Africa – the Evolution of a Continent and its Large Mammal Fauna

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Summary

Africa contains around 1,100 mammalian species, about a quarter of the worldwide total and a diversity unequalled elsewhere (Kingdon, 1997). Molecular analyses suggest a small number of these, including elephants, aardvarks and elephant shrews, form a unique group, the Afrotheria, with a restricted common ancestry there (Madsen *et al.*, 2001; Murphy *et al.*, 2001). Yet the African mammal fauna also shares elements with adjacent continents, the result of biogeographic changes induced by continental movements and climatic changes (Cox & Moore, 2004). We offer an illustrated overview, based on a more detailed study presented elsewhere (Turner & Antón, 2004), of the evolution of the continent and of its large-mammal fauna from around thirty million years ago (Mya).

Artwork by MA is based wherever possible upon the skeleton of the species being reconstructed to provide a clear guide for the placement and bulk of the muscles as a basis for the external features. More detail of methods and approach can be found elsewhere (Antón, 2003a, 2003b, Turner & Antón, 2004).

Samenvatting

Afrika herbergt rond de 1.100 zoogdiersoorten, ongeveer een kwart van het wereldwijde aantal en een diversiteit die nergens anders wordt geëvenaard (Kingdon, 1997). Moleculaire analyses suggereren dat een klein aantal van deze soorten, waaronder olifanten, aardvarkens en olifantspitsmuizen, een unieke groep vormen, de Afrotheria, met een beperkte gemeenschappelijke afstamming daar (Madsen *et al.*, 2001; Murphy *et al.*, 2001). Maar de Afrikaanse zoogdierfauna deelt ook elementen met aangrenzende continenten, wat het resultaat is van biogeografische veranderingen die geïnduceerd zijn door continentale bewegingen en klimaatveranderingen (Cox & Moore, 2004). We geven hier een geïllustreerd overzicht, gebaseerd op een meer gedetailleerde studie die elders uitgebracht is (Turner & Antón, 2004), van de evolutie van het continent en van zijn grote-zoogdierenfauna vanaf ongeveer dertig miljoen jaar geleden.

Plaatwerk door MA is, waar mogelijk, gebaseerd op het skelet van de gereconstrueerde soort om te dienen als leidraad voor de plaatsing en de massa van de spieren als basis voor de uitwendige kenmerken. Meer gegevens over de methode en benadering kan elders gevonden worden (Antón, 2003a, 2003b, Turner & Antón, 2004).

Africa – the background

The African plate, including the southern Arabian Peninsula, joined Eurasia in the early Miocene, around 25 - 18 Mya, closing the eastern Tethys Sea (Rögl, 1999). Changes in geography were complex, and movement across the shortening gap is evident from the presence of the Primates in Africa as early as 33 - 40 Mya in the Fayum of Egypt and possibly even slightly earlier in Algeria (Godinot & Mahboubi, 1992) together with anthracotheriid artiodactyls (Tabuc & Marivaux, 2005). Northward movement of Africa and India formed the mountain chains that run from southern Europe to the Himalayas, including the Taurus and Zagros mountains of Turkey and Iran that have combined with the frequently harsh conditions of the Arabian Peninsula to control movements into and out of Africa (Tchernov, 1992). Towards the end of the Miocene, during the Messinian, tectonic processes in the region closed the area of the present-day Gibraltar Straits and the Mediterranean began to dry up (Kirjksman *et al.*, 1999). During the early Pliocene the Mediterranean re-filled, while the Red Sea widened as the Arabian plate swung away and broke the Bab-el-Mandeb land bridge. Although a semi-complete land bridge existed across the Straits of Gibraltar at some point during the Messinian, there is no compelling evidence for one since then.

Africa is an elevated continent; almost half is over 1,000 m and most of the area south of the Sahara above 500 m. Highlands around the Rift Valley reach 5,000 m, eastern African savannas rise to 1,500 m and the Rift Valley lies at altitudes up to 2,000 m (Pritchard, 1979; Adams *et al.*, 1996). But until around 30 Mya the topography of eastern Africa was rather more even. At that time extensive volcanic activity occurred in the Ethiopia-Afar region (Hofman *et al.*, 1997) and the Rift Valley was well-established in

northern Ethiopia by the mid Miocene. Parts of the Afar Plateau in the north of Ethiopia were elevated by close to 2,000 m within the past 8 Mya, while the flanks of the eastern arm of the Rift grew mainly through volcanic activity from around 15 Mya onwards and substantial uplift within the past 3 Mya. The western arm of the Rift began to form later, around 12 Mya. Uplifting of the Rift flanks exceeded 4,000 m in the Ruwenzori Mountains of western Uganda, mostly between 3.0 and 2.0 Mya. By the end of the Miocene the topographic changes in eastern Africa were sufficient to have had a major impact on the climate of the region.

The folded mountains of northern Africa are a late Oligocene-age product of the contact with Europe. Folding lifted much of the northern region above the Tethys shoreline, although substantial areas east of the Atlas belt in Libya and Egypt were covered again by shallow Miocene seas. In southern Africa, large-scale Cainozoic uplift produced the highveld and the Drakensburg Escarpment, and there appears to have been a substantial Pliocene uplift of the south-eastern hinterland, perhaps by as much as 1,000 m superimposed on a Miocene rise of around 250 m (Partridge et al., 1995).

African biomes consist mainly of Mediterranean vegetation, desert, savanna and tropical lowland and montane rainforest, with swamplands locally important (Hamilton; 1982; Cox & Moore, 2004). Africa is relatively dry, and seasonal rainfall means that rivers vary greatly in water volume while vegetational distributions are essentially limited by the balance between water demands and availability (O'Brien & Peters, 1999) and extensive wet season rain produces swamplands like the Okavango in Botswana. Savanna grasses encourage a range of seasonal grazers, and zebras, wildebeests and gazelles in turn attract lions, cheetahs, leopards, hyaenas and wild dogs (Owen-Smith, 1999).

Changes in physical geography and climate would have affected past vegetation (Behrensmeyer et al., 1992; Cerling, 1992). The Antarctic ice sheet developed around 30-35 Mya, and led to the trend of global cooling marked by several downward steps that has continued to the present (Denton, 1999). One of the most significant steps took place between 3.0 Mya and 2.5 Mya (Shackleton, 1995), at the end of which the first major northern hemisphere glacial event is recorded. A second major event is recorded close to 0.9 Mya, with a further intensification of Northern Hemisphere glaciation so that the swing between interglacial and glacial conditions became more marked.

Each major ice age probably lowered temperatures and decreased precipitation in Africa (deMenocal, 1995; deMenocal & Bloemendal, 1995). Precise effects on plant growth are
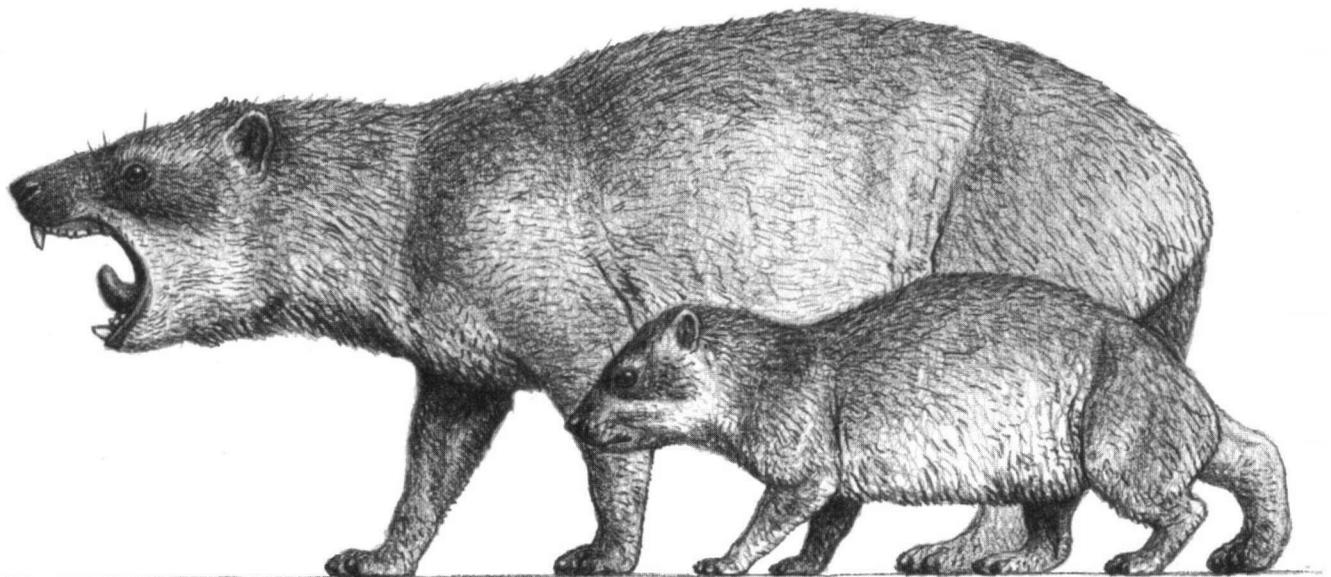

Fig 1 Comparison of size in living hyrax, *Procavia johnstoni* (right), and *Prohyrax hendeyi* from the Namibian early mid Miocene site of Arrisdrift. Reconstructed shoulder height of *Prohyrax* 37 cm.

Vergelijking van grootte van de nu levende klipdas, *Procavia johnstoni* (rechts) en *Prohyrax hendeyi* van de vroeg midden-Miocene site Arrisdrift in Namibië. Gereconstrueerde schouderhoogte van *Prohyrax* 37 cm.
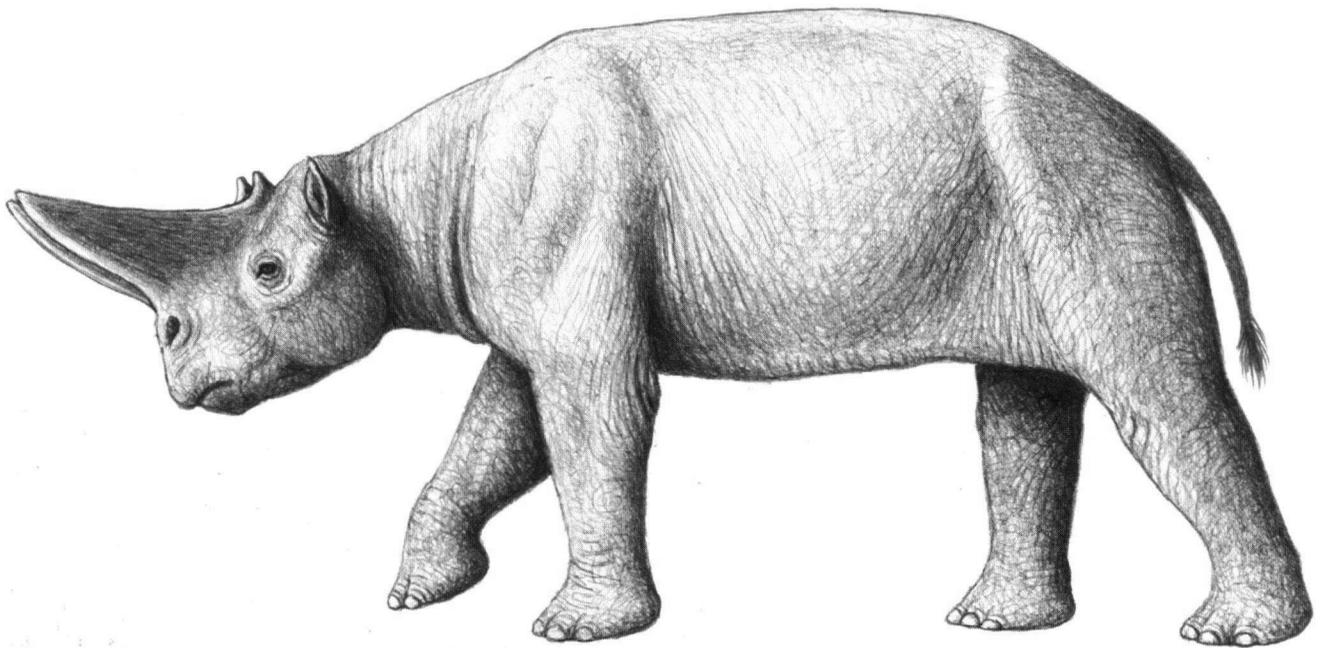
Fig 2 Life appearance of *Arsinoitherium zitteli* from the Fayum of Egypt. The "horns" were of solid bone, unlike the horns of rhinoceroses, while the columnar limbs ended in five-toed feet and resembled those of elephants. Reconstructed shoulder height 1.84 m.

