	Record of ancestral lineage in southern Eurasia	First appearance in East Africa	References
Lagomorpha	<i>Alilepus</i> , Late Miocene	<i>Alilepus</i> , <i>Serengetilagus</i> , c. 7 Myr	40
Hystriidae	<i>Hystrix</i> spp., 10 Myr	<i>Hystrix</i> spp., c. 7 Myr	40
<i>Plesiogulo</i>	<i>Plesiogulo</i> , Late Miocene	<i>Plesiogulo</i> , c. 6 Myr	41
<i>Agnotherium</i>	<i>Agnotherium</i> , Middle Miocene	<i>Agnotherium</i> , c. 13 Myr	42
<i>Agriotherium</i>	<i>Agriotherium</i> , Late Miocene	<i>Agriotherium</i> , c. 5 Myr	43
Canidae	<i>Canis</i> spp. Late Miocene	<i>Eucyon</i> , 6 Myr	41
Hyaenas	High diversity during Late Miocene	<i>Ikelohyaena</i> , c. 7 Myr	41
White rhinoceros	<i>Ceratotherium</i> spp., 10 Myr	<i>Ceratotherium praecox</i> , 7 Myr	44
Brachypotheres	<i>Brachypotherium</i> spp., Early Miocene	<i>Brachypotherium</i> , 20 Myr	44
Ancylotheres	<i>Ancylotherium</i> , Late Miocene	Ancylothere, c. 9.5–10 Myr	45
<i>Hipparion</i>	<i>Hipparion</i> , 11 Myr	<i>Hipparion</i> , 11 Myr	46, 47
<i>Equus</i>	<i>Equus</i> , 2.6 Myr	<i>Equus</i> , 2.6 Myr	48
Suidae	<i>Aureliachoerus</i> , Late Oligocene	<i>Nguruwe</i> , c. 20	49
Listriodontinae	<i>Listriodon</i> , MN 4a	<i>Listriodon</i> , c. 16 Myr	49
Tetraconodontinae	<i>Conohyus</i> , MN 5	<i>Nyanzachoerus</i> , c. 10 Myr	49
Suinae	<i>Potamochoerus</i> , Late Miocene	<i>Potamochoerus</i> , 4.5 Myr	50
Large doliochoeres	<i>Xenohyus</i> , Basal Miocene MN 2	<i>Kenypotamus</i> , c. 16 Myr	51
Small doliochoeres	<i>Doliochoerus</i> , <i>Choeromorus</i> , Oligo-Miocene	<i>Morotochoerus</i> , c. 17.5 Myr	52
Giraffes	High diversity in Late Miocene	<i>Giraffa</i> , c. 7 Myr <i>Sivatherium</i> , c. 6 Myr	53, 54
Camelidae	<i>Paracamelus</i> , Late Miocene	<i>Paracamelus</i> , Mid-Pliocene*	55
Camel	<i>Camelus</i> , Pliocene	<i>Camelus</i> , Pleistocene	56
Hippotragini	Hippotragines, 9–10 Myr	Hippotragini, c. 7 Myr	57
Caprini	Caprines, Late Miocene	Caprines, Plio-Pleistocene	58
Ovibovini	Ovibovini, Late Miocene	<i>Budorcas</i> , c. 3 Myr	59

*Camels reached north Africa and Chad by the end of the Miocene^{60, 61, 62} but the earliest record in East Africa is mid-Pliocene.⁵⁵**3. 'Hidden' origins** (possibly southern African on the argument that the better fossil records of eastern and northern Africa show no signs of these lineages prior to their appearance there).

Lineage	Earliest appearance in East Africa	References
<i>Hippopotamus</i>	<i>Hippopotamus</i> , c. 7 Myr	63
Colobines	<i>Microcolobus</i> , c.10 Myr	64
Papionines	<i>Parapapio</i> , c. 7 Myr	65
Reduncines	<i>Redunca</i> , c. 9.5 Myr	45
<i>Antidorcas</i>	<i>Antidorcas</i> , c. 3 Myr	66
<i>Paranthropus</i>	<i>Paranthropus</i> , c. 2.6 Myr	67
Tool-using <i>Homo</i>	<i>Homo</i> spp., c. 3–2.6 Myr	68

Geography of hominid origins**The East Side Story**

Because of its name, the best-known of the geographic scenarios about hominid origins is Coppens' East Side Story,⁶⁸ but there are others that can be summarized as the West Side Story⁶⁹ and the North Side Story (or Stories).^{70–76} There are even Far East Side Stories,^{77,78} which need not concern us here. There are differences between the evidential bases of these various hypotheses, most of them interpreting one or another fossil or group of fossils

as early hominids. The only scenario that did not have a particular hominid species in mind when it was formulated is the East Side Story (ESS). Coppens' hypothesis has three main elements and subsumes several others. The main ones are environmental, chronological and geographic, which are joined by biological concepts such as allopatric speciation, competitive exclusion, adaptation and extinction, and geological ones such as rift tectonics and epeirogenic uplift.

