

Encyclopedia of Human Evolution and Prehistory

Second edition

Editors

Eric Delson

Ian Tattersall

John A. Van Couvering

Alison S. Brooks

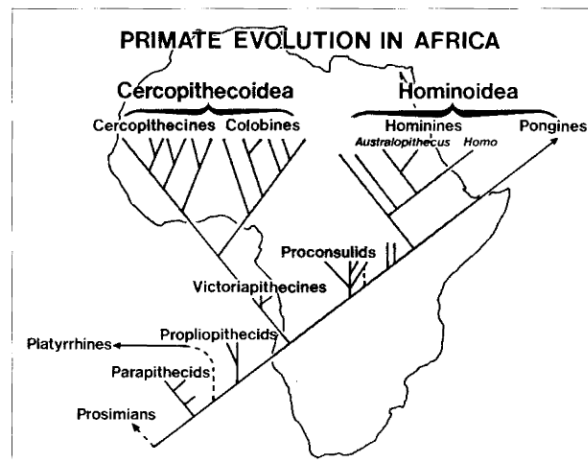
Garland Publishing, Inc.
A member of the Taylor & Francis Group
New York & London, 2000

Africa

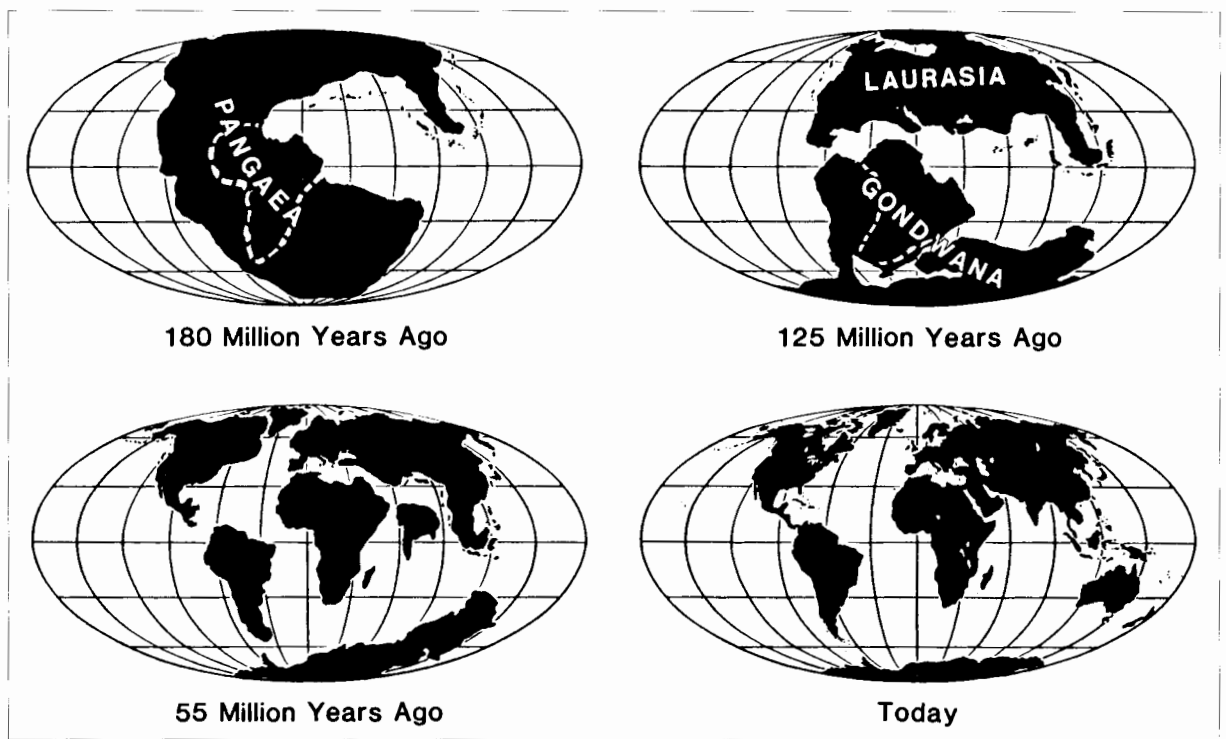
No other continent rivals Africa in its importance for human evolution and prehistory. Human evolution can be traced in the African fossil record from Paleocene euprimates to *Homo sapiens* (albeit with a frustrating pre-*Australopithecus* gap). Africa's role as evolutionary center for the higher primates is emphasized by the fact that only the Southeast Asian hylobatids and the South American platyrrhine monkeys have diversified outside of its bounds. Archaeological finds in Africa predate those in any other continent by at least 1 Myr, and a vast body of archaeological material is available to document progressive technological change on the continent from crudely chipped pebbles to iron and bronze casting. On the basis of fossils and tools, the continent would seem to have been the place of origin not only for genus *Homo*, but also, ca. 2.5 Myr later between 0.2 and 0.1 Ma, for modern humans as well.

Geology and Geography

The geology of Africa would seem to hold little promise for a notable Cenozoic vertebrate fossil record. The Afro-Arabian continent, segmented by the Red Sea stretch of the East African Rift system, is essentially a high plateau of Precambrian basement without significant Cenozoic deformation



Primate evolution in Africa: diagram of the relationships of higher primates, most of which evolved and differentiated in Africa. Courtesy of John G. Fleagle.

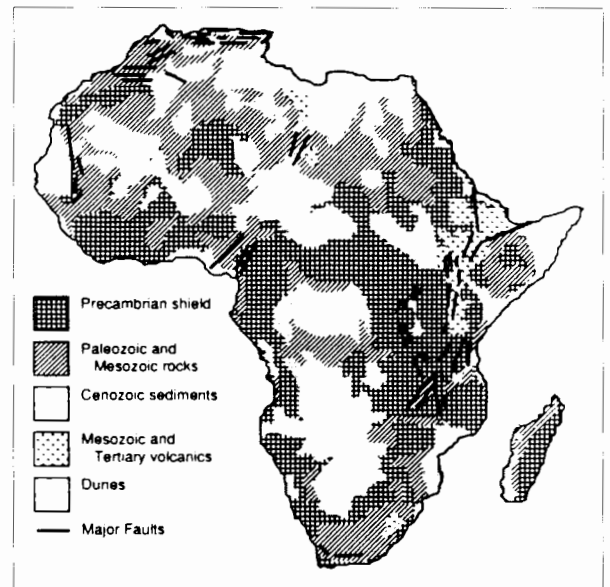


Effect of continental drift on Africa's position relative to that of other continents. Courtesy of John G. Fleagle.

except in the Atlas and the East African Rift Valley. A sizable portion of the plateau is masked by Saharan, Arabian, and Kalahari dune sands, and even more by the "calcaire continental," indurated, unfossiliferous veneers of dune-base material cemented by limy groundwater. Favorable locations are thus of relatively limited extent, but, in compensation, some of the deposits have proven to be incredibly prolific.

Fossiliferous continental Cenozoic deposits in Afro-Arabia fall into four principal groups. The most important by far are the thick sections of Miocene-to-Recent lacustrine and fluvial beds and alkali volcanics that accumulated in the linear depressions formed by the East African Rift from Israel to Malawi, and in the paravolcanic basins of rift-shoulder volcanic complexes. Another cluster of fossil sites occurs in shoreward facies of Cenozoic coastal-plain deposits of North Africa and, to a lesser extent, in Southwest Africa and Arabia. A third source of fossils (with an unusually high proportion of anthropoid remains) is in Plio-Pleistocene (and some Miocene) cave deposits within the karstic limestones of southern Africa. Finally, seismic and drilling programs have shown many thousands of meters of Cenozoic strata in the intracontinental "sags," or passively subsiding basins, that underlie the Sudd of the upper Nile, Lake Chad, and the Etosha Pan of northern Namibia. However, these basins are not subject to uplift tectonics, and only the Plio-Pleistocene outer margin of the Chad Basin has been exposed by erosion.

The geological and faunal connections between Afro-Arabia and other continents have been a topic of debate for centuries. As soon as accurate maps came into existence, the parallelism of the Atlantic coasts of Africa and South America inspired speculation about continental drift, and we now know that Africa was at the center of the Gondwana super-



Geological framework of Africa: areas of outcrop of African rocks by age; note the relatively small area of Cenozoic sediments. From Cooke, H.B.S., in V.J. Maglio and H.B.S. Cooke, eds. 1978, *Evolution of African Mammals*. Copyright © by the President and Fellows of Harvard College, reprinted by permission of Harvard University Press.

continent ca. 225 Ma. This was the Permo-Triassic interval, when Afro-Arabia (together with Iran, Anatolia, and much of what is now Greece and Italy) was joined with South America, Antarctica, Australia, and the Indian subcontinent. During the Mesozoic, rift valleys evolved into ocean basins, and the Gondwana continents and subcontinents began to separate. Since Gondwana was also separated from the northern supercontinent, Laurasia, by the Tethys Ocean, all of the

Gondwana continents became islands. One by one, they have moved across the Tethys gap to join against Laurasia, so that Australia and Antarctica are the only ones still islands today. Although geologically isolated until the Miocene, Africa seems to have been open to intermittent and probably selective faunal exchange with the north throughout the Mesozoic (as indicated by clear relationships among dinosaurs) and at several times in the Early Cenozoic. One of the earliest exchanges, at ca. 55 Ma, brought omomyid primates into the continent, and for the next 40 Myr this lineage diversified in relative isolation from the rest of the world.