Zo zag Arsinoitherium zitteli uit het Fayum van Egypte er uit. De "hoorns" waren van massief bot, anders dan de hoorns van neushoorns, terwijl hun pilaarvormige poten in vijftenige voeten eindigden en leken op die van olifanten. Gereconstrueerde schouderhoogte 1,84 m.

unclear (O'Brien & Peters, 1999), but such conditions probably fragmented the rainforests across the tropical region while allowing drier areas to the north and south to expand towards the equator. Fossil sand dunes show the Sahara desert extended 450 km further southwards around 20,000 years ago at the height of the last glaciation, matched by an expansion in southern desert areas (Hamilton, 1982). Each return to interglacial conditions would have reversed the process, rejoining areas of fragmented rainforest and driving the arid areas once more to the north and south. The present interglacial reached a peak around 6,000 years ago, when moisture seems to have made now barren areas of the Sahara habitable by plants, animals and humans (Hamilton, 1982). Intermediate conditions during interstadials would have produced similar change in the continent on a smaller scale. The climate, and with it the rainfall and vegetation, would effectively have pulsed on a timescale correlated with the glacial cycles, so that species adapted to rainforest, or even just to woodland cover, would have contracted their ranges during glacial phases, adapted to new and drier conditions or gone extinct. Species adapted to arid habitats would have faced the same problems during the swing back to interglacials, as expanding forests frag-

mented the arid habitats, and contracted ranges in both cases would have led to population fragmentation.

The evolving African large-mammal fauna

Around 30 million years ago

Africa today has the greatest diversity of ungulates, particularly antelopes, and the greatest diversity of large carnivores found anywhere (Kingdon, 1997). Yet thirty million years ago there were no antelopes, horses, rhinos or pigs there. Although there were artiodactyls in the form of the pig- or hippo-like anthracotheres, the dominant medium-sized herbivores were hyraxes, animals that today reach only the size of a small rabbit (Fig. 1).

Their Afrotherian contemporaries, the proboscideans, looked little like living elephants, although they were fairly large and had the typical pillar-like limbs. Another afrothere, the large *Arsinoitherium zitteli* (Fig. 2), best known from deposits at Fayum in Egypt, may have looked rhinoceros-like with its odd, double horn, but its skeleton and inferred locomotion were more elephant-like and it probably had a

very different, perhaps partly aquatic lifestyle. The carnivores were a bizarre collection of animals most of which did not even belong to the order Carnivora but instead to the Creodonta. Of all the mammals, the Primates were perhaps most like their living descendants in general appearance, although they seem to have been members of now extinct families, with primitive apes of the family Proconsulidae known from around 27 Mya.

These animals lived in a tectonically stable continent without the eastern and southern areas of uplift, no Saharan desert and little of the present vegetational zonation. Indeed much of Africa may have been covered in lowland tropical-temperate rain forest interspersed with drier woodland and scrub (Cerling, 1992). But the rainforest was increasingly interrupted as the connection between Africa and Eurasia closed the Tethys Sea and reduced the availability of moisture. Eastern African volcanism and rifting after 30 Mya added uplift to the effect of continental movement as rain shadow reduced moisture in the high plateau

areas of eastern Africa. The planet was cooling and the massive Antarctic ice cap was forming.

Around 20 million years ago

Immigrants from Eurasia at this time included perissodactyls, but the only recognisable members of this order were the earliest rhinos (Fig. 3). The rest were chalicotheres, bizarre animals with horse-like heads and clawed feet - a later, Pliocene-age species is shown in Fig. 14. More artiodactyls also appeared, with the giraffoide climacoceratids as well as true giraffids (Morales *et al.*, 1999; Fig. 3 here) and first bovids (Morales *et al.*, 1995; Antón, 2003) as well as primitive pigs of the genus *Nguruwe* which are known from Namibia and Kenya at around 17.5 Mya.

Cercopithecoid monkeys of the extinct family Victoriapithecidae, best represented by remains of *Victoriapithecus* from Maboko Island in Kenya (Fig. 4), replaced earlier primates around that time. Primitive proconsulid apes continued, best known from specimens of *Proconsul africanus* from Rusinga Island in Kenya (Fig. 5),
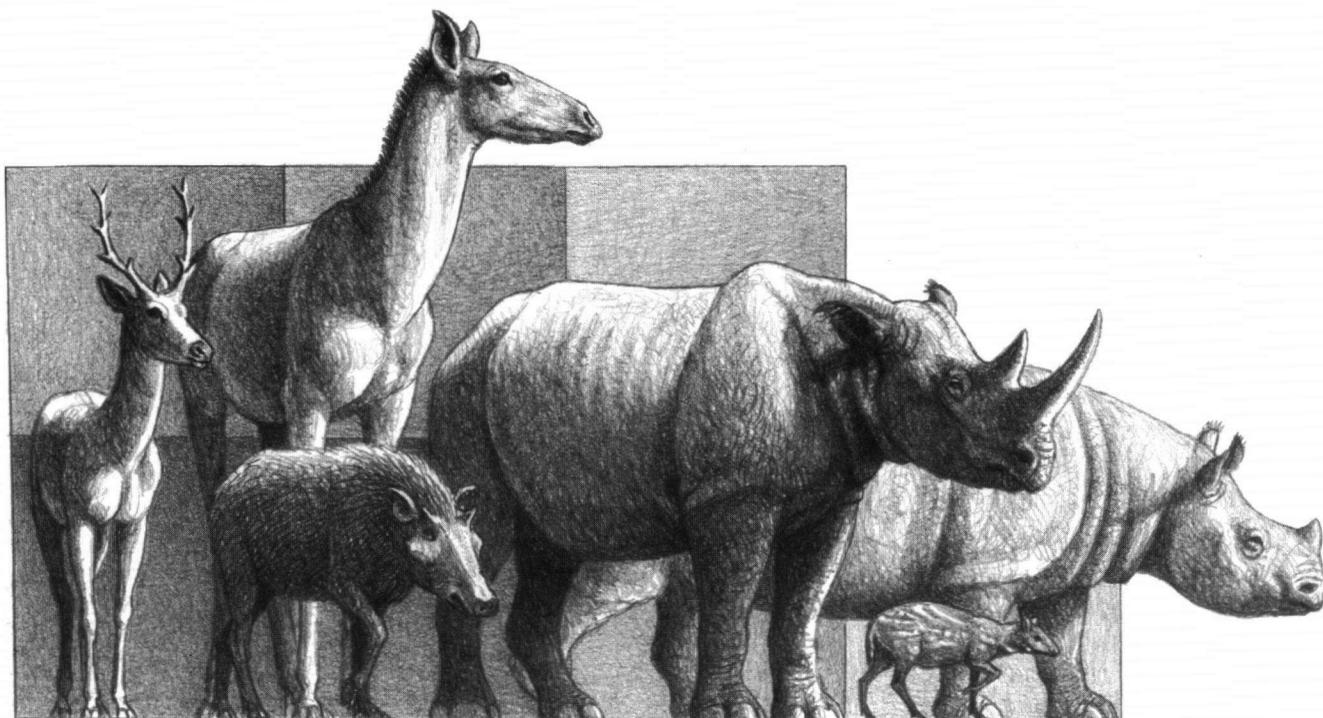

Fig 3 Some early Miocene ungulate species from Eastern Africa. From left to right: the climacoceratid *Climacoceras africanus*, the giraffid *Palaeotragus primaevus*, the suid *Kubanochoerus massai*, the rhino *Dicerorhinus leakeyi*, the chevrotain *Dorcatherium crassum* and the rhino *Brachypotherium heinzelini*. Each square measures 1 m on a side in this and subsequent group figures.

Enkele soorten vroeg-Miocene hoefdieren van Oost Afrika. Van links naar rechts: de climacoceratid *Climacoceras africanus*, de giraf *Palaeotragus primaevus*, het varken *Kubanochoerus massai*, de neushoorn *Dicerorhinus leakeyi*, het dwergmuskusdier *Dorcatherium crassum* en de neushoorn *Brachypotherium heinzelini*. Elk vierkant heeft een zijde van 1 m in deze en de volgende afbeeldingen van groepen.
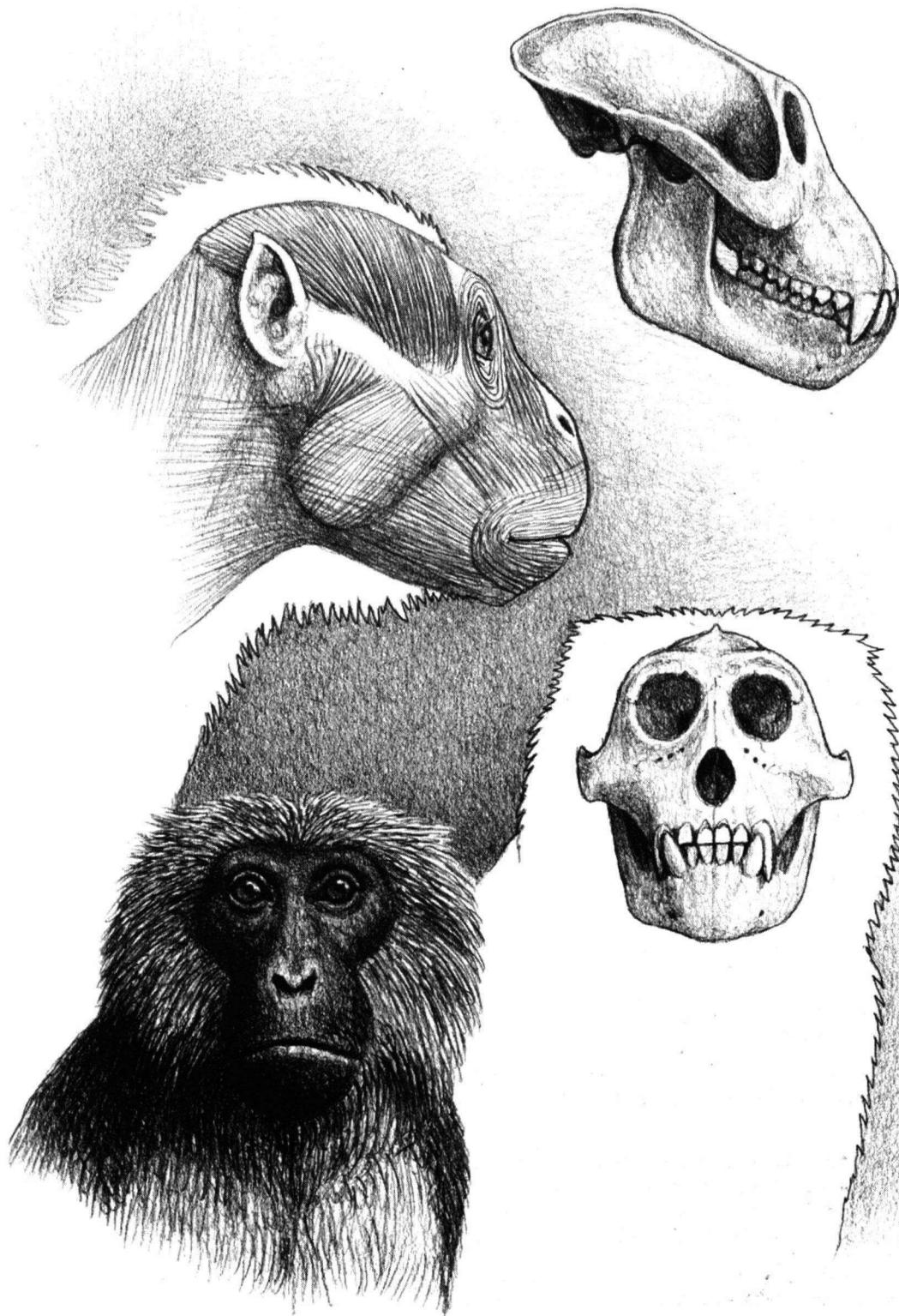
Fig 4 *Victoriapithecus* based on a well-preserved skull from Miocene deposits at Maboko Island, Kenya. Well developed nuchal and sagittal crests indicate very strong temporalis muscles, although in other respects the skull is typically cercopithecine-like, and the teeth suggest a mostly frugivorous diet. Total length of the skull about 12 cm.