There are several weak points to the ESS. First, the error margin of radioisotopic dates in the Cainozoic typically span

about 200 000 years, which is more than ample time for a species to spread from one end of Africa to the other, given suitable adaptations and habitats. For this reason it may be that we will never know the precise location or area in which the earliest humans evolved, unless we can find good evidence of their precursors in one area long before they occur elsewhere.

Second, the geological and climatic events that resulted in the environmental changes envisaged by Coppens (rifting, uplift of East Africa, desiccation of East Africa) were not the only ones that affected the continent. These regional causes of geological, climatic and biological change obtain support from studies of the Rift deposits and their contained fauna and flora, but there is little doubt that there were global changes that occurred at the same time, and which also contributed to climatic, vegetation and faunal changes. The growth of the Arctic Ice-cap to cover vast areas near the North Pole had a global effect, the main one of which was to squeeze the northern ecoclimatic belts equatorwards, thereby making the equatorial belts narrower than they were in the Middle Miocene (Fig. 1). A direct consequence of this polar ice-cap growth was the onset of aridification in what is now the Sahara c. 8 Myr, savanna and eventually desert replacing what used to be tropical forest.⁴ At about the same time, uplift of the Tibetan Plateau and other parts of the Alpine orogenic chain culminated in climatically critical relief being attained, which affected atmospheric circulation to such an extent that the monsoon system was created more or less in its present form, which is important for understanding the evolution of East Africa's climate.

Third, the lack of fossil sites in western tropical Africa means that there is no support for the contention that apes have lived in the west on a permanent basis since the Miocene. It is an assumption which is currently impossible to verify or refute.

Fourth, the assumption that the Late Miocene precursors of hominids were confined to the equatorial belt is not warranted. It has been known for several decades that the distribution of tropical forest and desert was dramatically different in the Middle and Late Miocene from what it is at present.⁷ Biondi *et al.*⁷⁹ and Koeniguer⁸⁰ documented the presence of rainforest tree species in Miocene deposits in many parts of central and northern Africa, proving that what is now hyper-arid Sahara was clothed in tropical forest during the Middle Miocene, and African tropical trees have even been recorded from Europe. What is at present the centre of the Congolian rainforest was dune desert during the Middle Miocene.⁸¹

Furthermore, hominoids survived throughout the mid-latitudes of Europe and Asia from about 14 to about 8 Myr, and this fact is the basis of the North Side Story.⁷¹

An essential element of the ESS is that as the east became drier, the vegetation became more open, thereby diminishing around the forest-dwelling hominoids that lived there. In other words, in the ESS concept the forest left the apes, the apes did not leave the forest. There were two possibilities, either the apes became extinct in the east, or they adapted to the new conditions. Most lineages did go extinct, but Coppens suggested that at least one survived, in the process evolving into hominids. This argument has a strong element of environmental determinism in it, and this is its weakest point. Open environments have existed in Africa from at least the beginning of the Middle Miocene, and there is good evidence that several lineages of hominoids became adapted to relatively open country, yet bipeds did not evolve until towards the end of the epoch.

The discovery of 8–7 Myr hominid fossils in the western, northern or southern parts of Africa might refute the geographical element of the ESS, but it would be illogical to claim on such a

basis that the hypothesis is totally wrong. This is because at heart the ESS is about environmental and chronological aspects of hominid origins, and these would need to be refuted on grounds related to such factors. Furthermore, such a demonstration would not affect the evidence related to rifting, uplift and climatic change that have been documented in East Africa^{82,83} and which are in general agreement with Coppens'⁶⁸ proposal.

The North Side and Far East Side stories

Several Eurasian Miocene Hominoidea have, at one time or another, been claimed as hominid ancestors including *Oreopithecus bambolii* by Hürzeler,⁷⁶ *Ramapithecus punjabicus* by Pilbeam,⁷⁷ *Dryopithecus fontani* by Begun,^{70,71} *Lufengpithecus lufengensis* by Wu,⁷⁸ and *Ouranopithecus macedoniensis* by De Bonis *et al.*^{74,75}