The African Fossil Record

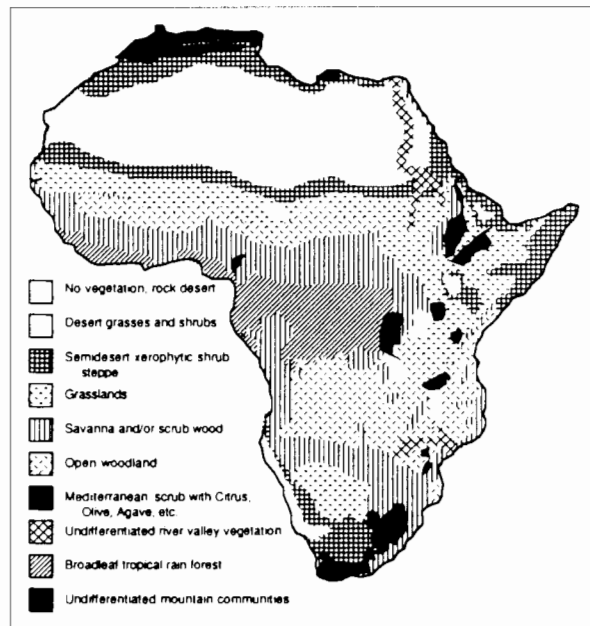
Mammalian paleontology in Africa dates from nineteenth-century descriptions of Eocene sirenians and cetaceans in Egypt and Late Pleistocene large mammals in the coastal terraces of Algeria and Morocco. In the 1920s, the discoveries of *Australopithecus* at Taung (South Africa) and of *Proconsul* at Koru (Kenya), as well as recognition of uniquely primitive lithic industries throughout the sub-Saharan region, began the vindication of Charles Darwin's prediction that Africa would prove to be the cradle of human evolution. In the years since World War II, a steady stream of discoveries has made Africa the focus of the most advanced multidisciplinary programs in paleoanthropology (human paleontology and Paleolithic archaeology), with significant carryover in the allied fields of vertebrate paleontology, paleoenvironmental studies, and Cenozoic geochronology.

By 1998, well over 100 collecting areas had yielded diverse and well-preserved local faunas of fossil mammals to document the Cenozoic history of African mammals—approximately half with primate remains—and there are as many or more that are of significant archaeological interest. As noted above, most sites are confined to the Rift Valley, to the narrow coastal plains, and to scattered exposures of cave deposits in southern Africa.

Archaeological sites are only slightly less concentrated in these geologically favored regions. A significant number of the more recent discoveries, however, have been reported from hitherto lightly explored regions of Arabia, the Atlas, and Central Africa, suggesting that the fossil and artifact map will continue to fill in across the continent.

THE AFRO-ARABIAN PALEOBIOLOGICAL REGION

Mainland Africa, Arabia, and the Levant were a single continental unit until the Early Miocene. During this early period, the African faunal realm may also have extended into microcontinents that were structurally tangent to Afro-Arabia, such as the central massifs of Iberia, Apulia, Yugoslavia, Romania, northern Greece, Turkey, and Iran, all of which are now sutured to southern Eurasia. Eocene mammals from scattered occurrences in these regions have strong affinities to Africa and not to coeval faunas in the lands to the north. Fossils from the Eocene of Indo-Pakistan, Burma, and Thailand also suggest a degree of mid-Paleogene communication with Afro-Arabia, involving exchange of early rodents, tethytheres (sirenians, proboscideans), anthracotheres, and adapiform or tarsiiform primates (e.g., *Pondaungia* in Burma and the *Hoanghoni* and *Eosimias* associations in China, all of Middle Eocene age).

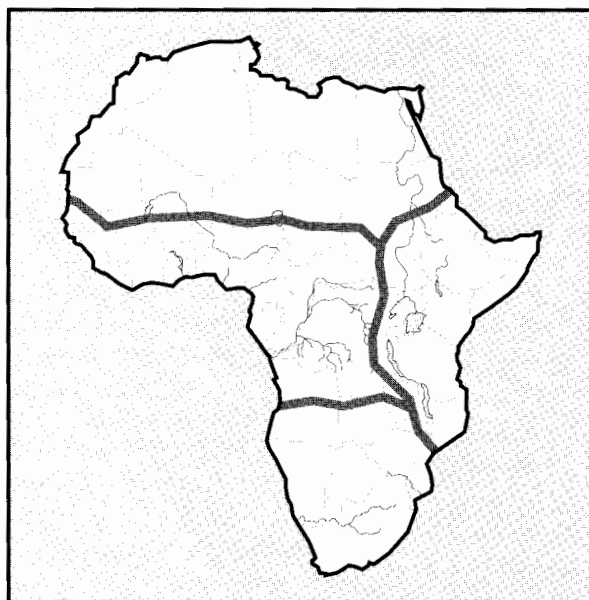


Major vegetation types of modern Africa. From Cooke, H.B.S., in V.J. Maglio and H.B.S. Cooke, eds. 1978, *Evolution of African Mammals*. Copyright © by the President and Fellows of Harvard College, reprinted by permission of Harvard University Press.

The Old World tropics was the only part of the world in which a diverse primate fauna survived the changing climates of the Oligocene. In the Late Eocene, the anthropoids and probably the strepsirhines were already present in Africa (including, presumably, lemuroids in Madagascar). From the Oligocene onward, seasonal and latitudinal differences intensified in Africa, but the primates, particularly the anthropoids (and lemurs), continued to thrive. Unfortunately, we know little or nothing of mammalian faunas outside of the coastal plains and the rift valley, and the paleoclimatic conditions and faunal assemblages of these regions are thus grossly overrepresented in the record.

REGIONAL SUBDIVISION

The latitude of the Afro-Arabian crustal plate changed very little during the Cenozoic, so that the present broad division into northern, equatorial, and southern environmental domains probably existed over the past 50 Myr. These domains have different environments and even more different fossil records due to regional taphonomic bias. The northern zone is equivalent to the Mediterranean coast and the great arid zone of the interior; for this work, we have selected its southern margin as a boundary that includes the Saharan Plateau, the Chad and Sudanese Basins, and the Arabian Peninsula save only Yemen. The 12° S parallel, which we have arbitrarily set as the boundary of the southern region from the west coast to the rift, lies slightly north of the known limit of the fossiliferous paleokarst, in southern Angola. The East African Rift ends at 15° S, not far below the environmentally transitional Pliocene faunas of Chiwondo in Malawi, and we have set the boundary of the southern Africa zone to angle towards this parallel from the rift to the east coast.



Eco-geographical regions of Africa as used in this encyclopedia. Clockwise from top, these are: North Africa, East Africa, Southern Africa, and West and Central Africa; of these, only the last is not treated in a separate entry. The boundaries of the first three regions are as discussed in their respective entries.

Between these two poleward zones lies the equatorial belt, here divided into eastern and West-Central Africa by the continental divide along the shoulder of the rift valley. East Africa is thus the region from the rift to the Indian Ocean between the 15th parallels. Unfortunately, so little is known of the paleontological history of the west-central region (and not much more of its earlier Palaeolithic archaeology) that there is no separate encyclopedia entry for it.

CLIMATIC HISTORY

At ca. 35.5 Ma, at the end of the Eocene, exposure of significantly colder Antarctic bottom water in the upwelling cells along the west coasts of Africa and India initiated a major shift in prevailing winds and rainfall. Cold winds from the Namib and Senegal-Mauritania cells created arid low-pressure cells over adjacent parts of southern and northern Africa, while warm air from counterflowing Atlantic surface waters near the equator provided moisture for seasonal southwesterly monsoons in Central Africa, with most rainfall in the west. Given this general pattern, intensified by the north-south highland divide of the rift shoulders, the west half of Africa will always have been characterized by extreme contrasts between high precipitation near the equator and low precipitation to the north and south, while the eastern half will have had less average rainfall in the equatorial zone and, consequently, less conspicuous latitudinal variation.

Superimposed on this pattern were migrations of ecological zones under the influence of short-term climate changes, most notably in the Late Cenozoic in response to the orbitally forced cycles of Pliocene and Pleistocene climate. In the equatorial region, ecozone shifts were essentially vertical, in synchrony with retreats and advances of moun-

tain glaciers and the declines and rises of pluvially controlled lakes. The presently extensive grasslands and xeric scrublands on the African high plains, for instance, were forced into coastal refugia during cold/pluvial events, and miombo and highland forests moved downslope from the mountainous regions to cover the plains. At higher latitudes, particularly in southern Africa, ecoplanes are tilted poleward, and the Late Cenozoic global climate cycles also involved notable lateral and altitudinal shifts.