Victoriapithecus, gebaseerd op een goed behouden gebleven schedel uit Miocene afzettingen op Maboko eiland, Kenia. Goed ontwikkelde nuchale en sagittale kammen wijzen op zeer krachtige temporalis kauwspieren, hoewel de schedel in andere opzichten typisch cercopithecine-achtig is, en de tanden een hoofdzakelijk uit fruit bestaand dieet doen vermoeden. Totale lengte van de schedel ongeveer 12 cm.
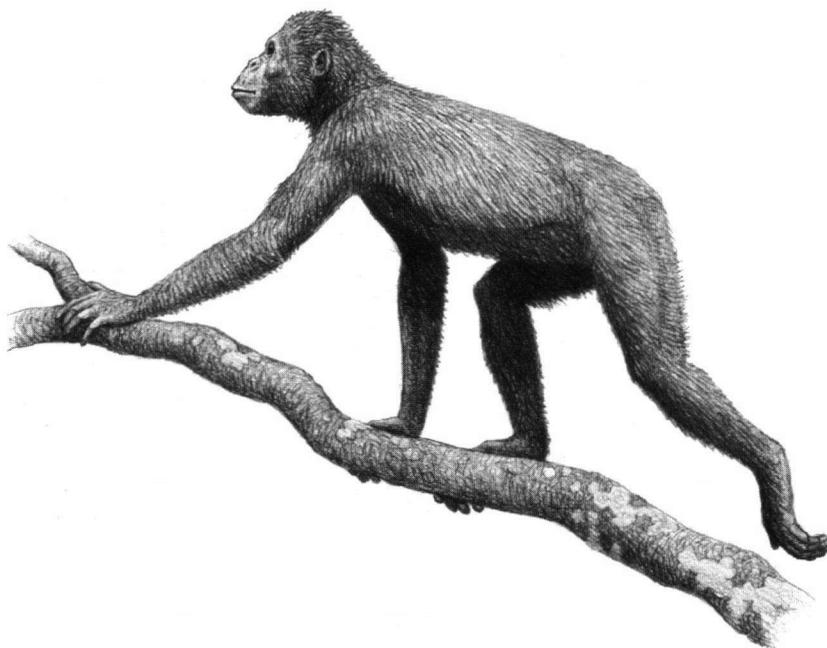
Fig 5 *Proconsul africanus*, based on cranial and postcranial remains from Rusinga Island in Kenya. The articulations of its limbs suggest locomotion resembling a macaque or even New World monkey more than an extant hominoid. Reconstructed shoulder height 45 cm.

Proconsul africanus, gebaseerd op schedel- en skeletresten van Rusinga eiland in Kenia. De gewrichten van zijn ledematen doen eerder een voortbeweging vermoeden lijkend op die van een makaak of zelfs van een aap uit de Nieuwe Wereld dan die van een huidige mensaap. Gereconstrueerde schouderhoogte 45 cm.
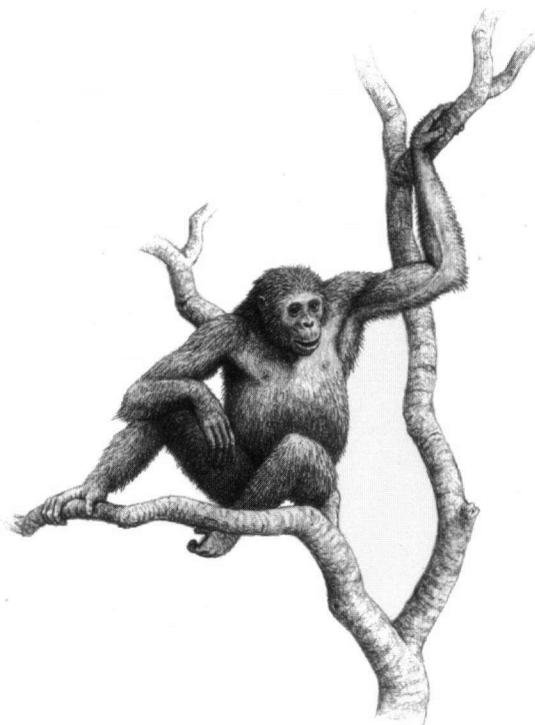

Fig 6 A life reconstruction of *Dryopithecus aietanus* based on material from Can Llobateres in Spain. This is a relatively primitive hominid, but shows incipient orangutan-like features, many of them being adaptations for an arboreal locomotion.

Een reconstructie van hoe *Dryopithecus aietanus* eruit gezien kan hebben, gebaseerd op materiaal van Can Llobateres in Spanje. Dit is een relatief primitieve mensachtige, maar toont al wel vroege orang-oetan-achtige kenmerken, voor een groot deel aanpassingen aan een voortbeweging in bomen.
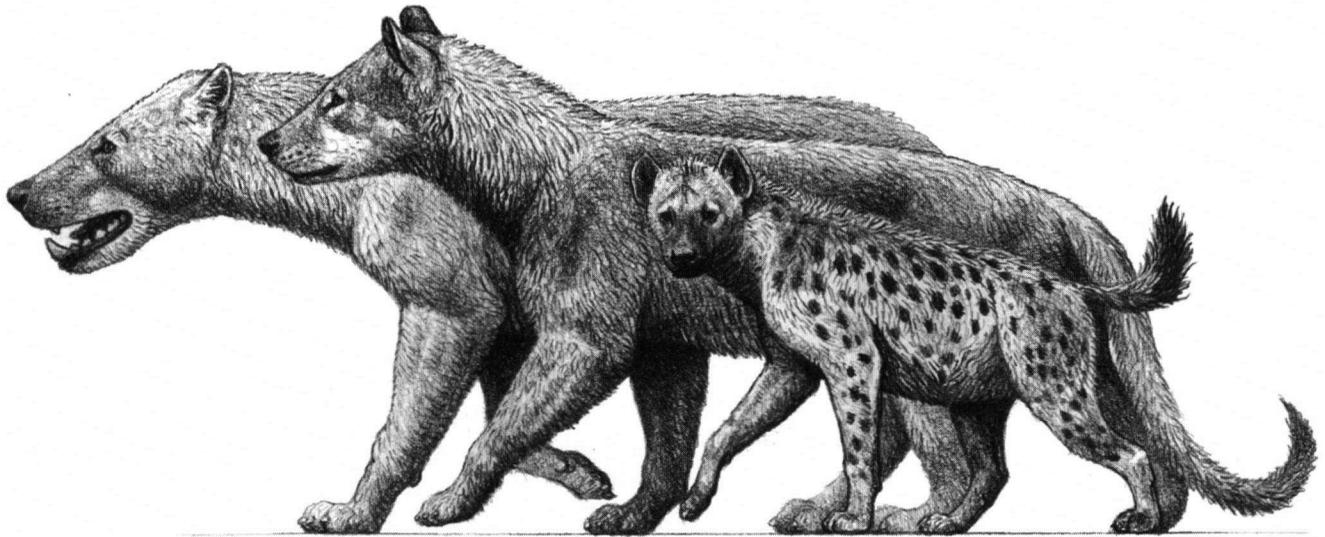
Fig 7 A life reconstruction of *Hyainailouros sulzeri* (left) compared with *Amphicyon giganteus* (centre) and a living spotted hyaena (*Crocuta crocuta*). Both it and *Amphicyon* would have dwarfed the hyaena, the largest living carnivore with a comparable combination of dental adaptations to eating meat and cracking bones. Reconstructed shoulder height of *Hyainailouros* 1.0 m.

Een reconstructie naar het leven van *Hyainailouros sulzeri* (links), vergeleken met *Amphicyon giganteus* (midden) en een nu levende gevlekte hyena (*Crocuta crocuta*). De eerste twee maken een dwerg van de hyena, de grootste nu levende vleeseter met een vergelijkbare combinatie van gebitsaanpassingen om vlees te eten en botten te kraken. Gereconstrueerde schouderhoogte van *Hyainailouros* 1,0 m.

and more advanced apes of the subfamily Dryopithecinae within the family Hominidae appeared.

The dryopithecine apes were quite diverse, with at least three tribes recognised. One, the Kenyapithecini, is known from Kenya, Turkey and southeastern Europe while another, the Dryopithecini, are only known from Europe. These distributions may indicate movement of the dryopithecines out of Africa. The tribe Dryopithecini have provided the best picture of the subfamily based on material from Can Llobateres in Spain (Fig. 6). The European distribution of the Dryopithecini raises an intriguing possibility for the later evolution of the Hominidae, including of course the subfamily Homininae, which encompasses ourselves and the living African great apes. The latter have no fossil history, and it is not clear what relationship if any they have with the various tribes within the Dryopithecinae although fossil apes are very scarce in Africa between around 15 Ma and the end of the Miocene (Andrews & Humphrey, 1999; Leakey & Harris, 2003). But the skeleton of the living African apes has some similarities to that of one species, *Dryopithecus fontani*, which could be taken to imply that the apparent African origins of humans and apes

owes itself to a later Miocene dispersion from Eurasia, as has indeed been suggested by Solounias *et al.* (1999).

Other emigrants from Africa around this time were the Proboscidea, whose subsequent history during the Miocene suggests a good deal of interchange with Eurasia.

True Carnivora entered the continent with the first appearance of cats, amphicyonid bear-dogs, mustelids and a group of so-called "false hyaenas", the Stenoplesictidae, that resembled the small, more primitive hyaenas of the later mid-Miocene (Antón, 2003; Morales, Pickford, Soria *et al.*, 1998). In north Africa at least, this immigration included the cat-like nimravids, but the creodonts continued as the dominant meat eaters (Morales, Pickford & Soria, 1998). The structure of the larger predator guild seems to have divided into flesh eaters among the early cats, nimravids and smaller creodonts, and bone-crunchers among the amphicyonids and larger creodonts, with the stenoplesictids perhaps falling somewhere in the middle. Some creodonts, like the widely distributed *Hyainailouros sulzeri*, were enormous animals, although large amphicyonids among the Carnivora rivalled them in size (Fig. 7), and the later, mid-Miocene diversity of the African
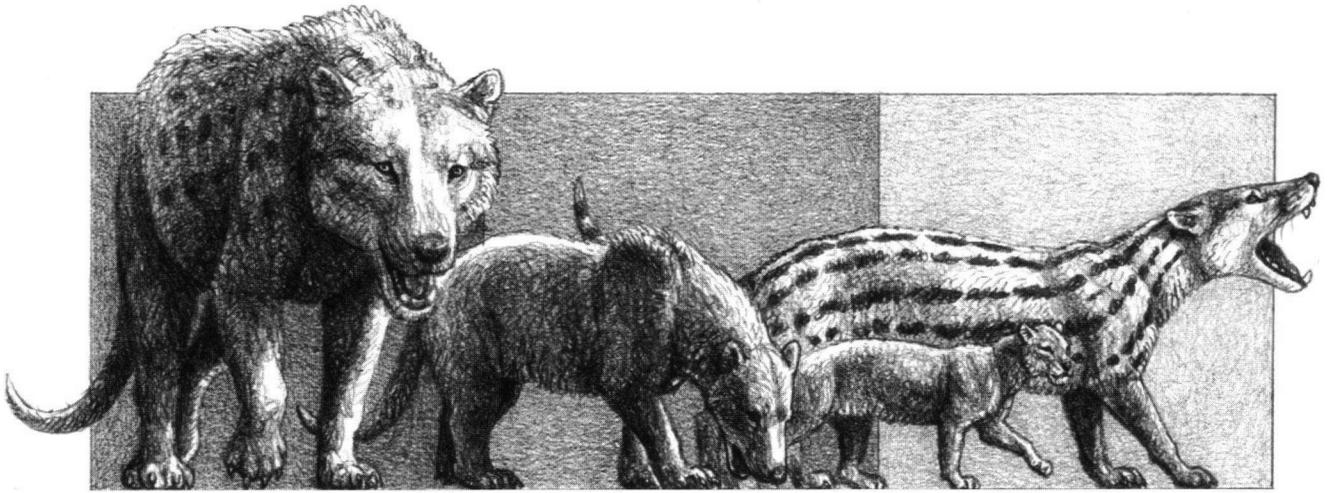
Fig 8 Representative species of Carnivora and hyaenodontid Creodonta from the early Miocene of East Africa. From left to right: the larger hyaenodontid *Hyainailouros sulzeri*, the amphicyonid bear-dog *Cynelos euryodon*, the felid *Afrosmilus africanus* and the smaller hyaenodontid *Hyainailouros napakensis*.