A common basis of all these claims is the perceived lack of hominoids in African Late Miocene deposits and their abundance and relatively high diversity in European and Asian deposits of the same age. Begun,⁷¹ for example, wrote that no hominoids have ever been found in African Late Miocene localities, yet the 6 Myr Lukeino molar⁸⁴ was described in 1975 it is now attributed to *Orrorin tugenensis*; *Samburupithecus kiptalami*, a gorilla-sized species, was described from the Namurungule Formation (9.5 Myr), Kenya, by Ishida and Pickford,³⁵ and subsequently others have been described from the Lukeino Formation, Kenya (*Orrorin tugenensis*),⁸⁶ the Western Margin of the Afar, Ethiopia (*Ardipithecus ramidus kadabba*),⁸⁷ and Toros-Menalla, Chad (*Sahelanthropus tchadensis*).⁶⁹ Latest Middle Miocene hominoids are also known in Africa, including *Otaviopithecus namibiensis* from Berg Aukas (12–13 Myr), Namibia⁸⁸ and an unnamed species from the Ngorora Formation, (12.5 Myr) Kenya. It is thus highly probable that there was no time during the Cainozoic when Africa was devoid of hominoids. Indeed, with the recent discoveries, it is becoming apparent that hominoids were probably more diverse in the Late Miocene of Africa than they were in Europe during the same period.

The resemblances of European *Dryopithecus* and *Ouranopithecus* (= *Graecopithecus* of some authors) to African apes and humans have been interpreted^{70,71,74,75} to mean that these European lineages re-entered Africa to re-populate a continent that had become devoid of hominoids. This now seems highly unlikely, and it is more probable that the resemblances noted by these authors are due to African lineages colonizing Europe rather than the other way round.

The Far East hominoids, *Ramapithecus* (now generally accepted as females of *Sivapithecus*) and *Lufengpithecus*, share important features with the orang utan, and are unlikely to have anything to do with the evolution of the extant African apes and hominids.

The West Side Story

Brunet *et al.*⁶⁹ suggested that the discovery of *Sahelanthropus tchadensis* in 7–6 Myr deposits in the Chad Basin refuted Coppens' East Side Story, and revealed that hominids might have originated instead in the west. Even if *Sahelanthropus* is a hominid, which has been disputed,⁸⁹ it would only refute the geographical element of the ESS. However, if it is an ape, as thought by Wolpoff *et al.*,⁸⁸ then its discovery comforts the ESS. It is thus essential to determine the familial affinities of *Sahelanthropus*, and for this, postcranial bones would be most useful, the presently available evidence as to its supposed bipedalism being extremely scanty.

Other vertebrates from Chad lend support to the ESS in the sense that they reveal that there was marked provincialism in

Africa during the Late Miocene. The anthacothere *Libycosaurus petrocchii* and the crocodile *Tomistoma coppensi*, for example, are abundant in Chad and western Uganda, but have never been found in the exceptionally rich fossil deposits of the same time span in Kenya, Ethiopia and Tanzania. There were thus significant differences between 'western' and 'eastern' faunas of Late Miocene Africa, and these differences were most probably related to environmental factors, as suggested by Coppens.⁶⁸

A South Side Story?

It is rare to read suggestions that hominids evolved in the south, yet the possibility exists. Not only have suitable open habitats ranging from desert to forest existed there for at least 16 Myr, but it is also now established that the southern half of the continent was home to hominoids during the Early and Middle Miocene. The Ryskop hominoid (c. 17 Myr), from Namaqualand, South Africa,⁸⁹ and *Otaviipithecus namibiensis* from Berg Aukas (13–12 Myr), Namibia³⁵ prove their presence in the subcontinent.

Otaviipithecus is particularly interesting since it has thick-enamelled cheek teeth with minor dentine penetrance, and it lived in an area that, although well vegetated, was unlikely to have been tropical forest. *Otaviipithecus* was arboreal and most likely frugivorous/omnivorous, eating sclerocarp fruit among other foods. It was somewhat smaller than a chimpanzee.

Robust australopithecines make a sudden appearance in East Africa about 2.6 Myr, with no signs that they evolved autochthonously from one of the East African Late Pliocene lineages. The fossil record for Pliocene hominids is remarkably comprehensive due to the intense activity that has been focused there for the past four decades, making it almost certain that the robust australopithecines evolved elsewhere and spread to East Africa only when conditions suitable for their existence developed there. On balance, it is more likely that they originated in the south than in the north or west.

The abrupt appearance of *Homo* (and stone tools) in East Africa about 2.6–3 Myr, with no convincing evidence that the genus evolved autochthonously, suggests that it may have originated elsewhere, and spread to East Africa at the end of the Pliocene. The north African and Eurasian fossil records of this period are well known and there are no signs that the genus evolved there. This leaves southern Africa as a prime candidate for the region in which *Homo* originated.