REGIONAL TAPHONOMIC BIASES

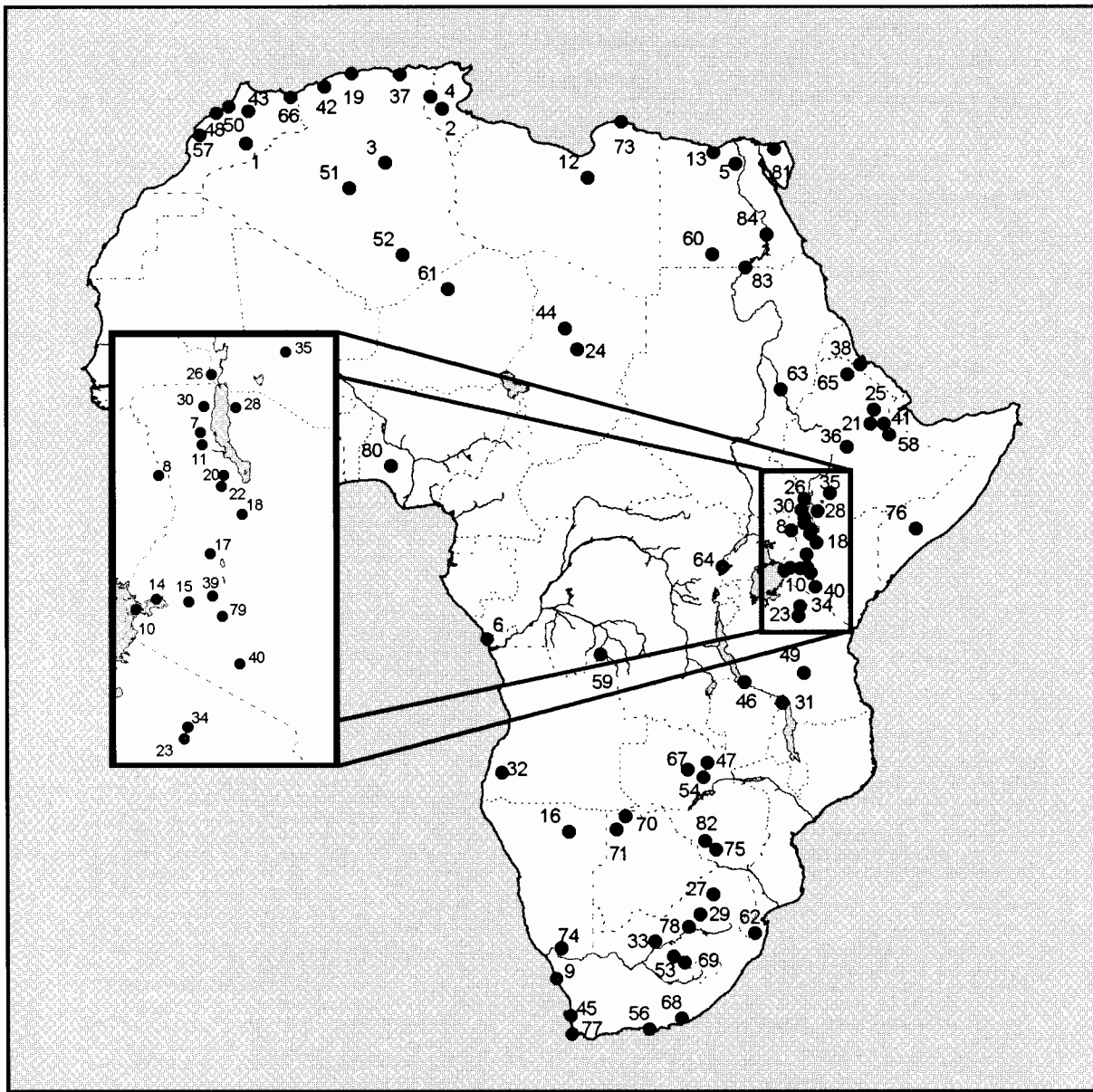
In the African fossil record, the regional ecological differences have been exaggerated by regional taphonomic biases. The paleontology of the equatorial region in East Africa, the standard for African mammal biochronology, is completely dominated by material collected from the volcanic highlands and rift valleys. Throughout this area, the fossils are found in strata that accumulated in volcanically active, ecologically fragmented, and topographically varied terrain. In the peculiar geology of the rift, hyperalkaline volcanic ejecta created fossilizing environments resembling desert playas in the midst of tropical forest and brushland, in a process termed *mock aridity*. The number and diversity of fossils from such localities are exceptional; postmortem sorting is minimal; and the contribution from normally underrepresented (i.e., rapidly decomposed) forest communities is unusually high.

By contrast, Paleogene and Neogene paleofaunas in the northern zone are almost exclusively from low-relief coastal lowland settings. The exception is that part of the Miocene small-mammal record recovered from karst fillings in the Atlas foothills. Aside from this, the northern sample represents swamp, forest, and interfluvial savannah habitats on coastal plains, in which postmortem damage, sorting, and preservation under the influence of coastal sedimentary regimes are highly variable. Mammal remains from highland communities were normally too distant, except in the Israel Miocene sample, to have contributed.

Knowledge of the southern paleofaunal zone is again strongly biased, because here the great majority of material was preserved in cave deposits, with a much lesser amount from estuarine and aeolian sites. The cave-preserved assemblages built up under strongly selective conditions in which nocturnal small mammals (mainly in raptor middens), hyaenas, leopards, terrestrial cercopithecoids, hominoids, and small herbivores are consistently among the best-represented groups. In the cave sites, postmortem integrity of larger species is only moderate, but preservation tends to be good to excellent.

AFRICAN LAND-MAMMAL AGES

A stable biochronological framework for the growing volume of paleontological, stratigraphical, and archaeological data from Africa has long been needed. Much of the collected fossil material, however, has yet to be adequately described. On the other hand, geochronometry in East Africa is extremely well developed, and isochronous correlations, from magnetostratigraphy and tephrachronology, connect a large number of sites. In view of this, a recent approach has



Major African fossil localities yielding primates (including hominins) and Paleolithic archaeological remains. Numbers represent site names (in approximate chronological order), as follows: 1, Adrar Mgorn 1; 2, Chambi; 3, Glib Zegdou; 4, Nementcha, Bir el Ater; 5, Fayum; 6, Malembe; 7, Lothidok; 8, Moroto; 9, Ryskop; 10, Rusinga; 11, Kalodirr; 12, Gebel Zelten; 13, Wadi Moghara; 14, Maboko; 15, Fort Ternau (also Koru, Songhor); 16, Berg Aukas; 17, Tugen Hills; 18, Samburu; 19, Meuacer; 20, Lothagam; 21, Aramis; 22, Kanapoi; 23, Laetoli; 24, Bahr el Ghazal; 25, Hadar, Gona; 26, Omo (Usno, Shungura, Kibish); 27, Makapan, Cave of Hearths; 28, Koobi Fora; 29, Sterkfontein, Swartkrans, Kromdraai; 30, Nachukui (West Turkana); 31, Chiwondo (Uraba); 32, Leba; 33, Taung; 34, Olduvai Gorge; 35, Konso; 36, Melka Kontouré; 37, Ain Hanech; 38, Buia; 39, Kilombe; 40, Ologresailie; 41, Bodo; 42, Tigbenif; 43, Ain Maarouf; 44, Yayo (Koro-Toro); 45, Saldanha (Hopesfield); 46, Kalambo Falls; 47, Kabwe; 48, Sidi Abderrahman, Thomas Quarries; 49, Isimila; 50, Salé; 51, Tachenghit; 52, Tihodaine; 53, Florisbad; 54, Twin Rivers; 56, Klasies River Mouth; 57, Jebel Irhoud; 58, Diré-Dawa; 59, Lupemba; 60, Bir Tarfawi; 61, Adrar Bous; 62, Border Cave; 63, Singa; 64, Katanda, Ishango; 65, Gobedra; 66, Taforalt; 67, Mumbwa; 68, Howieson's Poort; 69, Rose Cottage; 70, #Gi; 71, Tsodilo Hills; 73, Haau Freda; 74, Apollo-11; 75, Pomongwe, Bambata; 76, GoGoshis Qabe; 77, Cape Flats, Fish Hoek; 78, Boskop; 79, Gamble's Cave; 80, Iwo Eleru; 81, Musbabi; 82, Khami; 83, Wadi Halfa, Khor Musa; 84, Wadi Kubbaniya, Kom Ombo. Site contents not indicated here—see detailed maps in regional entries; Note: sites 55 and 72 deleted.

been to group the East African local faunas according to external rather than internal criteria of age. The boundaries between these units are defined by the oldest site of each group, without primary reference to the presently known age limit of any included taxon. In this way, faunal range limits may continue to change with new finds and revisions without destabilizing the age or definition of unit boundaries. With

regard to the most commonly observed fossils, a preliminary characterization of the units at the genus level can be proposed, and sites from northern and southern Africa can be assigned to the East Africa-defined regional land-mammal age units according to local geochronology and faunally based estimates of age.