Representatieve soorten van Carnivora en de hyaenodontide (= met hyena-achtig gebit) Creodonta van het Vroeg Mioceen van Oost Afrika. Van links naar rechts: de grotere hyaenadontide *Hyainailouros sulzeri*, de beer-hond *Cynelos euryodon*, de kat *Afrosmilus africanus* en de kleinere hyaenodontide *Hyainailouros napakensis*.
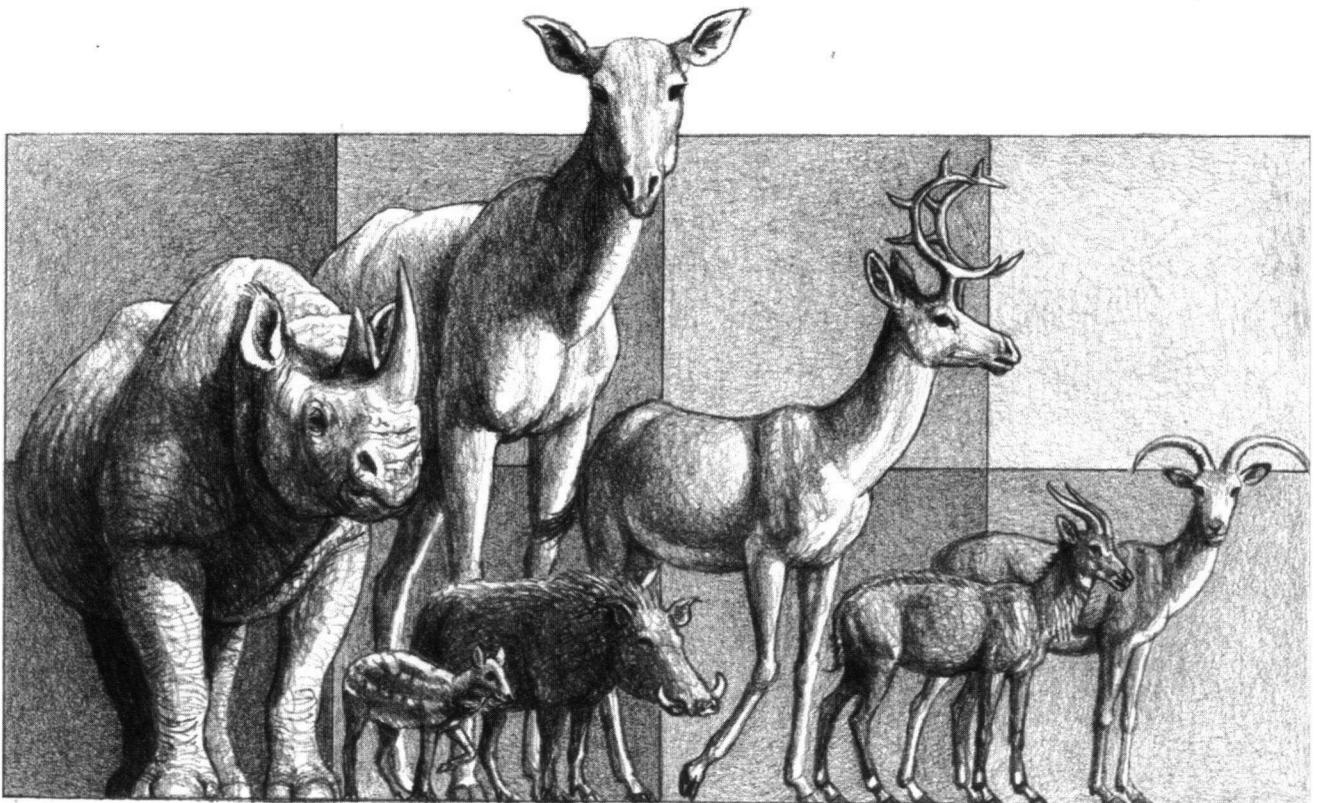

Fig 9 Some eastern African mid-Miocene ungulates. From left to right: the rhino *Paradiceros mukirii,* the chevrotain *Dorcatherium chappuisi*, the giraffid *Palaeotragus primaevus*, the pig *Listriodon akatikubas*, the deer-like ruminant *Climacoceras gentryi*, and the bovids *Kipsigicerus labidotus* and *Oioceros tanyceras*.

Enkele oost-Afrikaanse midden-Miocene hoefdieren. Van links naar rechts: de neushoorn *Paradiceros mukirii,* het dwergmuskusdier *Dorcatherium chappuisi*, de giraf *Palaeotragus primaevus*, het varken *Listriodon akatikubas*, de hertachtige herkauwer *Climacoceras gentryi*, en de runderen *Kipsigicerus labidotus* en *Oioceros tanyceras*.

creodonts was one of the most extensive undergone by the order. A number of east African early Miocene predators, including *H. sulzeri* and another, smaller bear-dog, are shown in Fig. 8.

The complex guild structure of the predators implies an equivalent complexity in the ecological relationships of predators and prey. Most of the ungulates do not look well adapted for speed, although the larger ones were perhaps difficult quarry. The predators do not look equipped to chase anything moving particularly fast - none of the cats or more cat-like members of other groups resembles a cheetah, for instance, so that a high-speed chase was clearly not possible. Given this, and given their success elsewhere, quite why the nimravids were unable to penetrate further into Africa remains something of a mystery. In the absence of dogs it is difficult to assess the extent to which pack hunting might have been possible, but dog-like animals such as the smaller hyaenas of the genera *Ictitherium, Hyaenictitherium, Lycyaena* and *Hyaenictis* only appear much

later in the late Miocene (Werdelin & Turner, 1996). Whether the larger amphicyonids would have operated co-operatively is unknown, but they would probably have taken a mixture of carrion and hunted meat. These observations are in keeping with interpretations of the earlier Miocene vegetation as generally more closed, circumstance in which neither pack hunting nor shorter, high-speed chases offer significant advantages.

Around 15 million years ago

By the middle part of the Miocene conditions in Africa had begun to change further. Drier and more seasonal weather patterns began to have a major effect as fragmentation of the forests continued. Grasslands began to appear as part of what was clearly a complex mosaic of vegetational types with woodland savannas on the interior plateau of southern Africa and grassed areas in the eastern parts of the continent (Cerling, 1992).

The fauna continued to evolve with fresh waves of immigrations. True hyaenas had appeared, although far removed in size, morphology or
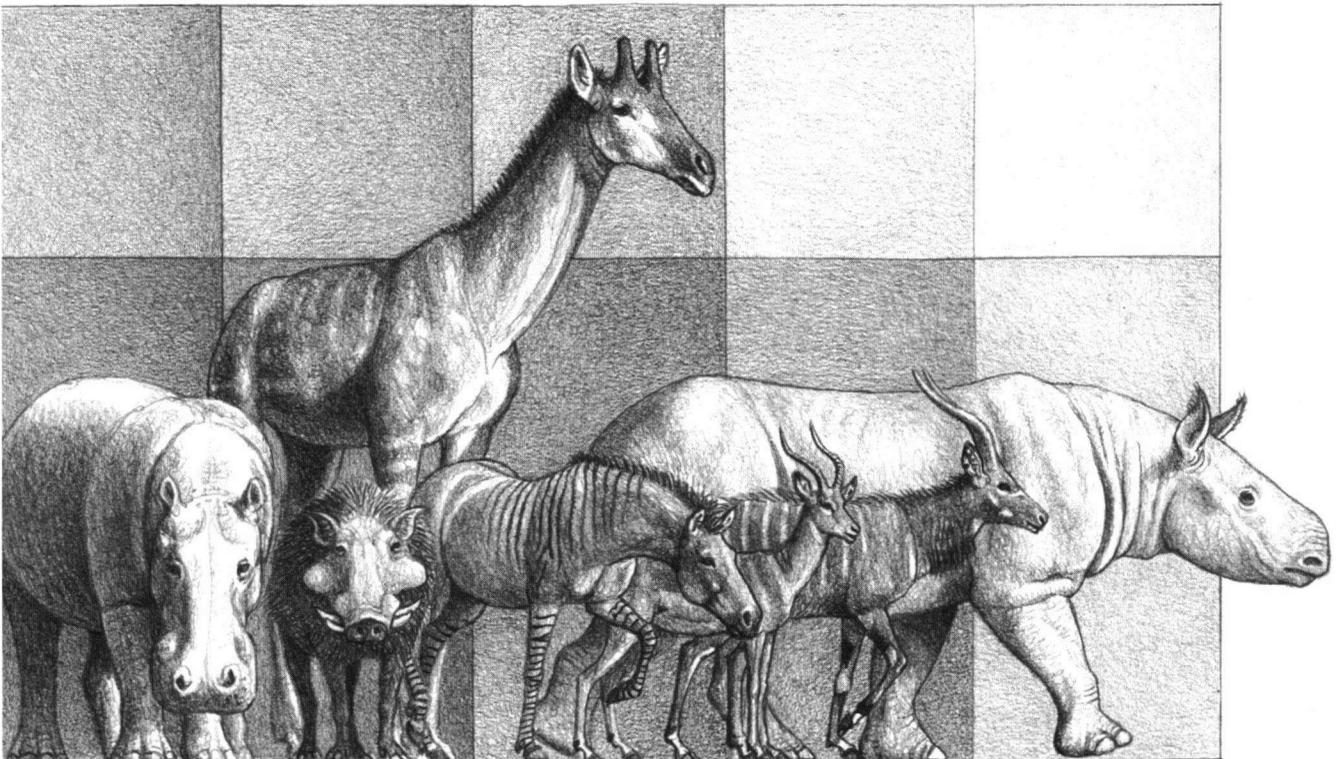

Fig 10 Some African Late Miocene ungulates. From left to right: the hippo *Hexaprotodon harvardii*, the pig *Nyanzachoerus syrticus*, the giraffid *Paleotragus germaini*, the equid *Eurygnathohippus turkanense*, the impala, *Aepyceros premelampus*, the antelope *Tragelaphus kyaloae*, and the rhino *Brachypotherium lewisi*.

Enkele Afrikaanse Laat-Miocene hoefdieren. Van links naar rechts: het nijlpaard *Hexaprotodon harvardii*, het varken *Nyanzachoerus syrticus*, de giraf *Paleotragus germaini*, het paard *Eurygnathohippus turkanense*, de impala, *Aepyceros premelampus*, de antilope *Tragelaphus kyaloae*, en de neushoorn *Brachypotherium lewisi*.
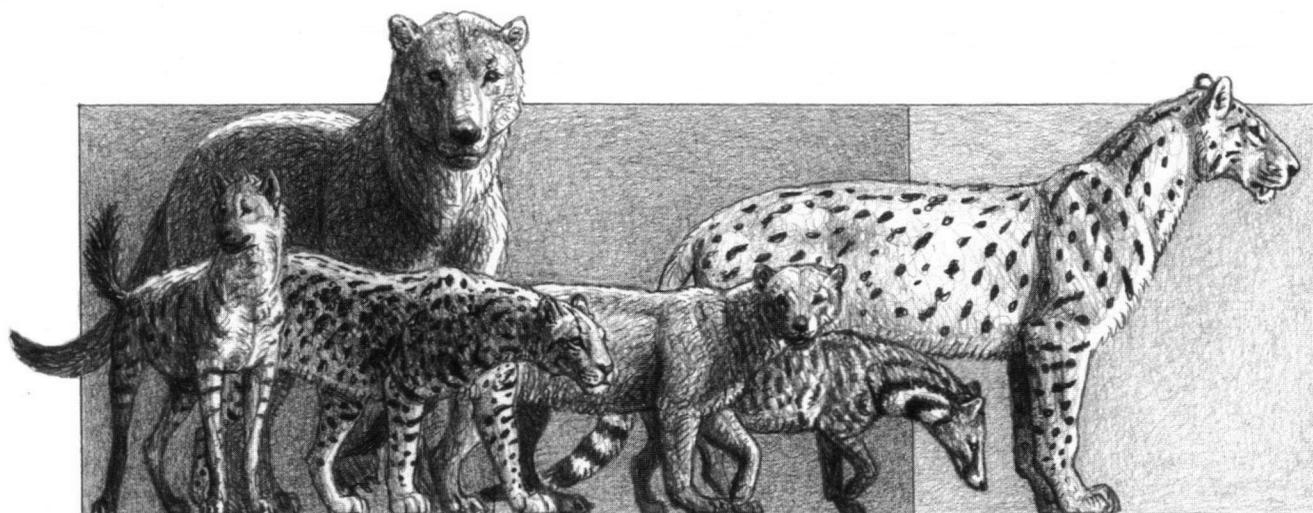
Fig 11 A selection of Late Miocene Carnivora from Eastern Africa. From left to right: the hyaena *Ictitherium ebu*, the bear-dog *Amphicyon* sp., the cat *Dinofelis* sp., the mustelid *Ekorus ekakeram*, the viverrid *Viverra leakeyi* and the sabretoothed felid *Lokotunjailurus emageritus*.

Een selectie van Laat-Miocene Carnivora van Oost Afrika. Van links naar rechts: de hyena *Ictitherium ebu*, de beer-hond *Amphicyon* sp., de kat *Dinofelis* sp., de marterachtige *Ekorus ekakeram*, de civetkat *Viverra leakeyi* en de sabeltandkat *Lokotunjailurus emageritus*.

function from those of today with the earliest civet-like (*Protictitherium*) and mongoose-like (*Proteles* lineage) species having the general appearance of insectivores or omnivores (Werdelin & Turner, 1996). These would have augmented the range of morphotypes previously represented by the stenoplesictids, although cursorial hunters were still absent. True elephants and hippos evolved and three-toed hipparionine horses invaded around 10 Mya. Many of the latter were well-adapted skeletally for running in open habitats and for grazing, with high-crowned teeth. The tetraconodont pigs of the genus *Nyanzachoerus* appeared, replacing earlier suid genera such as *Listriodon* and *Libyochoerus*. A selection of eastern African ungulates from around this period is shown in Fig. 9.

From this time onwards the artiodactyls, and above all the bovids, became a dominant feature of the larger mammal faunas, as new immigrants from Asia mixed with a smaller number of indigenous African forms to swell ungulate diversity (Vrba, 1985, 1995).

Around 8 million years ago

The end of the Miocene saw considerable further change in Africa. There was a global expansion in the biomass of C4 plants in tropics and subtropics at this time, measured directly from the isotopic composition of grazing herbivore dental enamel, and this trend continued

into the Pliocene of Africa with an increase in the proportion of savanna-mosaic herbivores (Cerling, 1992; Cerling *et al.*, 1997). The ancestral form of the white rhino occurs in late Miocene deposits, perhaps as a new immigrant from Arabia, and modern, long-necked giraffes too make their first appearance, perhaps as immigrants from Asia. Hippotragine, reduncine and tragelaphine antelopes rose to prominence from around 6.5 Mya, together with impalas, and perhaps somewhat later the alcelaphines. Solounias *et al* (1999) have suggested the origins of this incursion may lie in movements of what they term the Pikermi Biome, named after the late Miocene locality of Pikermi, and of course this dispersion into Africa may well have included the dryopithecine apes, which disappear in Eurasia towards the end of the Miocene, and thus the possible ancestors of the Homininae as mentioned above. Some typical ungulates of the period from eastern Africa are shown in Fig. 10.