Conclusions

Southern Africa was a region of marked endemism during the Miocene, and to some extent it still is. With a better understanding of the Miocene fossil record of the sub-region thanks to recent research in Namaqualand and Namibia, it is now clear that many lineages of vertebrates originated in the south and subsequently spread northwards into tropical Africa and beyond. For example, the Nile crocodile has its roots in the Middle Miocene *Crocodylus garipeensis* of southern Africa, and not in the Pliocene lineage of east and north Africa, *Crocodylus lloydi*, as once thought. The ostrich, *Struthio*, has a much earlier record in Namibia than anywhere else in the world. The same applies to Bovidae, Climacoceratidae, the black rhinoceros (*Diceros*) lineage, percrocutid carnivores, pliohyracid and procaviid hyracoids, the antbear (*Orycteropus afer*), and several rodents, in particular the bathyergids. One of the reasons for the precocious evolution of these lineages in southern Africa is that deserts and neighbouring ecosystems have been present in the region since the end of the Early Miocene, far longer than anywhere else on the continent, thus providing ample time for evolution to take its course. Moreover, the region is far removed

from the enormous genetic pools of Europe and Asia, which profoundly affected the northern African and tropical African faunas during the Miocene.

Because southwest Africa became arid appreciably earlier than other parts of the continent did, and since the area was well separated from arid areas in Eurasia, the flora and fauna had sufficient time to adapt to arid, unstable and open conditions in isolation from evolutionary activity elsewhere in the Old World. Having adapted to such conditions, these lineages were pre-adapted to spread into neighbouring areas as they, in their turn, became arid during the Late Neogene. Thus, as East Africa became more arid during the Late Miocene and Plio-Pleistocene, and its vegetation more open, southern African animals and plants simply spread northwards before local East African lineages could themselves adapt to the new conditions. By the Middle Miocene, a few southern African vertebrates had spread northwards into East Africa including struthionids, percrocutids, bovids and climacoceratids. During the Late Miocene and Pliocene, the rate of immigration accelerated and involved the Nile crocodile, several tribes of bovids, the black rhino, and probably hippos, colobines, papionines and perhaps even primitive hominids.

As East Africa became more and more arid during the Late Miocene and Pliocene, links were made not only with arid palaeoenvironments in southern Africa, but also with those in the northern hemisphere mid-latitude zones of Eurasia, with the result that a number of vertebrate lineages from this region spread southwards towards the tropics, including porcupines, hares, true hyaenas, white rhinos, suines, camelids and possibly giraffids.

Although mammals spread into East Africa throughout the Miocene epoch,⁵ the period from 8–7 Myr was particularly eventful as it saw the appearance of many of the classic African savanna mammals that still exist today. The region was subjected to invasions of fauna not only from the south but also from the north. Most local tropical vertebrate lineages could not cope with the invasions, or did not have time enough to respond to the changes before being pressured by the incoming lineages, which were well adapted to such conditions. Thus, through the Late Miocene and Pliocene, many of the archaic tropical African mammal lineages, that had survived for many millions of years in the tropics, disappeared from eastern Africa, either withdrawing to the west (such as tragulids) or going extinct (such as *Anancus*, chalicotheres, palaeotragines, and many others).

Because of the influence that southern African faunas had on the make-up of the Late Miocene, Plio-Pleistocene and modern tropical African fauna, it is evident that scenarios about the development of tropical lineages, including hominids, can no longer ignore possible contributions from southern Africa. Indeed, several hitherto intractable problems concerning the origins of certain groups of vertebrates that make a sudden appearance in the fossil record (that is, their origins are 'hidden'), including those of hippos, papionine baboons and even hominids, may eventually find their solution in southern Africa's fossil record.

Concerning human origins, I leave the second last word to Mayr:⁹⁰

[*Homo*] *rudolfensis* does not seem to have descended from any known species of *Australopithecus* in eastern or southern Africa. Rather, it seems to have invaded eastern Africa from somewhere else in Africa. Surely, there must have been australopithecine subspecies or allospecies in the tree savannas of western and northern Africa,

but no fossils have been found so far. Yet *Homo* must have evolved from some of these peripheral populations. This would explain why *Homo*, a far more advanced hominid, appears in eastern Africa so suddenly.

The last word is that, in my opinion, Mayr should have included South Africa in his list of possible centres of origin of humans. This implies that some, as yet unknown, precursor of *Homo* still remains to be discovered. Given the relative richness and completeness of the East African Pliocene fossil record allied to the 'sudden' appearance of *Homo* in the region about 3–2.6 Myr, it is probable that it did not originate there, just as Mayr suggested. The known southern African Pliocene fossil deposits occur in a very small part of the subcontinent (mainly in Gauteng province), which leaves a vast area where the genus could have evolved. Likewise, there are extensive areas of northern and western Africa which could have been the centre of origin, but the fact that the first record of *Homo* in north Africa is appreciably later than that of East Africa, suggests that the centre was not adjacent to the north. If this line of argument is valid, then it would reduce the chances that the genus *Homo* originated in either northern or western Africa, and would swing the balance of probability towards southern Africa.