(text continues on page 16)

KEY TAXA	EAST AFRICA	Age, Ma	OTHER AFRO-ARABIA	Age, Ma
Naivashan				
(♦) <i>Rusingonyx</i>	Naivasha Rockshelter	70.01	Casablanca Soltanian Morocco	0.07
(7) <i>Mustela</i> , <i>Nesokia</i> , <i>Sus</i>	OL Naisiusiu	~0.02	Melkbos; Swartklip S. Afr.	~0.06
(♣) <i>Megantereon</i> , <i>Praeomys</i> , <i>Paraethomys</i> , <i>Pelorovis</i> , <i>Megalotragus</i> , <i>Rabaticerus</i> , <i>Leptobos</i>	Mumba Cave-V Tanzania ET Galana Boi Omo Kibish Ethiopia +Laetoli Ngaloba Tanzania	~0.02 ~0.10 70.10 ~0.15	Border Cave S. Afr. Klasies River S. Afr.	~0.09 0.12 - 0.09
Natronian				
(7) <i>Ursus</i> , <i>Leptobos</i> , <i>Capra</i> , <i>Connochaetes</i>	OL Ndutu Beds (upper)	~0.25	Casabl. Presoltanian Morocco	0.18 - 0.15
(♣) <i>Machairodus</i> , <i>Irhoudia</i> , <i>Hexaprotodon</i> , <i>Kolpochoerus</i> , <i>Menelikia</i> , <i>Hipparion</i> , <i>Elephas</i>	Isimila Tanzania Lainyamok OL Ndutu Beds (lower) BA Kapthurin AW Melka Kunturé-5 AW Bodo Kariandusi SH Upper L; ET Silbo AW Melka Kunture-3; -4 OL Masek +Olorgesailie 1-14	~0.3 0.36 0.37 0.3 0.6 0.64 ~0.8 1.0 - 0.74 1.0 - 0.7 1.0 - 0.9 +0.99-0.49	Jebel Irhoud Morocco Florisbad S. Afr. Salé; Thomas 1 Morocco Rabat Morocco Kabwe (Broken Hill) Zambia Saldanha (Hopefield) S. Afr. Ternifine, Thomas "G" Morocco Vaal River (upper) S. Afr. Namib-IV Namibia Cornelia S. Afr.	0.2 - 0.125 ~0.25 ~0.28 ~0.3 ~0.5 0.7 - 0.5 ~0.7 ~0.7-0.2 ~0.7 71.0
Late Turkunan				
(♦) <i>Gorgopithecus</i>	Kanam Rawi, Kanjera North	71.2	Djebel Ressay 568 Tunisia	~1.2
(7) <i>Ourebia</i> , <i>Georhynchus</i> , <i>Meriones</i>	OL Bed III / IV	1.4-1.0	An Nafud Saudi Arabia	~1.3
(♣) <i>Dinofelis</i> , <i>Homo</i> , <i>Homotherium</i> , <i>Chasmapor-</i> <i>thetes</i> , <i>Rhinocolobus</i> , <i>Cercopithecoides</i> , <i>Paranthropus</i> , <i>Prolagus</i> , <i>Makapania</i> , <i>Deinotherium</i> , <i>Mammuthus</i> , <i>Anancus</i>	SH-L; ET Chari Konso (upper) Ethiopia WT Nariokotome Barogali Djibouti AW-Melka Kunture-2/1 Peninj Tanzania Gadeb Ethiopia OL Bed II (upper) SH-J/K; ET Okote BA Chesowanja (=Chemoigut) WR Nyabusosi ET Fejej-1 Konso (lower) Ethiopia Anabo Koma Djibouti OL Bed I, lower Bed II +ET-KBS; SH-H	1.4-1.3 1.45-1.3 1.33 1.5 1.5-1.1 1.5 1.5 1.6-1.4 1.64-1.4 ~1.8 ~1.8-1.3 1.88 1.9 1.9 1.9-1.6 1.9-1.65	'Ubediya Israel Kromdraai A, Swtkr. 2-3 S. Afr. Ain Hanech Algeria Yayo Chad Humpata (Leba) Angola Djebel Ressay 1 Tunisia Irhoud Ocre Morocco Sterkfontein 5 S. Afr. Swartkrans I S. Afr. Kromdraai B S. Afr.	~1.4 ~1.5 ~1.5 ~1.5 ~1.5 ~1.6 ~1.6 ~1.6 ~1.6 ~1.8
Early Turkunan				
(♦) <i>Protomys</i>	Kanjera South	72.0	Swartkrans II, Bolt's 6 S. Afr.	~2.0
(7) <i>Rhynchocyon</i> , <i>Erinaceus</i> , <i>Paranthro-</i> <i>pus</i> , <i>Homo</i> , <i>Vulpes</i> , <i>Lycaon</i> , <i>Otocyon</i> , <i>Proteles</i> , <i>Alcelaphus</i>	ET Upper Burgi BA Chemeron (upper) AW Matabaieitu, K. Hadar (upp.) WR Hohwa, Kaiso Chiwondo 3A Malawi Marsabit (Algas) WT Lokaiabei, Kalochoro +SH-D/G	2.0 ~2.4 2.5-2.3 2.5-2.0 ~2.5 ~2.5 2.52-2.35 2.52-2.33	Langebaan upper S. Afr. Ouadi Dardemi, Koula Algeria Taung S. Afr. Constantine, Ain Jourdel Alger. Ain Brimba Tunisia Ahl al Oughlam Morocco	~2.0 ~2.0 72.0 ~2.3 ~2.3 ~2.5 ~2.5
Late Afarian				
(7) <i>Crocidura</i> , <i>Elephantulus</i> , <i>Suncus</i> , <i>Rhinocolobus</i> , <i>Cercopithecus</i> , <i>Cercop-</i> <i>ithecoides</i> , <i>Papio</i> , <i>P. (Dinopithecus)</i> , <i>Steatomys</i> , <i>Arvicanthus</i> , <i>Grammomys</i> , <i>Equus</i> , <i>Phacochoerus</i> , <i>Camelus</i> , <i>Menelikia</i> , <i>Antidorcas</i>	Laetoli Ndolanya Tanzania ET Hasuma; SH C WR Kyeoro Kesem-Kebena 1 Ethiopia AW Kada Hadar (lower) AW SHT/Denen D WT Lomekwi ET Tulu Bor; SH B AW Maka WR Warwire +ET Lokochot; SH A	~2.6 2.85-2.6 ~3.0-2.5 ~3.0-2.5 3.18-2.95 3.39-3.2 3.39-2.6 3.39-2.9 3.4 ~3.5-3.0 3.5-3.39	Sterkfontein-4 (main) S. Afr. Ain Boucherit Algeria O. Fouarat, O. Akrech Morocco Makapansgat-II / lwr. IV S. Afr. Gcwihaba Botswana Lac Ichkeul Tunisia Bahr el-Gazal Chad	~2.6 73.0 73.0 ~3.0 ~3.0 73.5 ~3.5
Early Afarian				
(♦) <i>Praedamalis</i>	Karmosit	~3.6	Vaal River, Lower S. Afr.	74.0-3.5
(7) <i>Mungos</i> , <i>Ictonyx</i> , <i>Panthera</i> , <i>Chasma-</i> <i>porhethes</i> , <i>Canis</i> , <i>Galago</i> , <i>Theropithecus</i> , <i>Serengetilagus</i> , <i>Pedetes</i> , <i>Xerus</i> , <i>Oenomys</i> , <i>Thallomys</i> , <i>Notochoerus</i> , <i>Potamochoerus</i> , <i>Metridiochoerus</i> , <i>Pelorovis</i>	Laetoli (upper) Tanzania AW Belohdelie Ethiopia Ekora AW Sagantole Ethiopia +ET Moiti; Omo U-1	3.7-3.5 3.8 3.8 4.0-3.6 3.96-3.40		
(♣) <i>Miotragocerus</i> , <i>Stegodon</i>				

African Land Mammal Ages (LMAs). The time frame is based on the well-calibrated sequence of local faunas in East Africa (Kenya, except where noted). Many of the East African "local faunas" identified by site names (col. 2) were actually collected from many sub-sites in the same stratigraphic unit. Local faunas outside of East Africa (col. 4) are mostly not directly dated, and are positioned here according to faunal correlation. The age limits of each unit are set by the index fauna at the base (marked with +), following the principle of "base defines boundary." Prior to the Fayum fauna, data are insufficient to justify setting firm boundaries, and names have been given to arbitrary spans of time that contain roughly comparable sites in North Africa. The range limits of Key genera, in the left side column, are selected from the known record because of their significance, either because they are abundant or because they are informative for diversity, habitat, or biogeography. Primates are shown in **bold**. In the pre-Fayumian sites, all identified genera are considered significant. The relationship of these LMAs to calibrated chronostratigraphy, magnetostratigraphy, and paleoclimatology, and to LMAs of other regions, is shown in the "Time Scale" section of the Introduction. Note that the upper and lower age range limits of the noted genera are not necessarily coincident with the upper or lower boundaries of the relevant mammal age.