It is during this period too that the more dog-like hyaenas, the genera *Ictitherium, Hyaenictitherium, Lycyaena* and *Hyaenictis* appear (Werdelin & Turner, 1996), together with the large felid genera *Dinofelis, Machairodus* and *Homotherium* (Turner, 1990). An odd felid, with something of a mixture of features seen in the latter two genera, has been referred to a new genus and species, *Lokotunjailurus emageritus* (Fig. 11), although so far it is only known from
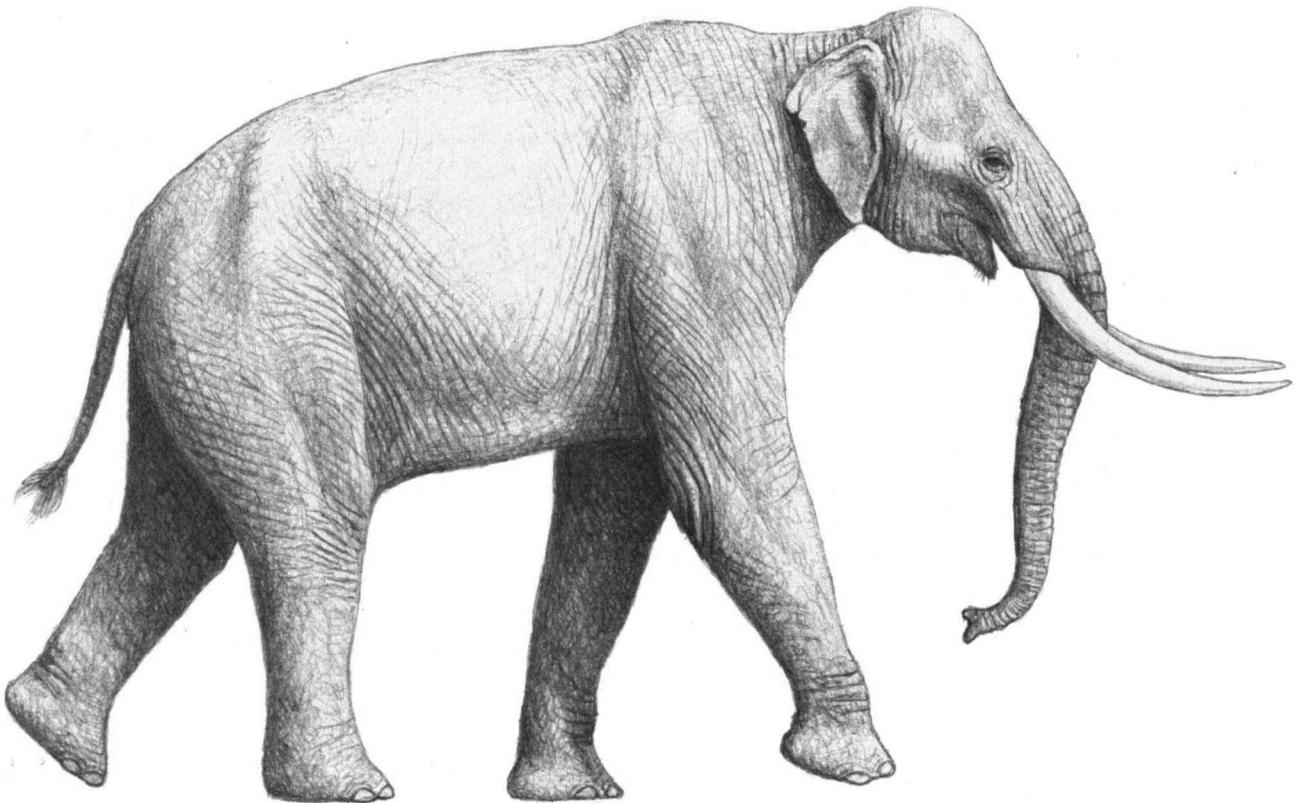
Fig 12 Life appearance of *Elephas recki*, based on a nearly complete skeleton found at Koobi Fora. The body proportions were unlike those of modern elephants, with a disproportionately small head and tusks, an inflated forehead and low-placed orbits, elongated forelimbs and a somewhat sloping back. Reconstructed shoulder height 4.5 m.

Zo zag *Elephas recki* eruit, gebaseerd op een vrijwel compleet skelet gevonden in Koobi Fora. De lichaamsverhoudingen waren anders dan die van moderne olifanten, met een naar verhouding klein hoofd en stoottanden, een bol voorhoofd en laaggeplaatste oogkassen, verlengde voorpoten en een ietwat aflopende rug. Gereconstrueerde schouderhoogte 4,5 m.

Lothagam in Kenya (Werdelin, 2003). Towards the very end of the Miocene dogs appear in Africa, although only in the form of small foxes. *Adcrocuta eximia,* the first of the large, bone crushing hyaenas, appears together with a late member of the stenoplesictid false hyaenas, the large *Percrocuta,* although both are only known from the Libyan site of Sahabi. The mustelids included *Ekorus ekakeram* from Lothagam in Kenya (Werdelin, 2003), which was big enough to deserve inclusion in the guild of larger species (Fig. 11). In all, a significant immigration from Eurasia is indicated, even if *Dinofelis* may have its origins in Africa, and truly cursorial predators had become established members of the large carnivore guild.

The effects of continued uplift operated in combination with further aridification as the Antarctic ice sheet grew, global sea level dropped and the Mediterranean became a land-locked sea that gradually evaporated. The Mediterranean eventually regained contact with the Atlantic, but the process of change in Africa was continued by the swing to even colder global conditions after 3.0 Mya. The Sahara became a desert, and by the period 2.5 - 2.0 Mya the effect on the African biota was marked. Vrba (1993) identified this late Pliocene event as a "faunal-turnover pulse", a significant evolutionary change across numerous lineages involving extinctions, speciations, dispersions and changes within lineages (Turner, 1995, 1999; Vrba, 1995, 1999). In the next section we turn our attention to the relationship between changes in ungulates and changes in predators, and go on from there to the question of evolution within our own tribe, the Homininae, which may be seen as part of this turnover.

Plio-Pleistocene faunal turnover

The Ungulates

Throughout the Pliocene the eastern African elephants show a trend towards high-crowned and folded teeth with extensive enamel cutting ridges, but the rate of this change increases markedly in the later Pliocene, especially after around 2.3 Mya. At that time the lineage represented by the now extinct *Elephas recki* (Fig. 12) became dominant, while the forerunners of the living African elephant genus, *Loxodonta*, declined (Beden, 1983).

This pattern of massive dental development is also seen in pigs, with several species undergoing increases in tooth size and crown height during the Pliocene and an increase in the rate of change at this time (Harris, 1983). There was also considerable turnover in the suid fauna of the later Pliocene in Africa between around 2.0 Mya and 1.6 Mya (Bishop, 1999), with members of the *Nyanzachoerus-Notochoerus* lineage, *Notochoerus euilus* and *N. scotti*, going extinct, the appearance of *Kolpochoerus majus*, the extinction of *Metridiochoerus andrewsi* and the appearance of *M. modestus*, *M. hopwoodi*, and *M. compactus*.

rily absent (Schaller, 1972, Estes, 1992). Some of the extinct species, especially those of the genus *Notochoerus*, were huge animals up to perhaps 450 kg in weight and therefore relatively immune to predation (Fig. 13), although the young may have been a valuable source of food for any open country predator. Large piglets of larger species would have represented a good return on energy expended in capture, and a turnover in the suid component of the ungulate fauna that removed larger pigs from the fauna would have had important consequences for predators (Turner & Antón, 1999), as we discuss further below.

Horses of the living genus *Equus* first appear in Africa around 2.3 Mya, following a dispersion across Eurasia from the Americas, with high crowned teeth well-equipped for consumption of abrasive fodder (Eisenmann, 1983). The equids of the hipparionine group co-existed with the newcomers for some time (Bernor & Armour-Chelu, 1999), their pattern of dental development matching that of the pigs and elephants during this period. At the same time, the white rhinoceros, *Ceratotherium simum*, exhibited changes in the structure of the skull (Harris, 1983), which became longer and
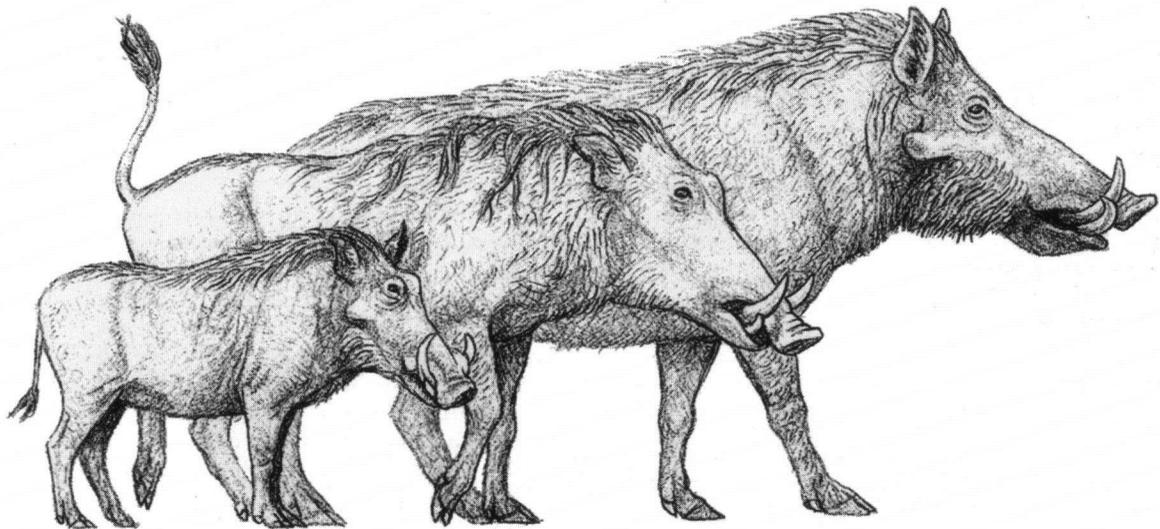

Fig 13 The extant warthog, *Phacochoerus aethiopicus*, in comparison with the extinct *Metridiochoerus andrewsi* and *Notochoerus eulius*.

Het huidige wrattenzwijn, *Phacochoerus aethiopicus*, in vergelijking met de uitgestorven *Metridiochoerus andrewsi* en *Notochoerus eulius*.

The pigs, a major element of the Plio-Pleistocene fauna of Africa, are likely to have been particularly important as prey. Today warthogs figure largely in the diet of lions, especially in areas where other prey are scarce or tempora-