Research authorization for Kenya was provided by the Ministry of Education, Science and Technology, and research affiliation is with the Community Museums of Kenya (E. Gitonga). Thanks to the members of the Kenya Palaeontology Expedition for their help in the field and laboratory. I thank all members of the Namibia Palaeontology Expedition for their participation and support. I am anxious also to acknowledge the help of the Geological Survey of Namibia (G. Schneider), Namdeb (R. Burrell, R. Spaggiari, K. Kotze), the Namibian National Monuments Council (G. Hoveka), the Collège de France (Y. Coppens), the Département Histoire de la Terre of the Muséum national d'Histoire naturelle, Paris (Ph. Taquet, S. Sen, B. Senut), the French Mission for Cooperation in Windhoek (T. Gervais de Lafont, F. Gheno) and the CNRS (D. Gommery).

Received 13 January. Accepted 16 March 2004.

- Meester J. (1965). The origins of the southern African mammal fauna. *Zool. afr.* **1**, 87–98.
- Roberts A. (1937). The old surviving types of mammals found in the Union. *S. Afr. J. Sci.* **34**, 73–88.
- Pickford M. and Senut B. (2000). Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia* **18**, 1–155.
- Pickford M. and Senut B. (2003). Geology and Palaeobiology of the Central and southern Namib. Vol. 2: Palaeontology of the Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia* **19**, 1–398.
- Pickford M. and Morales J. (1994). Biostratigraphy and palaeobiogeography of East Africa and the Iberian Peninsula. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **112**, 297–322.
- Brain C.K. (1981). The evolution of man in Africa: was it a consequence of Cainozoic cooling? *Alex. L. Du Toit Memorial Lecture, 17. Annex. Trans. Geol. Soc. S. Afr.* **84**, 1–19.
- Pickford M. (1999). Aubréville's hypothesis of a southwards shift of Africa's vegetation belts since the Miocene. In *Wood to Survive: Liber Amicorum Roger Dechamps*, eds F. Maes and H. Beekman, *Ann. Sci. Econ. Mus. R. Afr. Centr. Terouren* **25**, 195–212.
- Dechamps R. (1987). Xylotomy of fossil wood from the Sahabi Formation. In *Neogene Paleontology and Geology of Sahabi*, ed. N. Boaz, pp. 37–41. Alan Liss, New York.
- Pickford M. (1995). Fossil land snails of East Africa and their palaeoecological significance. *J. Afr. Earth Sci.* **20**(3–4), 167–226.
- de Broin F. (2003). Miocene Chelonians from southern Namibia. *Mem. Geol. Surv. Namibia* **19**, 67–102.
- Meylan P.A. and Auffenberg W. (1986). New land tortoises (Testudines, Testudinidae) from the Miocene of Africa. *Zool. J. Linn. Soc.* **86**, 279–307.
- Pickford M. (2003). A new species of crocodile from Early and Middle Miocene deposits of the lower Orange River Valley, Namibia, and the origins of the Nile crocodile (*Crocodylus niloticus*). *Mem. Geol. Surv. Namibia* **19**, 43–50.
- Tchernov E. (1976). Crocodylians from the late Cenozoic of the Rudolf Basin. In *Earliest Man and Environments in the Lake Rudolf Basin*, eds Y. Coppens et al., pp. 370–378. University of Chicago Press, Chicago.
- Storrs G. (2003). Late Miocene–Early Pliocene crocodylian fauna of Lothagam, southwest Turkana Basin, Kenya. In *Lothagam: The Dawn of Humanity in Eastern Africa*, eds M. Leakey and J. Harris, pp. 137–159. Columbia University Press, New York.
- Pickford M. (1994). Late Cenozoic crocodiles (Reptilia: Crocodylidae) from the Western Rift, Uganda-Zaire. In *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*, vol. 2: *Palaeobiology-Paléobiologie*, eds B. Senut, and M. Pickford. *Occas. Publ. CIFEG* **29**, 137–155.
- Mourer-Chauviré C., Senut B., Pickford M. and Mein P. (1996). Le plus ancien représentant du genre *Struthio* (Aves, Struthionidae), *Struthio coppensi* n. sp. du Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris* **322**, 325–332.
- Pickford M. (1986). Cainozoic palaeontological sites of Western Kenya. *Münchener Geowiss. Abh.* **A 8**, 1–151.
- Pickford M. (1975). New fossil Orycteropodidae (Mammalia, Tubulidentata) from East Africa. *Neth. J. Zool.* **25**, 57–88.