Key to notation			
(♦)	Characterizing taxon: apparently restricted to this time interval, in Africa	AW	Awash - eastern Ethiopian Rift basin, Ethiopia
(7)	FAD: earliest known African occurrence of taxon is within this interval	BA	Baringo - Lake Baringo basin & Tugen Hills, Kenya
(♣)	LAD: last known African occurrence of taxon is within this interval	ET	East Turkana - northeast Lake Turkana basin, Kenya-Ethiopia
taxon	Known range includes East Africa during this interval	OL	Olduvai - Eyasi basin, northern Tanzania
taxon	Known range only in southern and/or northern Africa during this interval	SH	Shungura - lower Omo River basin, southern Ethiopia
?	Questionable date	WR	Western Rift - Lake Albert basin, western Uganda, NE Zaire
-	Approximate date	WT	West Turkana - western Lake Turkana basin, Kenya

KEY TAXA	EAST AFRICA	Age, Ma	OTHER AFRO-ARABIA	Age, Ma
Kerian				
(◆) <i>Ardipithecus</i> , <i>Stegodibelodon</i>	Kanapoi	4.12	Hamada Damous Morocco	?4.5
(?) <i>Parapapio</i> , <i>Australopithecus</i> , <i>Herpestes</i> , <i>Helogale</i> , <i>Mellivora</i> , <i>Torolutra</i> , <i>Lutra</i> , <i>Megantereon</i> , <i>Crocota</i> , <i>Nyctereutes</i> , <i>Prolagus</i> , <i>Lepus</i> , <i>Tatera</i> , <i>Mastomys</i> , <i>Koipo-</i> <i>choerus</i> , <i>Syncerus</i> , <i>Redunca</i> , <i>Elephas</i> , <i>Loxodonta</i>	Omo Mursi Ethiopia Aterir WT/ET Lonyumun AW Aramis Kanam Homa Chiwondo 2 (Uraha) Malawi BA Tabarin AW Kuseralee WR Ongoliba Zaire Manonga Kilolele Tanzania +Lothagam Apak	4.2?-4.0 4.2?-4.0 4.35-4.0 4.4 ~4.5 ?4.5 4.5 ~5.0-4.5 ~5.0 ~5.0 ~5.0-4.5	Bochianga; Kolinga Chad Ain Guettara Morocco Argoub Kemellal Algeria Douaria Tunisia Amama-2 Algeria Kolié Chad	?4.5 ?4.5 ~4.5 ~4.5 ~4.5 ~4.5
(♣) <i>Agriotherium</i> , <i>Zramys</i> , <i>Progonomys</i> , <i>Brachypotherium</i> , <i>Dicerorhinus</i> , <i>Stegotetra-</i> <i>belodon</i>				
Baringian				
(◆) <i>Libypithecus</i> , <i>Ailepus</i> , <i>Kanisamys</i> , <i>Cainotherium</i> , <i>Damalacra</i> , <i>Chemositia</i>	Manonga Tinde Tanzania WR Nyawiega WR Nkondo Manonga Ibole Tanzania Lukeino	~5.3 ~5.5 ~6.0 ~6.0 6.0	Langebaan "E" S. Afr. Sahabi Libya Wadi Natrun Egypt Hondeklip 30m S. Afr. Amama-1 Algeria	~5.3 ~5.3 ~5.3 ?5.3 ~6.5
(?) <i>Civettictis</i> , <i>Agriotherium</i> , <i>Hyaena</i> , <i>Dinofelis</i> , <i>Macaca</i> , <i>Hystrix</i> , <i>Heterocephalus</i> , <i>Thryonomys</i> , <i>Mus</i> , <i>Rattus</i> , <i>Saccostomus</i> , <i>Ancylotherium</i> , <i>Sivatherium</i> , <i>Giraffa</i> , <i>Mad-</i> <i>oqua</i> , <i>Miotragocerus</i> , <i>Tragelaphus</i> , <i>Kobus</i> , <i>Aepycoerus</i> , <i>Raphicerus</i> , <i>Primelephas</i> , <i>Mammuthus</i>	Lothagam Nawata upper Kanam West Lothagam Nawata lower +BA Mpesida	6.2-5.5 ~6.2 ~7.0-6.6 7.0-6.5	Menacer (Marceau) Morocco Klein Zee S. Afr. Banyunah Abu Dhabi	?7 ?7 ~7
(♣) <i>Sayimys</i> , <i>Africanomys</i> , <i>Myocricetodon</i> , <i>Libycosaurus</i>				
Sugutan				
(◆) <i>Indarctos</i> , <i>Samburupithecus</i> , <i>Micro-</i> <i>colobus</i> , <i>Nakalimys</i> , <i>Kenyantherium</i>	Nakali BA Ngeringerowa +Namurungule (Baragoi)	?8.0 ~9.0 ~9.5	Khendek el-Ouaich Algeria Sidi Salem Algeria Dj. Krechem Tunisia	7.4 ~8.0 ~9
(?) <i>Paraethomys</i> , <i>Hippopotamus</i> , <i>Hipparion</i> , <i>Zygolophodon</i> , <i>Stegodon</i>				
(♣) <i>Paranomalurus</i> , <i>Tetralophodon</i>				
Tugenian				
(◆) <i>Vishnuonyx</i> , <i>Otaviipithecus</i> , <i>Damalav-</i> <i>us</i>	BA Ngorora D/E AW Ch'orora WR Kakara (Mohari) +BA Ngorora A/C	~11-10 10.6 ~12 12.8-11.6	Oued Zra Algeria Oued Mya Algeria Bou Hanifa Algeria Jebel Hamrin Iraq Beglia sup. Tunisia Hondeklip 50m S. Afr. Beglia inf. Tunisia Berg Aukas Namibia	9.7 ~10 ~10 ~10 ~10 ?12 ~12 ~12
(?) <i>Canis</i> , <i>Mellivora</i> , <i>Progonomys</i> , <i>Nyanza-</i> <i>choerus</i> , <i>Miotragocerus</i> , <i>Prostrepsiceros</i> , <i>Paleotragus</i> , <i>Stegotetralodon</i>				
(♣) <i>Dissopsalis</i> , <i>Victoriapithecus</i> , <i>Kenya-</i> <i>pithecus</i> , <i>Vulcaniscius</i> , <i>Nquruwe</i> , <i>Nasus</i> , <i>Kenyapotamus</i> , <i>Dorcatherium</i> , <i>Canthu-</i> <i>meryx</i> , <i>Chilotheridium</i> , <i>Prodeinotherium</i>				
Tinderetian				
(◆) <i>Paradiceros</i>	BA Alengerr	13	Pataniak-6 Algeria	~13
(?) <i>Genetta</i> , <i>Machairodus</i> , <i>Percrocuta</i> , <i>Kenyapithecus</i> , <i>Kenyapotamus</i> , <i>Climaco-</i> <i>ceras</i> , <i>Samotherium</i> , <i>Heterohyrax</i> , <i>Choerolophodon</i> , <i>Anancus</i>	Kirimun Fort Ternan WR Kisege Nyakach (Sondu) Nachola BA Muruyur, Kipsaramon +Maboko-Majiwa	13.5 14.0 ~14 ~15 15 ~15.5 15.3	Testour Tunisia Cherichera Tunisia Beni Mellal Algeria Hofuf Saudi Arabia	~13.5 ?13.5 ~14 ~15
(♣) <i>Hyainailourous</i> , <i>Anasinopa</i> , <i>Komba</i> , <i>Limnopithecus</i> , <i>Micropithecus</i> , <i>Procon-</i> <i>sul</i> , <i>Simiolus</i> , <i>Paraphiomys</i> , <i>Diamantomys</i> , <i>Myophiomys</i> , <i>Notocricetodon</i> , <i>Namachoer-</i> <i>us</i> , <i>Libycochoerus</i> , <i>Eotragus</i> , <i>Aceratherium</i> , <i>Miorhynchocyon</i> , <i>Pachyhyrax</i>				
Kisingirian				
(◆) <i>Afrocyon</i> , <i>Afrosmilus</i> , <i>Kichechia</i> , <i>Luo-</i> <i>gale</i> , <i>Dendropithecus</i> , <i>Rangwapithecus</i> , <i>Prohylobates</i> , <i>Morotopithecus</i> , <i>Afropith-</i> <i>ecus</i> , <i>Turkanapithecus</i> , <i>Kenyalagomys</i> , <i>Kenyamys</i> , <i>Kenyasus</i> , <i>Hyoboops</i> , <i>Prohyrax</i>	Ombo, Mariwa Rusinga Kulu, Uyoma Kajong (Mwiti) Loperot Kalodirr (Muruarot) Locherangan Rusinga Hiwegi, Karungu Bukwa Uganda Moroto Uganda Napak Uganda Songhor, Koru +Meswa	~16 16 ~17 17 17 17.5 17.8 ?18 ?18 ~19 ~19 ~20	Arrisdrift-Rooilepei Namibia Jebel Zelten, Siwa Libya Hadrukh - AsSarrar Saudi Ar Huqf - Ghaba Oman Negev Rotem Israel Jebel Mrhila Tunisia Wadi Moghara Egypt Auchas Namibia Sperrgebiet Namibia Hondeklip 90m S. Afr. J. Midrash Shamali Saudi Ar.	~16 ~18 ~18 ~18 ~18 ?18 ~18 ~18 ~18 ?20
(?) <i>Hyainailourous</i> , <i>Komba</i> , <i>Limnopithec-</i> <i>us</i> , <i>Micropithecus</i> , <i>Proconsul</i> , <i>Victoria-</i> <i>pithecus</i> , <i>Simiolus</i> , <i>Paranomalurus</i> , <i>Mega-</i> <i>pedetes</i> , <i>Paraphiomys</i> , <i>Diamantomys</i> , <i>Myophiomys</i> , <i>Atlantoxerus</i> , <i>Vulcaniscius</i> , <i>Notocricetodon</i> , <i>Nasus</i> , <i>Nquruwe</i> , <i>Nama-</i> <i>choerus</i> , <i>Libycochoerus</i> , <i>Dorcatherium</i> , <i>Canthumeryx</i> , <i>Prolibytherium</i> , <i>Paleotragus</i> , <i>Eotragus</i> , <i>Gazella</i> , <i>Aceratherium</i> , <i>Brachypo-</i> <i>therium</i> , <i>Miorhynchocyon</i> , <i>Gomphotherium</i>				
(♣) <i>Apterodon</i> , <i>Phiomys</i> , <i>Afromeryx</i> , <i>Eozygodon</i> , <i>Archaeobelodon</i>				