enabled the species to graze on shorter grasses more easily, features duplicated to some extent among hipparionine horses of the genus *Eurygnathohippus*.
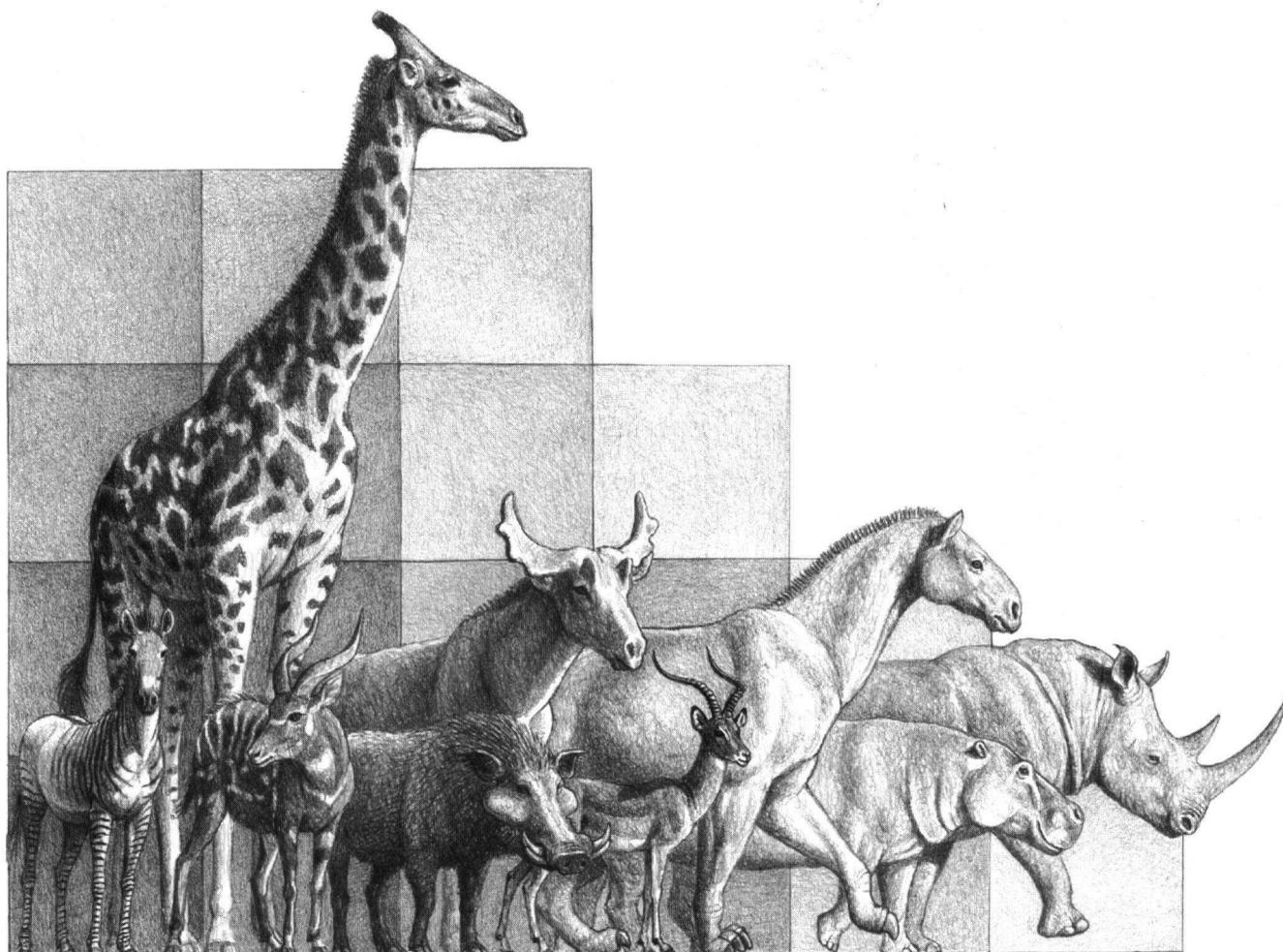
Fig 14 A selection of ungulates from the Pliocene of eastern Africa. From left to right: the hipparion *Hipparion cornelianum*, the giraffe *Giraffa jumae*, the bovid *Tragelaphus nakuae*, the pig *Kolpochoerus limnetes*, the giraffid *Sivatherium maurisium*, the bovid *Aepyceros melampus*, the chalicothere *Ancylotherium hennigi*, the hippo *Hexaprotodon aethiopicus* and the rhino *Ceratotherium praecox*.

Een selectie van hoefdieren uit het Plioceen van Oost Afrika. Van links naar rechts: het drie-tenige paard *Hipparion cornelianum*, de giraf *Giraffa jumae*, de koedoe *Tragelaphus nakuae*, het varken *Kolpochoerus limnetes*, de giraf-achtige *Sivatherium maurisium*, de impala *Aepyceros melampus*, de chalicothere *Ancylotherium hennigi*, het nijlpaard *Hexaprotodon aethiopicus* en de neushoorn *Ceratotherium praecox*.

Bovids, the most diverse of the African larger mammals are likely to have been the most important prey species for all the larger predators. A major change in the bovid fauna has been identified by Vrba (1985, 1995) between 3.0 and 2.0 Mya, involving speciation events, immigrations of antilopine and caprine taxa and extinctions. As conditions cooled, new taxa appeared and began to show adaptations to more open conditions, producing a predominance of more open country, larger bovids especially among the Alcelaphini and Hippotragini. These may have been faster or more efficient in their locomotion, changes perhaps linked to increases in foraging range or to predator avoidance in more open country. These changes in the structure of the bovid fauna are matched by changes in the dentition in later species of lineages, such as a shift in emphasis to molars at the expense of premolars in alcelaphines like *Connochaetes*, the wildebeest. Such changes often involve loss of the lower second premolar and reduction of the third premolar to a peg-like structure, an emphasis on the molar toothrow that seems to indicate increasing adaptation towards coping with the food available in more open grasslands (Vrba, 1984; Harris, 1991).

Analyses of postcranial characters suggest that some locomotory changes took place slightly later (Plummer & Bishop, 1994), but investigations of bovid feeding mechanisms tend to
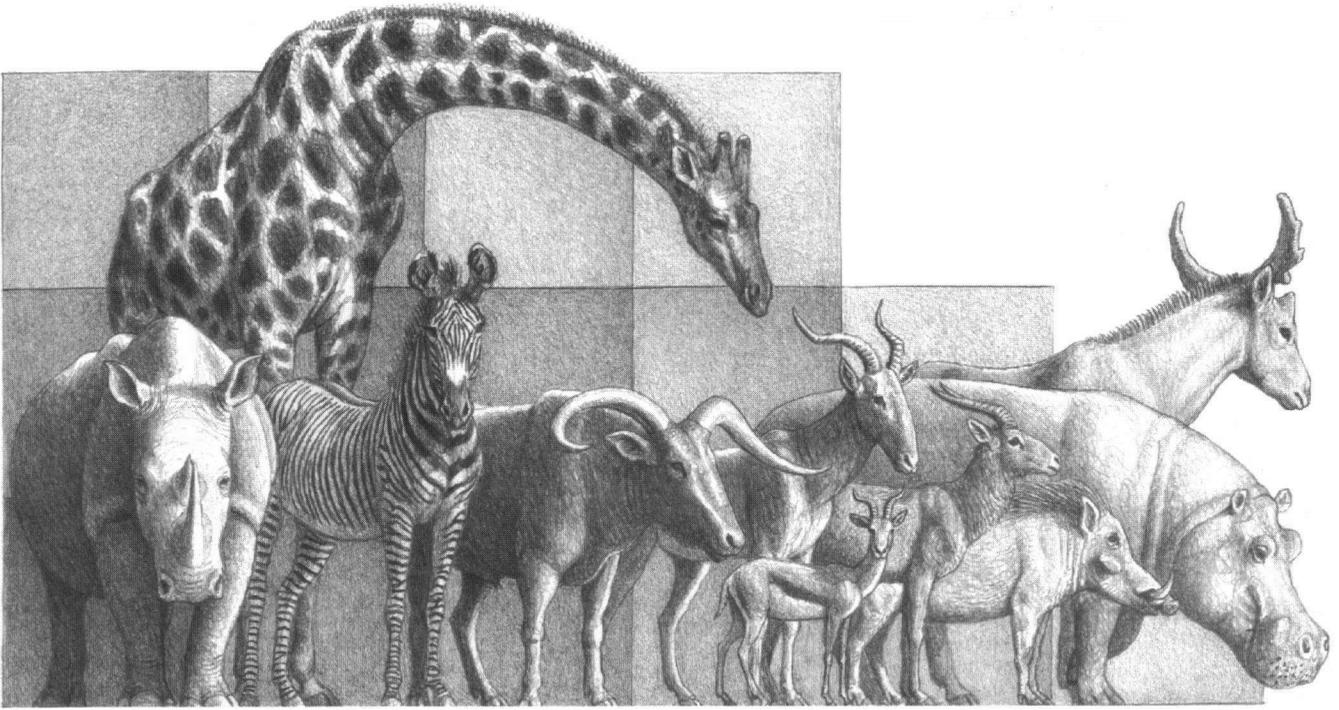
Fig 15 A selection of ungulates from the Pleistocene of Eastern Africa. From left to right: the rhino *Ceratotherium simum*, the giraffe *Giraffa camelopardalis*, the horse *Equus koobiforensis*, the bovids *Pelorovis olduvaiensis*, *Megalotragus issaci*, *Antidorcas recki*, and *Menelikia lyrocera*, the pig *Metridiochoerus andrewsi*, the hippo *Hippopotamus gorgops* and the giraffid *Sivatherium maurisium*.

Een selectie van hoefdieren uit het Pleistoceen van Oost Afrika. Van links naar rechts: de neushoorn *Ceratotherium simum*, de giraf *Giraffa camelopardalis*, het paard *Equus koobiforensis*, de rundachtigen *Pelorovis olduvaiensis*, *Megalotragus issaci*, *Antidorcas recki*, and *Menelikia lyrocera*, het varken *Metridiochoerus andrewsi*, het nijlpaard *Hippopotamus gorgops* en de giraf-achtige *Sivatherium maurisium*.

support arguments for environmentally induced turnover in the period prior to 2.0 Mya, and the weight of the evidence across so many groups reinforces the point (Turner, 1995, 1999). Further changes occurred in the Bovidae after 2.0 Mya, with immigrations of yet more open country species of Ovibovini and Caprini seen in various horizons at West Turkana and in Shungura Member H (Vrba, 1995). Such changes in the structure of the bovid guild, like those among the pigs, would have directly affected members of the large carnivore guild.

An overview of some of the Pliocene ungulates of eastern Africa is shown in Fig. 14, while those of Pleistocene age are shown in Fig. 15.

The Carnivores

The African large predator guild has changed markedly from 5 Mya (Turner, 1990; Turner & Antón, 1999; Werdelin & Turner, 1996). At its beginning there were no living species of cats, dogs or hyaenas, and the hunting and scavenging roles were occupied by sabre-toothed cats, medium-sized hunting hyaenas, smaller hyaenas with moderate bone destroying abilities and the large *Adcrocuta eximia* and false hyaena *Percrocuta*, although these are only known from northern Africa. By around 3.5 Mya *Adcrocuta* and *Percrocuta* had disappeared, but most of the living species were then also present in a rich carnivore fauna almost twice the size of today. For the next two million years modern elements coexisted with some of the more archaic elements such as the machairodont cats of the genera *Homotherium*, *Megantereon* and *Dinofelis*, as well as the so-called hunting hyaenas of the genus *Chasmaporthetes* and the giant hyaena *Pachycrocuta*, a species well known in Eurasia. A range of typical predators from the larger carnivore guild of the latter part of the Pliocene is shown here in Fig. 16.

As an interesting aside we may mention here in passing the recent suggestion by Hemmer *et al* (2004) that late Pliocene material from Sterkfontein and perhaps Laetoli, previously placed by us in *Panthera* (Turner, 1990) should more properly be referred to *Puma* along with a

variety of European specimens, following a revision of the fossil evidence for the genus in Eurasian and African deposits. However, we note that only the material from the French locality of St Vallier provides sufficiently complete material for clear referral, and that many of the other identifications have essentially been made by default, rather than by posi-

tive matching with known characters of *Puma*. We therefore do not consider that *Puma* can be identified as a member of the African Carnivora.

The next major event was the extinction of the machairodont cats and of the remaining archaic hyaenas such as *Chasmaporthetes* and
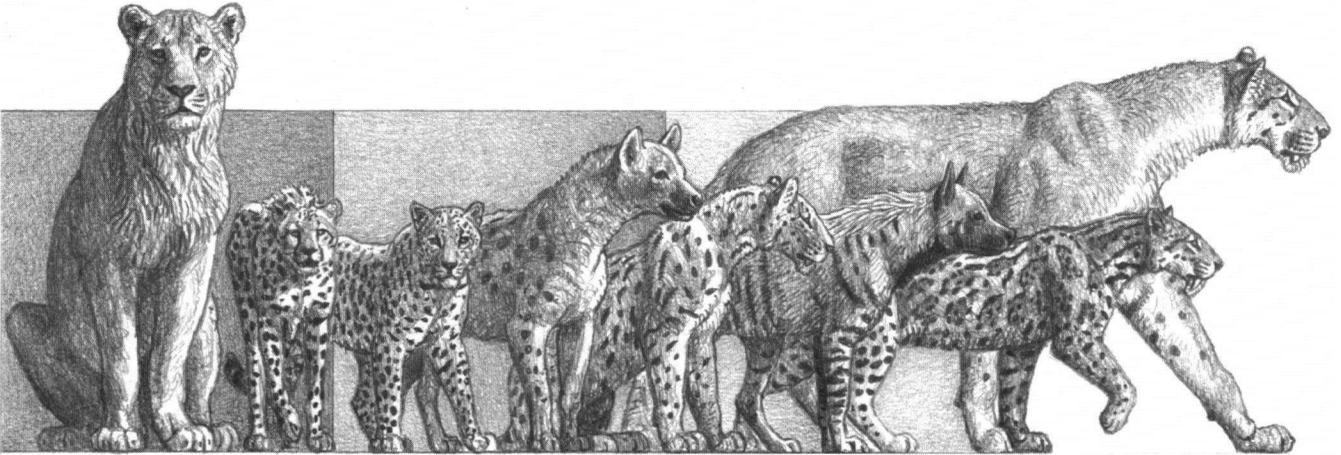

Fig 16 A selection of carnivores, living and extinct, from the Pliocene of East Africa. From left to right: lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*), the false sabretoothed cat *Dinofelis* sp., striped hyaena (*Hyaena hyaena*), the dirk-toothed cat *Megantereon cultridens* and the sabretoothed *Homotherium latidens*.