- Pickford M. (2003). Minute species of *Orycteropus* from the early Middle Miocene at Arrisdrift, Namibia. *Mem. Geol. Surv. Namibia* **19**, 195–198.
- Stromer E. (1926). Reste Land- und Süßwasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. In *Die Diamantenwüste Südwest-Afrikas*, ed. E. Kaiser, **2**, 107–153. Reimer, Berlin.
- Pickford M. (1994). A new species of *Prohyrax* (Mammalia, Hyracoidea) from the Middle Miocene of Arrisdrift, Namibia. *Commun. Geol. Surv. Namibia* **9**, 43–62.
- Pickford M. (2003). Middle Miocene Hyracoidea from the lower Orange River Valley, Namibia. *Mem. Geol. Surv. Namibia* **19**, 199–206.
- Rasmussen D.T., Pickford M., Mein P., Senut B. and Conroy G. (1996). Earliest known procaviid hyracoid from the Late Miocene of Namibia. *J. Mammal.* **77**, 745–754.
- Fischer M. (1986). Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria. *Cour. Forsch. Senckenb.* **84**, 1–132.
- Guérin C. and Pickford M. (2003). *Ougandatherium napakense* nov. gen. nov. sp. le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Ann. Paléont.* **89**(1), 1–35.
- Guérin C. (2000). The Neogene rhinoceroses of Namibia. *Palaeont. afr.* **36**, 119–138.
- Harris J.M. and White T.D. (1979). Evolution of Plio-Pleistocene African Suidae. *Trans. Am. Phil. Soc. n.s.* **69**, 1–128.
- Gentry A. (1980). Fossil Bovidae (Mammalia) from Langebaanweg, South Africa. *Ann. S. Afr. Mus.* **79**, 213–337.
- Gentry A. (1990). Evolution and dispersal of African Bovidae. In *Horns, Proghorns and Antlers: Evolution, Morphology, Physiology and Social Significance*, eds G. Bubenik and A. Bubenik, pp. 195–233. Springer-Verlag, New York.
- Gentry A. (1978). The fossil Bovidae of the Baringo Area, Kenya. In *Geological Background to Fossil Man*, ed. W.W. Bishop, pp. 294–308. Scottish Academic Press, Edinburgh.
- Harris J.M. (1991). *The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments*. In *Koobi Fora Research Project*, vol. 3, ed. J.M. Harris, pp. 139–320. Clarendon Press, Oxford.
- Morales J., Pickford M., Fraile S., Salessa M.J. and Soria D. (2003). Creodonts and Carnivora from Arrisdrift, early Middle Miocene of Southern Namibia. *Mem. Geol. Surv. Namibia* **19**, 177–194.
- Aguirre E. and Leakey P. (1974). Nakali: nueva fauna de *Hipparion* del Rift Valley de Kenya. *Estudios geológicos* **30**, 219–227.
- Pickford M., Moya Sola S. and Mein P. (1997). A revised phylogeny of Hyracoidea (Mammalia) based on new specimens of Pliohyracidae from Africa and Europe. *N. Jb. Geol. Paläont. Abh.* **205**, 265–288.
- Conroy G., Pickford M., Senut B., Van Couvering J. and Mein P. (1992). *Otaoipithecus namibiensis*, first Miocene hominoid from southern Africa (Berg Aukas, Namibia). *Nature* **356**, 144–148.
- Morales J., Soria D. and Pickford M. (1999). New stem giraffoid ruminants from the Lower and Middle Miocene of Namibia. *Geodiversitas* **21**, 229–254.
- MacInnes D.G. (1936). A new genus of fossil deer from the Miocene of Africa. *J. Linn. Soc. Zool.* **39**, 521–530.
- Morales J., Soria D., Pickford M. and Nieto M. (2003). A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae. *Mem. Geol. Surv. Namibia* **19**, 371–384.
- Thomas H. (1984). Les Giraffoidea et les Bovidae Miocènes de la formation Nyakach (Rift Nyanza, Kenya). *Palaeontographica* **A183**, 64–89.
- Winkler A. (2003). Lagomorpha and Rodentia. In *Lothagam: The Dawn of Humanity in Eastern Africa*, eds M. Leakey and J.M. Harris, pp. 169–198. Columbia University Press, New York.
- Morales J., Pickford M. and Soria D. (in press). Carnivores from the Late Miocene and Basal Pliocene of the Tugen Hills, Kenya. *Estudios geológicos* (Madrid).
- Pickford M. and Senut B. (1997). Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeont. afr.* **34**, 199–217.
- Petter G., Pickford M. and Senut B. (1994). Présence du genre *Agriotherium* (Mammalia, Carnivora, Ursidae) dans le Miocène terminal de la Formation de Nkondo (Ouganda, Afrique orientale). *C. R. Acad. Sci. Paris* **319**, 713–717.
- Hooijer D.A. (1978). Rhinocerotidae. In *Evolution of African Mammals*, eds V.J. Maglio and H.B.S. Cooke, pp. 371–378. Harvard University Press, Cambridge, MA.