KEY TAXA	EAST AFRICA	Age, Ma	OTHER AFRO-ARABIA	Age, Ma
Turkwelian				
(◆) <i>Kamoyapithecus</i>	Lothidok	~26	Wadi Sabyah Saudi Arabia	723
(♣) <i>Afromeryx</i> , <i>Prodeinotherium</i> , <i>Eozygodon</i> , <i>Archaeobelodon</i>				
Qatranian				
(◆) <i>Metapterodon</i> , <i>Afrotarsius</i> , <i>Omanodon</i> , <i>Shizarodon</i> , <i>Parapithecus</i> , <i>Apidium</i> , <i>Propiipithecus</i> , <i>Metoldobotes</i> , <i>Selenohyrax</i>	(None)		Taqah Oman Thaytiniti Oman Malembe Angola (Cabinda) Zallah Libya	~31 33 733 ~33
(♣) <i>Pachyhyrax</i>			Gebel Qatrani-4 (I,M) Egypt	
(♣) <i>Qatrania</i> , <i>Oligopithecus</i> , <i>Metaphiomys</i> , <i>Megalohyrax</i> , <i>Titanohyrax</i> , <i>Sagatherium</i> , <i>Thyrohyrax</i> , <i>Bunohyrax</i> , <i>Barytherium</i> , <i>Paleomastodon</i>			+Gebel Qatrani-3 (E,V) Egypt	~33 ~34
Fayumian				
(◆) <i>Ptolemaia</i> , <i>Hyaenodon</i> , <i>Biretia</i> , <i>Aframonius</i> , <i>Anchomomys</i> , <i>Wadilemur</i> , <i>Plesiopithecus</i> , <i>Arsinoea</i> , <i>Serapia</i> , <i>Catopithecus</i> , <i>Nementchamys</i> , <i>Herodotius</i> , <i>Arsinoitherium</i> , <i>Moeritherium</i>	(None)		Gebel Qatrani-2 (A,B,C) Egypt Gebel Qatrani-1 (L-41) Egypt Dur at-Talha Libya Nementcha -Bir el Ater Algeria In Tafidet Mali	~35 ~37 ~37-35 738 738
(♣) <i>Apterodon</i> , <i>Qatrania</i> , <i>Oligopithecus</i> , <i>Phiomys</i> , <i>Metaphiomys</i> , <i>Bothriogenys</i> , <i>Thyrohyrax</i> , <i>Barytherium</i> , <i>Paleomastodon</i>			+Qasr el-Sagha Egypt	~38
Numidian				
(◆) <i>Azibius</i> , <i>Algeripithecus</i> , <i>Tabelia</i> , <i>Glibia</i> , <i>Glibemys</i> , <i>Zegdoumys</i> , <i>Microhyrax</i>	(None)		M'Bodione Dadere Senegal Gour Lazib-Glib Zegdou Algeria	744 744
(♣) <i>Megalohyrax</i>				
(♣) <i>Numidothierium</i>				
Tebessan				
(◆) <i>Kasserinotherium</i> , <i>Garatherium</i> , <i>Koholia</i> , <i>Djebellemur</i> , <i>Chambius</i> , <i>Seggeurius</i>	(None)		Chambi (Kasserine) Tunisia El Kohol Algeria	746 750
(♣) <i>Titanohyrax</i> , <i>Numidothierium</i>				
Tingitanian				
(◆) <i>Afrodon</i> , <i>Todralestes</i> , <i>Cimolestes</i> , <i>Palaeoryctes</i> , <i>Tachyoryctes</i> , <i>Khamsaconus</i> , <i>Abolyolestes</i> , <i>Adapisoriculus</i> , <i>Altiatlasius</i> , <i>Phosphatherium</i>	(None)		N'Tagourt 2 Morocco Adrar Mgor 1 Morocco Ouled Abdoun Morocco	~54 ~57 ~57

African Land Mammal Ages (LMAs). The time frame is based on the well-calibrated sequence of local faunas in East Africa (Kenya, except where noted). Many of the East African "local faunas" identified by site names (col. 2) were actually collected from many sub-sites in the same stratigraphic unit. Local faunas outside of East Africa (col. 4) are mostly not directly dated, and are positioned here according to faunal correlation. The age limits of each unit are set by the index fauna at the base (marked with +), following the principle of "base defines boundary." Prior to the Fayum fauna, data are insufficient to justify setting firm boundaries, and names have been given to arbitrary spans of time that contain roughly comparable sites in North Africa. The range limits of Key genera, in the left side column, are selected from the known record because of their significance, either because they are abundant or because they are informative for diversity, habitat, or biogeography. Primates are shown in bold. In the pre-Fayumian sites, all identified genera are considered significant. The relationship of these LMAs to calibrated chronostratigraphy, magnetostratigraphy, and paleoclimatology, and to LMAs of other regions, is shown in the "Time Scale" section of the Introduction. Note that the upper and lower age range limits of the noted genera are not necessarily coincident with the upper or lower boundaries of the relevant mammal age.

Key to notation			
(◆)	Characterizing taxon: apparently restricted to this time interval, in Africa	AW	Awash - eastern Ethiopian Rift basin, Ethiopia
(♣)	FAD: earliest known African occurrence of taxon is within this interval	BA	Baringo - Lake Baringo basin & Tugen Hills, Kenya
(♣)	LAD: last known African occurrence of taxon is within this interval	ET	East Turkana - northeast Lake Turkana basin, Kenya-Ethiopia
taxon	Known range includes East Africa during this interval	OL	Olduvai - Eyasi basin, northern Tanzania
taxon	Known range only in southern and/or northern Africa during this interval	SH	Shungura - lower Omo River basin, southern Ethiopia
?	Questionable date	WR	Western Rift - Lake Albert basin, western Uganda, NE Zaire
-	Approximate date	WT	West Turkana - western Lake Turkana basin, Kenya

African Fossil Primates and Faunas

PALEOGENE

The early record of African primates begins with later Paleocene (Tingitanian) small-mammal faunas in Morocco that contain the indeterminate euprimate *Altiatlasius*, together with palaeoryctids and todralestids very close to Thanctian forms in western Europe. The earliest known proboscidean, *Phosphatherium*, is from this level as well. The adapiform status of *Djebellemur*, from the late Early Eocene (Tebessan) fauna of Chambi (Morocco), has been controversial, but recovery of an undoubted cercamoniine, *Aframonius*, from the

Late Eocene (Fayumian) fauna in the lower part of the Fayum sequence, and the probable cercamoniines *Omanodon* and *Shizarodon* from the Early Oligocene (Qatranian) fauna of Oman, suggests that adapiforms may indeed have been a significant component of primate faunas in the Old World tropics. The two parapithecids from the late Middle Eocene (Numidian) fauna of Glib Zegdou in Algeria may be the oldest certain anthropoids.