Een selectie van roofdieren, nu levende en uitgestorven, uit het Plioceen van Oost Afrika. Van links naar rechts: leeuw (*Panthera leo*), jachtluipaard (*Acinonyx jubatus*), luipaard (*Panthera pardus*), gevlekte hyena (*Crocuta crocuta*), de valse sabeltandkat *Dinofelis* sp., gestreepte hyena (*Hyaena hyaena*), de kleine sabeltandkat *Megantereon cultridens* en de sabeltandkat *Homotherium latidens*.
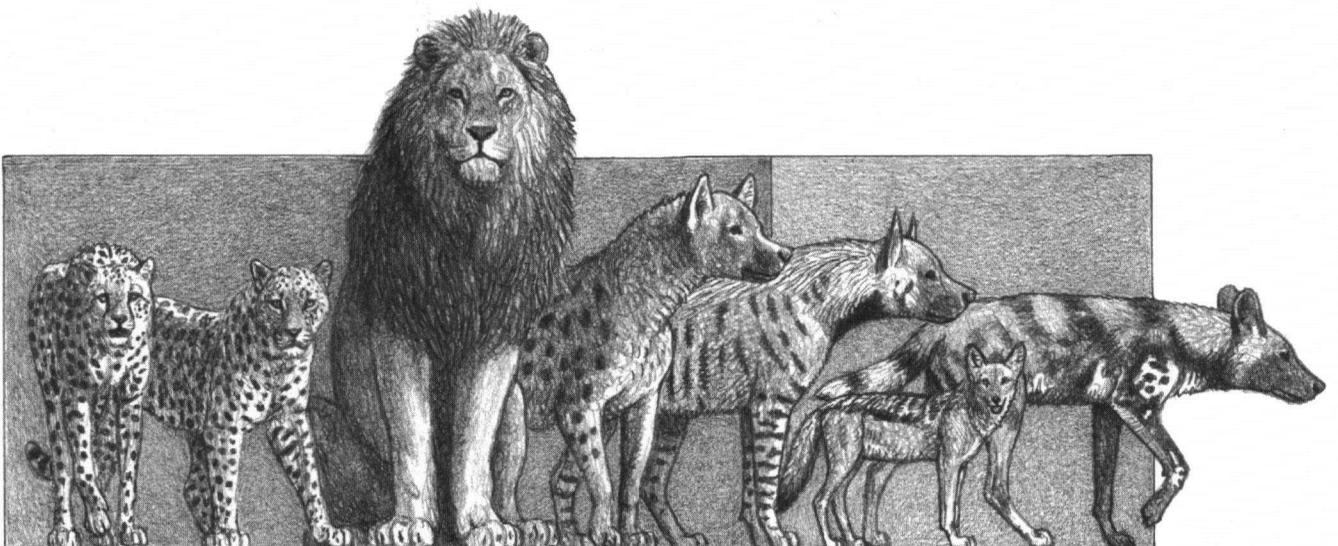
Fig 17 A selection of African Pleistocene carnivores. These animals, which form the living guild of larger predators, are from left to right: cheetah, leopard, lion, spotted hyaena, striped hyaena, black-backed jackal (*Canis mesomelas*) and African hunting dog (*Lycaon pictus*).

Een selectie van Afrikaanse Pleistocene roofdieren. Deze dieren, die de nu levende gilde van grotere roofdieren vormen, zijn van links naar rechts: jachtluipaard, luipaard, leeuw, gevlekte hyena, gestreepte hyena, zadeljakhals (*Canis mesomelas*) en de hyenahond (*Lycaon pictus*).

Pachycrocuta by around 1.5 Mya. This change left the structure and content of the large predator guild in its modern form (Fig. 17), with clear implications for change in predator-prey interactions (Turner & Anton, 1999). In this view we would of course differ quite radically from the interpretation of Pliocene and Pleistocene species deployment in the Carnivora proposed by Werdelin & Lewis (2005), who believe that many of the extant taxa had a much more recent origin on the continent.

Extinction of the machairodonts has long fascinated observers, and the African evidence may shed some light on this. Larger living cats use a killing bite at the neck or clamp the muzzle to induce suffocation despite any struggle. But both *Dinofelis* and *Megantereon* had a strong body with a short back, large claws and - especially in the case of *Megantereon* and *Dinofelis piveteaui* – long but fragile canine teeth. They were built for capturing using a short rush and considerable strength to bring down and hold their prey before killing by some form of slashing bite. Any attempt to clamp the muzzle would have risked biting into bone, and only with prey held essentially still could they have slashed or bitten into the neck to induce blood loss and shock or suffocation without risking damage to the canines as a result of striking bone or through torsion (Turner & Antón, 1997).

Homotherium also had elongated, flattened and potentially breakable upper canines as well as a strong back, although it differed from the other machairodonts in having more slender limbs (Antón & Galobart, 1999, Antón *et al.*, 2005). The front limb was elongated and the claws relatively small, suggesting a more cursorial and perhaps social predator operating in more open terrain and needing larger group size to deter scavengers. But none of these cats could have killed like a lion or a leopard without risking damaging its teeth, and the most probable habitat for *Megantereon* and *Dinofelis* would have been more closed vegetation, permitting a close stalk of a carefully selected prey followed by a short dash from cover and firm seizure. For *Homotherium*, group action in more open areas of vegetation would have achieved the same end, with the prey subdued by weight of numbers.

Megantereon and *Dinofelis* would therefore have been badly affected by reductions in vegetational cover and change in size and anti-predator response of prey species, especially by changes among the bovids and pigs and perhaps also by increasingly frequent encounters in more open terrain with large competitors such as *Homotherium*, lions and hyaena clans. *Homotherium* is likely to have been badly affected by reductions in resident prey biomass in successive years of increased dry-season drought and by increased clashes with open-terrain predators. But it took the combined effects of changes in climate, vegetation and prey composition and structure to drive the machairodonts extinct in Africa (Turner & Antón, 1999), and even then they managed to continue to exist on other continents – in the Americas to within the past 20,000 years (Kurtén & Anderson, 1980). Theirs was no evolutionary short-term success story for a set of what have often been characterised as bizarrely adapted animals. They are extinct, but so are most things that have ever lived.

Human evolution in Africa

Earliest stages in human evolution

Our African ancestors and relatives changed from generalised apes to more sophisticated tool-using apes between perhaps 7 and 2.5 Mya (Andrews, 1996), and only became really recognisably human at around 1.8 Mya with the earliest representative there of *Homo erectus*, known by some authors as *Homo ergaster* (Wood, 1992). This transition included shifts to an upright stance and bipedal walking, best seen in the 1.5 Mya-old youth from West Turkana (Fig. 18), and an increase in relative and absolute brain size, suggesting that physical manifestations of change were accompanied by alterations in behaviour, social interactions and intelligence. However, the extent to which these latter changes in non-physical attributes paralleled any given physical change in locomotion or brain size remains unknown.

Traditional interpretations of this larger evolutionary pattern of ape-like to human-like primate emphasise the adaptive necessity for an increasingly terrestrial lifestyle that included the eating of meat, and the archaeological record appears to support this view. According to interpretations of material referred to *Ardipithecus ramidus*, this attachment to the woodland habitat persisted until close to 4.0 Mya (WoldeGabriel *et al.*, 1994). The develop-
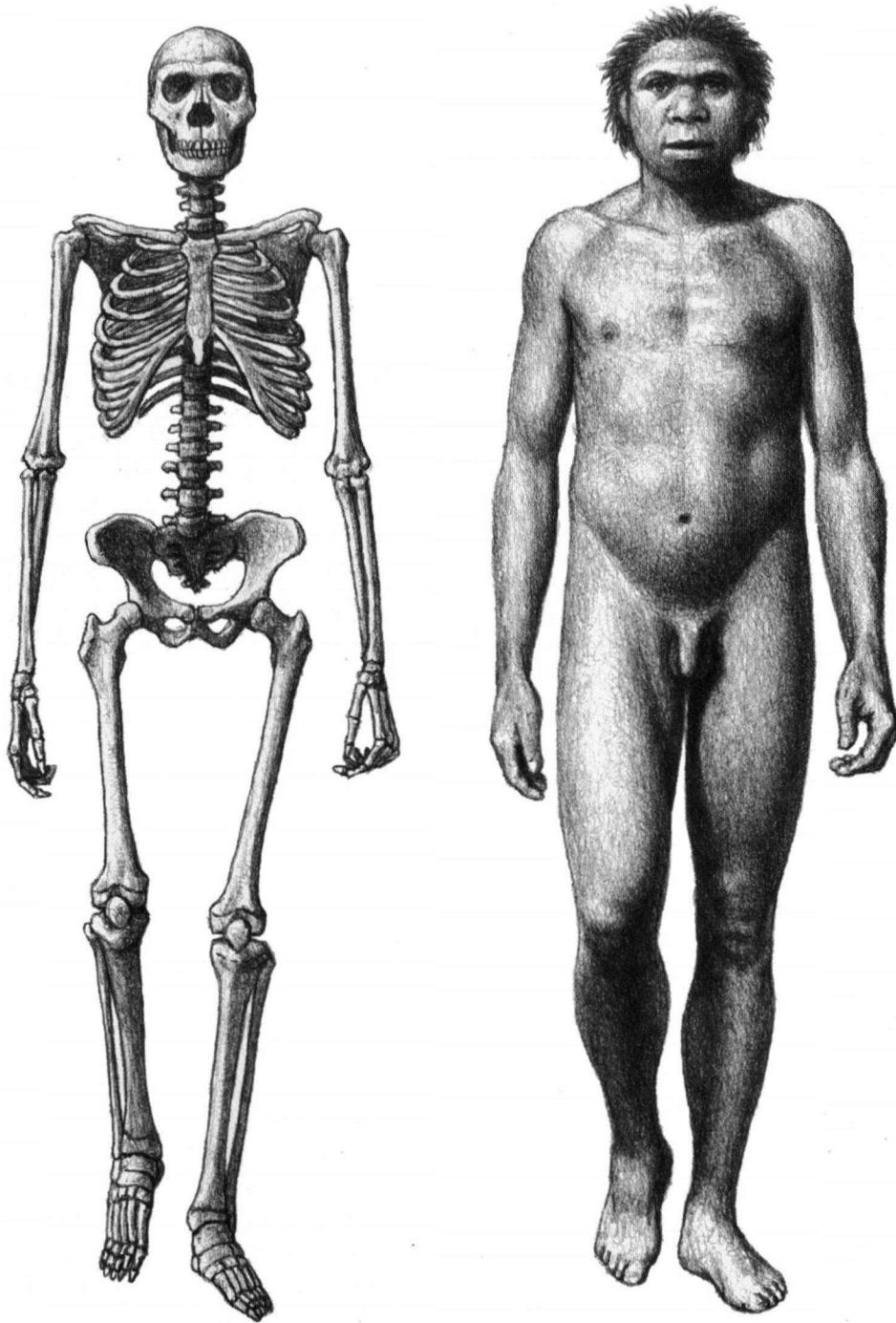
Fig 18 Skeleton and a life reconstruction of the *Homo erectus* youth from Nariokotome, West Turkana. He had relatively long legs and short arms, as in modern humans, and it was originally proposed that the pelvis was narrow, as in modern humans also (Walker & Leakey, 1993). But the bone is damaged, and interpretation open to question. Later discovery of a complete pre-Neanderthal pelvis from Atapuerca in northern Spain (Arsuaga *et al.*, 1999) suggests wide illia were probably the general condition among early hominins, and it seems likely that a narrow pelvis only appeared with *Homo sapiens*. Reconstructed height 1.6 m.

Skelet en reconstructie van de jeugdige *Homo erectus* van Nariokotome, West Turkana. Hij had relatief lange benen en korte armen, zoals in moderne mensen, en aanvankelijk werd verondersteld dat het bekken smal was, eveneens zoals in moderne mensen (Walker & Leakey, 1993). Maar het bot is beschadigd, en de interpretatie staat ter discussie. De latere ontdekking van een compleet pre-Neanderthal bekken van Atapuerca in Noord Spanje (Arsuaga *et al.*, 1999) doet vermoeden dat brede heupbeenderen waarschijnlijk de algemene toestand was onder vroege mensachtigen, en het lijkt waarschijnlijk dat het smalle bekken pas verscheen met *Homo sapiens*. Gereconstrueerde hoogte 1,6 m.

ment of a stone tool technology can now be traced back in Africa to close to 2.6 Mya at Gona and Bouri in Ethiopia, while bones of large mammals at the latter have damage marks suggesting the use of such tools (Semaw, 2000). What happens in the intervening period either to assist or to motivate the move to more open terrain is however unclear, although it is always possible to suggest some increasing use of technology involving organic materials. Conventionally, the oldest members of our genus and contemporaries of these earliest stone tools are the species *Homo habilis* and *H. rudolfensis* (Wood, 1992), although Wood & Collard (1999) have argued that these should be removed from the genus *Homo* and perhaps placed in the more primitive *Australopithecus*. If so, then logically the earliest stone tools were either made by members of some other genus or another, as yet unknown species of our own genus.