45. Nakaya H., Pickford M., Nakano Y. and Ishida H. (1984). The late Miocene large mammal fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *Afr. Studies Monogr. Suppl.* 2, 87–131.
46. Hooijer D.A. (1975). The *Hipparion* of the Baringo Basin sequence. *Nature* 254, 211–212.
47. Pickford M. (2001). Equidae in the Ngorora Formation, Kenya, and the first appearance of the family in East Africa. *Rev. Espanola de Paleont.* 16, 339–345.
48. Eisenmann V. (1980). Les chevaux (*Equus sensu lato*) fossiles et actuels: crânes et dents jugales supérieurs. *Cahiers paléont.*, pp. 1–186. CNRS, Paris.
49. Pickford M. (1986). A revision of the Miocene Suidae and Tayassuidae (Artiodactyla, Mammalia) of Africa. *Tertiary Res. Spec. Pap.* 7, 1–83.
50. Brunet M. and White T. (2001). Deux nouvelles espèces de Suini (Mammalia, Suidae) du continent Africain (Ethiopie, Tchad). *C. R. Acad. Sci. Paris* 332, 51–57.
51. Pickford M. (1983). On the origins of the Hippopotamidae together with descriptions of two new species, a new genus and a new subfamily from the Miocene of Kenya. *Geobios* 16, 193–217.
52. Pickford, M. (1998) A new genus of Tayassuidae (Mammalia) from the middle Miocene of Uganda and Kenya. *Ann. Paléont.* 84, 275–285.
53. Harris J. (2003). Lothagam Giraffids. In *Lothagam: The Dawn of Humanity in Eastern Africa*, eds M. Leakey and J.M. Harris, pp. 523–530. Columbia University Press, New York.
54. Geraads D. (1994). Girafes fossiles d'Ouganda. In *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*, vol. 2, *Palaeobiology*, eds B. Senut and M. Pickford, pp. 375–381. CIFE, Orléans.
55. Harris J. M. (1987). Fossil Giraffidae and Camelidae from Laetoli. In *Laetoli: A Pliocene Site in Northern Tanzania*, eds M.D. Leakey and J.M. Harris, pp. 358–377. Oxford University Press, Oxford.
56. Harris J. M. (1991). Family Camelidae. In *Koobi Fora Research Project 3. The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments*, ed. J.M. Harris, pp. 86–92. Clarendon Press, Oxford.
57. Harris J. (2003). Bovidae from the Lothagam Succession. In *Lothagam: The Dawn of Humanity in Eastern Africa*, eds M. Leakey and J.M. Harris, pp. 531–579. Columbia University Press, New York.
58. Harris J. M. (1991). Family Bovidae. In *Koobi Fora Research Project 3. The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments*, ed. J.M. Harris, pp. 139–320. Clarendon Press, Oxford.
59. Gentry A.W. (1996). A fossil *Budorcas* (Mammalia, Bovidae) from Africa. In *Paleoecology and Palaeoenvironments of Late Cenozoic Mammals: Tribute to the Career of C.S. (Rufus) Churcher*, eds K. Stewart and K. Seymour, pp. 571–587. Toronto University Press, Toronto.
60. Stromer E. (1913). Mitteilung über die Wirbeltierreste aus dem Mittelpiocän des Natrontales (Ägypten). *Zeitschr. Deutsch. Geol. Ges.* 65, 350–372.
61. Pickford M., Morales J. and Soria D. (1995). Fossil camels from the Upper Miocene of Europe: Implications for biogeography and faunal change. *Geobios* 28, 641–650.
62. Likius A.N., Brunet M., Geraads D. and Vignaud P. (2003). Le plus vieux Camelidae (Mammalia, Artiodactyla) d'Afrique: limite Mio-Pliocène, Tchad. *Bull. Soc. géol. Fr.* 174, 187–193.
63. Coryndon S.C. (1978). Fossil Hippopotamidae from the Baringo Basin and relationships within the Gregory Rift, Kenya. In *Geological Background to Fossil Man*, ed. W.W. Bishop, pp. 279–292. Scottish Academic Press, Edinburgh.
64. Benefit B. and Pickford M. (1986). Miocene fossil cercopithecoïdes from Kenya. *Am. J. Phys. Anthropol.* 69, 441–464.
65. Leakey M.G., Teaford M. and Ward C. (2003). Cercopithecoïdes from Lothagam. In *Lothagam: The Dawn of Humanity in Eastern Africa*, eds M. Leakey and J.M. Harris, pp. 201–248. Columbia University Press, New York.
66. Gentry A.W. (1985). The Bovidae of the Omo Group deposits, Ethiopia. *Les faunes Plio-Pléistocènes de la Basse Vallée de l'Omo, (Ethiopie)*, vol. 1, Périssodactyles, Artiodactyles (Bovidae). CNRS, Paris.
67. Walker A., Leakey R., Harris J.M. and Brown F. (1986). 2.5 Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature* 322, 517–522.