The world's most diverse and well-documented Paleogene anthropoid fauna has been collected in the Jebel Qatrani Formation of Egypt. In the lower part of the se-

quence, sites assigned to the Fayumian contain a number of parapithecoid and oligopithecoid taxa. The degree to which these are replaced by propliopithecoids in the Qatranian faunas from the upper part of the section is consistent with the passage of several million years at the observed replacement rate in the Miocene paleofaunas. While a Late Eocene (Priabonian) age is widely attributed to the Fayum sites, the correlation is broad enough to raise the question as to whether the upper Fayum (Qatranian) levels should also be dated to the later Priabonian or to the earliest Oligocene. The younger age is suggested by a preliminary magnetostratigraphic analysis; in addition, the Omani Thaitinitis and Taqah sites, which are faunally close, if not identically similar, to the Jebel Qatrani assemblages, are bracketed by Early Oligocene nummulite microfauna. A possible equivalent in sub-Saharan Africa is the Malembe faunule from Angola, with one debatable primate tooth.

The Middle-to-Late Oligocene is not well represented in Africa, and the first post-Fayum land mammal fauna is at Lothidok in East Africa (ca. 26 Ma). This small sample, the only one so far of Turkwelian age except for an even smaller collection from the Red Sea coast of Saudi Arabia, includes the earliest proconsulid, *Kamoyapithecus*, but none of the Fayum primate groups.

MIOCENE

Early Miocene Kisingirian localities provide the first pancontinental picture for Afro-Arabia, with fossil faunas from northern, equatorial, and southern regions. Evidence for a major post-Qatranian immigration and naturalization of Eurasian mammal lineages is apparent in the diversity of endemic genera of fissiped carnivores, sciurognath rodents, suids, ruminants (including the first known tragulids, bovids, and giraffids) and perissodactyls, none of which have ancestors in the Qatranian. A pronounced paleoecological difference between the tropical highlands and the pericontinental coastal environments is also evident in the Kisingirian faunas. Extremely well-preserved fossil mammal faunas (Koru, Songhor, Napak, Rusinga) from alkali-volcanic "mock arid" basins, in what were heavily forested volcanic highlands on the pre-rift Kenya Dome, contain abundant and largely arboreal proconsulids, archaic catarrhines (here included in the "*Dendropithecus*-group"), and strepsirhines, together with phylogenetically conservative, forest-adapted early ruminants, small carnivores, creodonts, hyraxes, rhinos, and proboscideans. A markedly different association has been sampled in the rift basin of northern Kenya, where the first hominid (*Afropithecus*) and the archaic catarrhine *Turkanapithecus* occur together with the first cercopithecoid (*Prohylobates*) in association with suids, ruminants, and carnivores that are clearly more advanced in their adaptations to open country. The nonprimate taxa correlate closely to Lower Miocene coastal-plain sites in Namibia, northern Africa, Israel, and the Persian Gulf (with *Heliopithecus*). None of the latter are closely dated, but the sites in North Africa, Israel, and Saudi Arabia are all well correlated to Late Burdigalian (ca. 17 Ma) marine strata. In Kenya, radiometric dates on the main "upland" sites range from 20 to 18 Ma, with

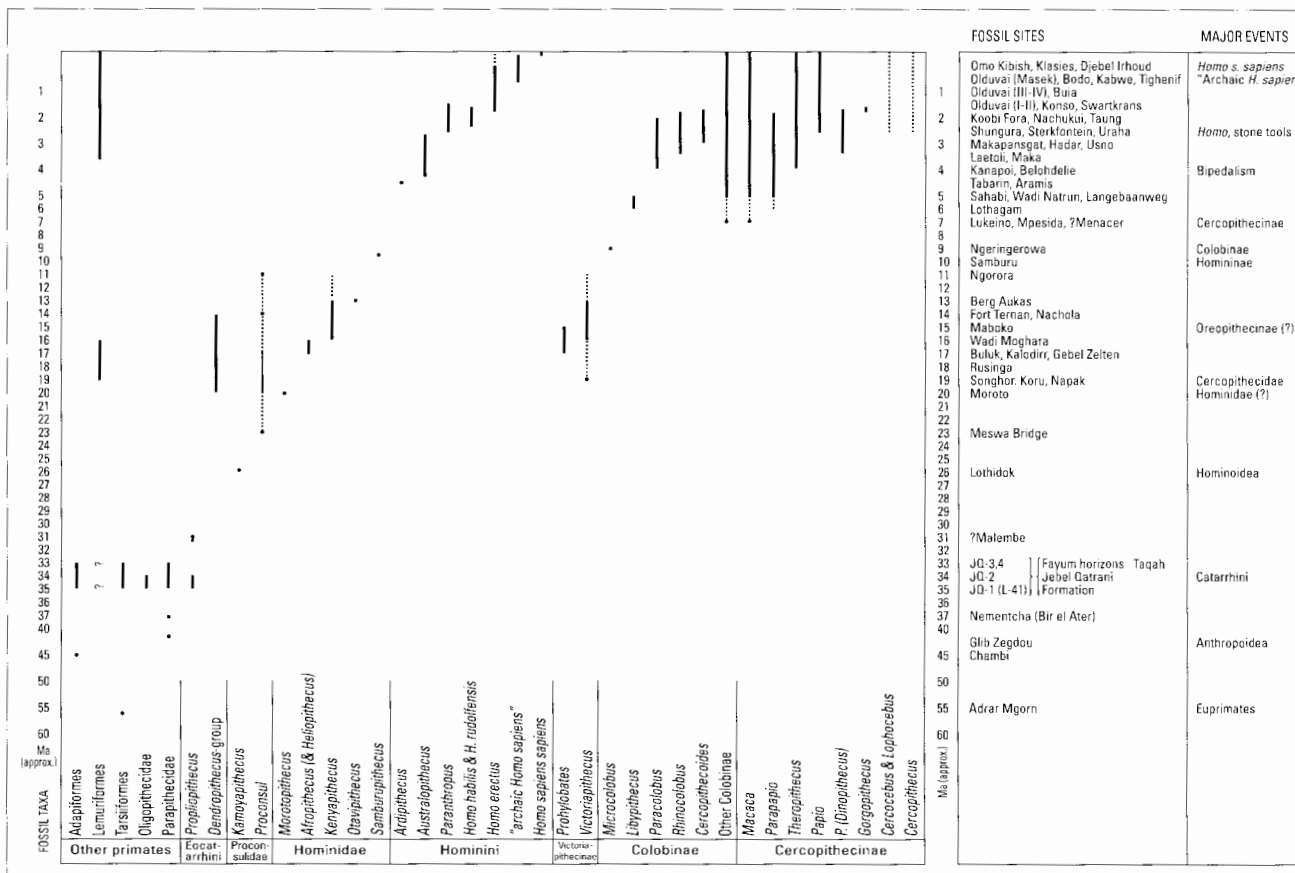
others known from ca. 16 Ma, while the "lowland" sites fall into the 18–17 Ma span. The radical differences between the two groups of Kenya Kisingirian local faunas have been attributed to evolutionary succession, but it seems preferable under the narrow time constraints to consider them as coeval ecofacies at different elevations. This grouping is entirely coincident with the paleotopography, so far as it is known, and the fact that the "upland" association continues to the end of the Kisingirian in the Kenya Dome cannot be ignored.

Beginning in the early Middle Miocene and continuing through the Late Miocene, the Tunderetian, Tugenian, Sugutan, and Baringan samples show less regional or environmental difference than in the Kisingirian. This may reflect the expansion of open-country habitat in the tropical highlands, as evidenced in the general, if not complete, replacement of the conservative forest-adapted genera in the Kisingirian with more advanced forms descended from the "lowlands" fauna (seen primarily in the rodents, bovids, giraffids, and proboscideans) together with new groups such as hyaenas, hippos, and (in the Tugenian) canids and equids. In the primate-bearing Tunderetian sites, whether on the dome (Maboko, Fort Ternan) or in the central rift (Muruyur, Alengerr, Nachola), *Kenyapithecus* is the sole hominid, together with the cercopithecoid *Victoriapithecus* and the last proconsulids. In Namibia, *Otaviapithecus* may represent the local kenyapithecine. From 13 Ma until the end of the Miocene, however, primates are extremely rare. Hominids are virtually unknown, other than a partial maxilla of a potential hominine from Baragoi (Samburu Hills) and isolated teeth in the Tugen Hills sequence. By contrast, the open-country cercopithecids (i.e., *Macaca* but also more arboreal colobines) become more common at the end of the Miocene (Menacer in Algeria; Wadi Natrun in Egypt; Sahabi in Libya; Lothagam in Kenya), which suggests that the sampled environments may simply have been unsuitable for contemporaneous hominids. The latest Miocene (Baringian) interval, from ca. 7 to 5 Ma, was marked by an increase in the rate of apparent origination, with the earliest (or sole) records of at least 48 new genera, including the first true elephantids (*Primelephas*, *Mammuthus*, and *Loxodonta*) and, at Lothagam, indeterminate indications of what may be the earliest hominin.