What is clear about the fossil and archaeological evidence is that it cannot be interpreted to show a simple, linear sequence of development in either hominin anatomy or technology that takes us from ape-like to human-like by way of the various forms seen in the fossils. Indeed it becomes evident that a variety of evolutionary solutions were developing among the Pliocene hominins, and this variety may well extend back into the Miocene if the fragmentary material referred to *Orrorin tugenensis* (Senut *et al.*, 2001) and *Sahelanthropus tchadensis* (Brunet *et al.*, 2002) bears continued scrutiny as hominin. The course of our own lineage seems to have involved an evolution towards greater ecological generalisation coupled to an emphasis on stone tool technology and an increase in brain size. At the same time the robust australopithecines of the genus *Paranthropus* appear to have followed a path towards larger jaws and teeth, presumably coping with food acquisition and processing by means of such an anatomical development, what Tobias (1991) termed a 'hypermasticatory trend'. At least one hominin species traditionally placed in the genus *Homo*, the east African *Homo rudolfensis* (Fig. 19), seems to have followed something of the same path as the paranthropines in the time range between 2.5 and 1.8 Mya with its own enlarged teeth, and even if it is now removed from *Homo* we cannot escape the fact that it does have a relatively large brain as well (Wood & Collard, 1992). If *H. rudolfensis* is linked to the earlier *Kenyanthropus platyops* and placed in that genus, as Leakey *et*

al. (2001) have suggested, then we may very well have evidence of a separate lineage within which brains and teeth both developed.

We may therefore identify at least three different evolutionary developments within Pliocene hominins, but the most interesting point about them is that all may be seen as responses to a similar problem, the one of dealing with changing climate and habitats faced by the other members of the mammalian fauna. The only lineage to survive ultimately was that of our own genus, *Homo*, but the various species of *Paranthropus* had a very reasonable measure of success too before ultimately becoming extinct by around 1.0 Mya in both southern and eastern regions; perhaps they also managed some form of tool-making to augment their physical abilities.

Earliest human dispersions from Africa

The earliest well-established hominin species appear to have been more restricted in their distributions within Africa, with *Ardipithecus ramidus, Australopithecus afarensis, A. africanus,* species of the robust genus *Paranthropus* and *H. rudolfensis* being variously recorded only from eastern and southern parts of the continent (Turner & Wood, 1993). It is easy to read too much into the face-value distribution of what are after all relatively scarce fossils, but there are good reasons for expecting new sexually reproducing species to originate in a restricted area, one with a preferred habitat to which the specific-mate recognition system is closely adapted (Turner & Paterson, 1991). Any greater range for a species must then be achieved by a process of dispersion, but the species with the more general repertoire of adaptations may be in the best position to disperse most rapidly and most successfully. Use of a stone tool technology may be argued to be one of the ways in which some of the hominins, including members of our own lineage, began to extend the range of their adaptive repertoire towards the end of the Pliocene. In the absence of such technology, earlier hominin species would have been more constrained in their range of options for dispersion.

The timing of earliest human emergence from Africa remains the subject of intense debate (Turner, 1999; Dennell, 2003). The best attested and most widely accepted evidence for early appearance outside Africa remains that from Dmanisi in Georgia dated to between 1.8 and 1.6 Mya and 'Ubeidiya in Israel dated to around
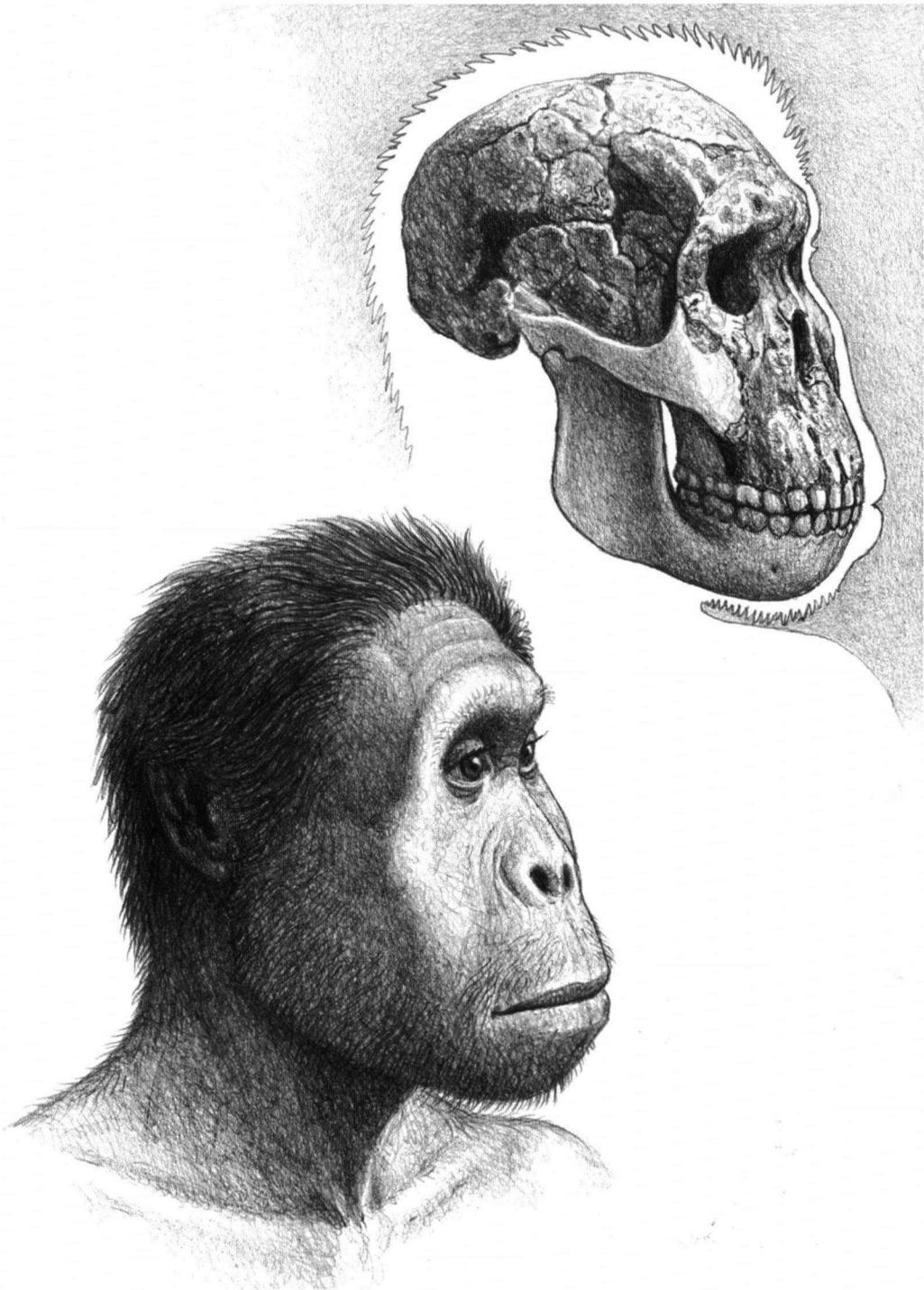
Fig 19 Life reconstruction of the head of *Homo rudolfensis* based on cranium KNM ER1470 from eastern Lake Turkana. It has a primitive look, but its brain is large, its face long and flattened and the crests for muscular insertions rather faint.

Reconstructie van het hoofd van *Homo rudolfensis*, gebaseerd op schedel KNM ER1470 van het oostelijke Turkana meer. Hij had een primitief aanzien, maar zijn hersenen zijn groot, zijn gezicht is lang en plat en de kammen voor spieraanhechtingen tamelijk zwak ontwikkeld.

1.4 Mya. The human remains from 'Ubeidiya are meagre, but are reinforced by the presence of Acheulean stone tools. Dmanisi has provided several specimens (Vekua *et al.*, 2002), including an almost complete skull with mandible, although the stone tool assemblage from this site has no Acheulean affinities (Gabunia *et al.*, 2000). Some of the material is reminiscent of specimens from Koobi Fora localities of similar age, especially the youth from West Turkana.

The complete skull, however, is of a smaller individual, and raises the question of whether this simply represents the female form of a fairly dimorphic species or a different species. Such questions bedevil palaeontology, but the most plausible interpretation surely has to be a single species. The most likely candidate at both these localities then really has to be *H. erectus*. Nevertheless, such finds say relatively little about the true earliest date of emigration. For one thing, they are unlikely to record the earliest movement and almost certainly do not do so. To proceed further in understanding the timetable we must look at the wider picture.

If we look at the larger pattern of mammalian dispersions between Africa and Eurasia we see that the Arabian Peninsula, an arid region closed off to its north by the great arcs of the Taurus and Zagros mountains of present-day Turkey and Iran, would have presented a formidable barrier to interchanges (Tchernov, 1992). The evidence for movements by other mammalian species suggests that this barrier was at its most impenetrable during the earliest Pleistocene, while the later part of the Pliocene appears to have been a time of perhaps greater movement across the region. Horses of the genus *Equus* successfully colonised Africa at that time, while mammoths and some African bovids moved out to the north, and if hominins were also dispersing at that time, then the earliest species to get out of Africa may not even have been a member of the genus *Homo* (Turner, 1999). In fact, renewed suggestions that the origins of hominins and of the genus *Homo* in particular may actually lie outside Africa have been made recently by Dennell (2004; Dennell & Roebroeks, 2005). But while it is clear that the genus *Homo* does seem to make an oddly abrupt appearance in the fossil record, as Dennell & Roebroeks (2005) stress, and that the later Pliocene appears to offer a more suitable time for movements into (or, conceivably, out of) Eurasia, it remains equally clear that interpretations of origin based the geographic patterning seen in the fossil evidence are difficult. The latter authors argue that the absence of a likely ancestor outside Africa may rest in part upon taphonomic factors, but while that could be true we must be careful not to argue that the best evidence for presence in an area is absence from the fossil record. The apparent extinction of dryopithecine apes in Eurasia at the end of the Miocene linked to the possible re-immigration of the group into Africa makes it less prob-

able that in any sense a more ultimate origin for *Homo* will be found outside Africa, beyond that possibly stemming from a late Pliocene movement of an australopithecine-grade hominin ancestor into Eurasia.

The appearance of the modern African mammalian fauna

Finally, we turn to the appearance of the modern African mammalian fauna. Europe, Asia and the Americas all witnessed massive changes in their large-mammal faunas as recently as the end of the last ice age, in the period between 20,000 - 10,000 years ago, when impressive numbers of large animals became totally or locally extinct. Examples include mammoths, mastodonts, camels, various species of deer, horses, species of bears, sabre-toothed cats, a cheetah-like cat and lions in North America (Kurtén & Anderson, 1980), and mammoths, woolly rhinoceros, musk oxen, species of deer and bears, hyaenas, lions and leopards in Eurasia (Kurtén, 1968). The modern mammalian fauna of these areas, in other words, is a very recent, postglacial phenomenon with a very reduced number of species.

The African pattern is very different. Although a relatively small number of species - mainly ungulates - became completely or locally extinct there around 10,000 years ago (see below), the changes at the beginning of the Pleistocene were virtually the last of any major significance. We pointed out above that once the sabre-toothed cats and remaining archaic hyaenas disappeared around 1.5 Mya, the large predator guild had taken on its present composition and structure, and this modern stamp begins to be reflected in the fauna as a whole. The archaic-looking trunked deinotheres together with the gomphotheres and chalicotheres disappeared, as did three-toed hipparionine horses, while the pigs and giraffes were eventually reduced in numbers and diversity to the present small range of species. Among our own fossil relations the robust australopithecine hominins of the genus *Paranthropus* were among the larger primates that went extinct. At the same time, however, species that had appeared on the continent during the later stages of the Pliocene survived in greater numbers down to the present day. Africa therefore began to look modern at a

substantially earlier date than Eurasia or the Americas while still retaining a larger proportion of its older range of larger mammals.

The African end-Pleistocene extinctions involved no more than perhaps ten or a dozen complete disappearances of species, animals such as *Pelorovis antiquus*, the long-horned buffalo which had previously been widely recorded in northern, eastern and southern parts of the continent and *Megalotragus priscus*, the giant hartebeest. However, localised extinction was a far more common phenomenon, with animals like elephant, zebras and giraffes disappearing from the Maghreb, kobs and lechwes from the Sudan and white rhinos, black wildebeest and springboks from the Cape region. Human activity has been invoked to explain some or all of these late extinctions, in part because such species clearly survived earlier fluctuations in environment and habitat of the kind that occurred at the end of the last ice age, but the evidence is circumstantial rather than direct.

Modern-day Africa is one of the richest biotic regions on Earth, although its mammalian abundance shrinks in comparison with the range of species that have come and gone there over a geologically short period. Africa without sabre-toothed cats, giant hyaenas, deinotheres, three-toed horses, chalicotheres, pigs the size of a small cow, sivatheres or robust australopithecines is very different from the Africa of only two million years ago when the earliest known members of our own genus were appearing and beginning to move into other continents. But what remains is still our oldest living mammalian fauna, with a higher proportion of Pliocene species than anywhere else in the world, with clear implications for the importance of conservation on the continent.

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