68. Coppens Y. (1994). East side story: the origin of humankind. *Sci. Am.* May 1994, 88–95.
69. Brunet M., Guy F., Pilbeam D., Mackaye H., Likius A., Ahounta D., Beauvilain A., Blondel C., Bocherens H., Boisserie J.-R., de Bonis L., Coppens Y., Dejax J., Denys C., Düringer P., Eisenmann V., Fanone G., Fronty P., Geraads D., Lehmann T., Lihoreau F., Louchart A., Mahamat A., Merceron G., Mouchelin G., Otero O., Pelaez-Campomanes P., Ponce de Leon M., Rage J.-C., Sapanet M., Schuster M., Sudre J., Tassy P., Valentin X., Vignaud P., Viriot L., Zazzo A. and Zollikofer C. (2002). A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418, 145–151.
70. Begun D. (1994). Relations among the great apes and humans: new interpretations based on the fossil great ape *Dryopithecus*. *Yrbk Phys. Anthropol.* 37, 11–63.
71. Begun D. (2002). European hominoids. In *The Primate Fossil Record*, ed. W.C. Hartwig, pp. 339–368. Cambridge University Press, Cambridge.
72. Begun D. and Gülec E. (1998). Restoration of the type and palate of *Ankarapithecus meteai*: taxonomic and phylogenetic implications. *Am. J. Phys. Anthropol.* 105, 279–314.
73. Begun D. and Kordos L. (1997). Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominoids. In *Function, Phylogeny, and Fossils*, eds D.R. Begun, C.V. Ward and M.D. Rose, pp. 291–316. Plenum Press, New York.
74. de Bonis L., Bouvraïn G., Geraads D. and Koufos G. (1990). New hominid skull material from the Late Miocene of Macedonia in northern Greece. *Nature* 345, 712–714.
75. de Bonis L., Johanson D., Melentis J. and White T. (1981). Variations métriques de la denture chez les Hominidés primitifs: comparaison entre *Australopithecus afarensis* et *Ouranopithecus macedoniensis*. *C. R. Acad. Sci. Paris* 292, 373–376.
76. Hürzeler J. (1960). The significance of *Oreopithecus* in the genealogy of man. *Triangle* 4, 164–174.
77. Pilbeam D. (1966). Notes on *Ramapithecus*, the earliest known hominid, and *Dryopithecus*. *Am. J. Phys. Anthropol.* 25, 1–5.
78. Wu R. (1987). A revision of the classification of the Lufeng great apes. *Acta anthropologica sinica* 6, 263–271.
79. Biondi E., Koeniguer J.-C. and Privé-Gill C. (1985). Bois fossiles et végétations arborecentes des régions méditerranéennes durant le Tertiaire. *Giorn. Bot. Ital.* 119, 167–196.
80. Koeniguer J.-C. (1966). Etude paléoxylologique de la Libye, I. Sur un bois fossile de l'Oligocène de Dor El Abd (Syrte) *Bridelioxylon arnouldii* n. sp. II. Sur la présence de *Dombeyoxylon oweni* (Carr.) Kräusel, 1939, dans le Tertiaire de la Syrte. III. Sur la présence de *Sapindoxylon* sp. dans le Tertiaire du Nord du Tibesti. *C. R. 91ème Congr. nat. Soc. Sav. Rennes, 1966*, 3, 153–172.
81. Pickford M. (1992). Evidence for an arid climate in Western Uganda during the middle Miocene. *C. R. Acad. Sci. Paris* 315, 1419–1424.
82. Pickford M. (1990). Uplift of the Roof of Africa and its bearing on the evolution of mankind. *Hum. Evol.* 5, 1–20.
83. Pickford M., Senut B. and Hadoto D. (1993). *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire, Orléans, CIFE, Publ. Occas.* 1993/24, 1–190.
84. Pickford M. (1975). Late Miocene sediments and fossils from the Northern Kenya Rift Valley. *Nature* 256, 279–284.
85. Ishida H. and Pickford M. (1997). A new late Miocene hominoid from Kenya: *Samburupithecus kiptalami* gen. et sp. nov. *C. R. Acad. Sci. Paris* 325, 823–829.
86. Senut B., Pickford M., Gommery D., Mein P., Cheboi K. and Coppens Y. (2001). First hominid from the Miocene (Lukeino Formation, Kenya). *C. R. Acad. Sci. Paris* 332, 137–144.
87. Haile-Selassie Y. (2001). Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* 412, 178–181.
88. Wolpoff M., Senut B., Pickford M. and Hawks J. (2002). Palaeoanthropology (communication arising): *Sahelanthropus* or *Sahelpithecus*? *Nature* 419, 581–582.
89. Senut B., Pickford M. and Wessels D. (1997). Pan-African distribution of Lower Miocene Hominoidea. *C. R. Acad. Sci. Paris* 325, 741–746.
90. Mayr E. (2001). *What Evolution Is*. Basic Books, New York.