PLIOCENE

The Pliocene begins with Kerian faunas in East Africa that show a continued sharp increase in the rate of diversification and the earliest well-documented record of hominines. There are no sites of this age in the southern region, and most, but not all, of the nine major Kerian sites in North Africa yield only small mammals. Even so, the appearance of *Australopithecus* and *Ardipithecus* in East Africa seems to document a hominid breakthrough into seasonally dry, open-country environments.

The Early Pliocene peak in generic origination rates contrasts with the termination rate, which showed a modest and regular increase until the Pleistocene. This is clear evidence for ecological fragmentation and niche diversification, at least in the open-country faunas that make up the known record.



Known ranges of African fossil primate genera (and some higher taxa) and major sites and events in African primate and human evolution.

The African Pliocene is characterized by the evolutionary radiations of two major groups of higher primates, Old World monkeys and hominines. The rich Pliocene sites in Ethiopia, Kenya, Tanzania, and South Africa document a diversity of both colobines and cercopithecines, many of which were considerably larger than their extant relatives. *Parapapio* is known from the southern sites of Sterkfontein and Makapansgat, as well as from Hadar and the Turkana Basin. In eastern and southern Africa, fossil geladas (*Theropithecus*) were quite abundant, along with large colobines (*Cercopithecoides*, *Paracolobus*, and *Rhinopithecus*; the latter two are as yet known only from eastern African localities). The genus *Cercopithecus*, which is so successful in Africa today, is known from only a handful of fossils, and *Papio* also is generally not common, except in the latest Pliocene of the southern region.

Early Pliocene (ca. 4.4 Ma) fossils from Aramis in the Ethiopian Middle Awash Valley, named *Ardipithecus ramidus*, are the most conservative of any material assigned to Hominini. This form combines reduced canines and anteriorly positioned foramen magnum with "primitive" retentions such as apelike dp_3 morphology, as well as thin enamel on canines and molars, which may be conservative or secondarily reduced. It is not yet certain if this taxon represents a distant side branch or a twig on the "main line" of human evolution.

Slightly younger fossils from Kanapoi and Allia Bay, Kenya, have been assigned to *Australopithecus anamensis*, the

oldest species of that basal hominin genus. A mandible, a maxilla, and a tibia from Kanapoi date ca. 4.2 Ma, while other specimens may range up to 3.9 Ma or younger. They differ from *A. ramidus* in known features especially by having thicker dental enamel, while the more elongate and parallel-sided tooth rows help distinguish them from younger species.

The largest collections of mid-Pliocene hominins, all attributed to *Australopithecus afarensis*, have been recovered from sites in the Hadar Formation, the sites of Belohdelie and Maka in the Middle Awash, Fejej, the Usno Formation (all Ethiopia), the Koobi Fora Formation (Kenya), and the Laetoli Beds (Tanzania). These fossils span the period between ca. 3.8 and 2.95 Ma, while slightly younger fossils from Member B in the Shungura Formation (Ethiopia) have been tentatively assigned here as well. *A. afarensis* appears to have occupied both closed-forest and open-savannah habitats. Its postcranial skeleton attests to both bipedal and climbing locomotor repertoires, and it shows considerable sexual dimorphism. A partial mandible and an isolated tooth from the Koro-Toro area of Chad have been named *A. bahrelghazali*, which is distinguished from *A. afarensis* by several dental features. The Chad faunal assemblage is said to most closely resemble those from Hadar, suggesting a date of ca. 3.5–3 Ma.

The South African sites of Taung, Makapansgat, and Sterkfontein, which have been faunally dated to between ca. 3 and 2.3 Ma, contain fossils of *Australopithecus africanus*. There is as yet no convincing evidence for *A. africanus* in eastern Africa. Faunal evidence indicates a closed-brush-

wood environment for *A. africanus*. This species is postcranially similar to *A. afarensis*, and it also shows evidence of strong sexual dimorphism. There are differences between the two taxa in vault roundness, forehead shape, mastoid projection, and development of the P₃ metaconid.

Two “robust australopith,” or *Paranthropus*, species are known from the Pliocene of eastern Africa. *P. aethiopicus* is represented by a cranium from the Lomekwi Formation (Kenya) and a mandible and numerous isolated teeth from the Shungura Formation that are dated to ca. 2.7–2.3 Ma. *P. boisei*, which is better known in Pleistocene-age sediments from eastern Africa, is also represented in Pliocene deposits from the Shungura Formation, the Koobi Fora Formation, and Bed I of Olduvai Gorge. The earliest fossils attributed to *P. boisei* date to ca. 2.3 Ma, and this species appears to have occupied both open and closed habitats.

The earliest evidence for the genus *Homo* derives from Pliocene deposits in eastern Africa. The earliest representatives of this genus are presently attributed to the species *H. rudolfensis*, known from ca. 2.4 to 1.9 (perhaps to 1.6) Ma in the Omo Shungura Formation and perhaps at Hadar (Ethiopia), the Koobi Fora Formation and the upper Chemeron Formation (Kenya), and the Chiwondo Beds (Malawi). It is probably not coincidental that the earliest lithic artifacts date to ca. 2.6–2.3 Ma at sites in the Omo and Afar (Gona) regions of Ethiopia, at Lokalalei west of Lake Turkana, and possibly at Senga-5 in northern Zaire. These stone tools, like those from Olduvai Gorge and Koobi Fora (Karari), appear to represent the opportunistic flaking of small cobbles (Mode 1), and a small proportion of animal bones that are associated with these Oldowan artifacts show evidence of stone-tool cutmarks.

The very end of the Pliocene (ca. 1.9–1.8 Ma) saw the apparent coexistence of up to two additional species of *Homo* in eastern Africa. Both *H. habilis* and *H. erectus* may have their earliest records in the Turkana Basin about this time and both extended well into the Pleistocene. Considering the range of *H. rudolfensis* and *P. boisei*, the overlap of four hominin species for up to 250 Kyr is unexpected, to say the least. Perhaps the three species assigned to *Homo* were adapted to different microenvironments around Lake Turkana and seldom, if ever, occupied the same territory at any time.

PLEISTOCENE

The fossil record during the Pleistocene shows further evolutionary radiations of Old World monkeys (especially modern genera such as *Papio*, *Cercocebus*, *Cercopithecus*, and *Colobus*, as well as ever-larger *Theropithecus*) and hominins. The latter were characterized by increasing reliance on technology, resulting in an abundant archaeological record. Although the global definition of the Plio-Pleistocene boundary is fixed at ca. 1.8 Ma, there is little overall change in Africa at that precise horizon, even though it marked the end of at least two species of *Homo* and the succession of *H. erectus* as the dominant, and soon the only, representative of the genus.

Fossils of *Paranthropus boisei* are known from Early Pleistocene deposits in the Turkana Basin and the Olduvai Gorge, as well as from the Humbu Formation at Peninj (Tan-

zania) and Chemoigut Formation at Chesowanja (Kenya). *P. boisei* is not represented in the fossil record after ca. 1.4 Ma. In South Africa, *P. robustus* is known from the sites of Swartkrans and Kromdraai, dated to ca. 1.8–1.5 Ma, where it appears to have inhabited comparatively open environments.

Both species of *Paranthropus* appear to have coexisted with one or more species of *Homo*. A single fragment is assigned to *H. rudolfensis* from a 1.6 Ma horizon at Koobi Fora. *Homo habilis*, however, is relatively common at Olduvai between 1.8 and 1.6 Ma, though it is not definitively recognized in contemporaneous deposits in the Turkana Basin. Specimens of early *Homo erectus* (sometimes termed *H. ergaster*) are known from the Turkana Basin and the upper Bed II at Olduvai Gorge at ca. 1.8–1.5 Ma. Contemporaneous nonrobust fossils from Swartkrans Members 1–3 and Sterkfontein Member 5 are often allocated to *H. erectus* as well, but some recent studies have questioned these identifications. Most of the artifacts found alongside or coeval with these early *Homo* fossils are still part of Mode 1 assemblages, including the so-called Developed Oldowan A. The earliest Acheulean (proto)bifaces are known from sites dated to ca. 1.6–1.4 Ma, such as EF-HR at Olduvai (middle Bed II) and Konso (Ethiopia).

Younger human fossils from Olduvai (Beds III–IV), the upper Shungura Formation, Gomboré II at Melka Kontouré (Ethiopia), and perhaps Yayo (Chad) and Tighenif (Algeria) are generally regarded as representing later *H. erectus*, with greater similarity to East Asian members of that taxon. African *H. erectus* fossils thus span a considerable period of time, from ca. 1.9 to 0.7 Ma. Many of these fossils derive from deposits that contain lithic artifacts of the Acheulean tradition, and countless sites from this period throughout northern, eastern, and southern Africa preserve Acheulean artifacts and extensive fauna but no hominid remains (e.g., Ologresailie). In contrast to the opportunistic flaking that appears to have been a feature of the Oldowan tradition, the Acheulean assemblages (Mode 2) are generally characterized by well-formed handaxes and cleavers, and there is evidence that a much wider landscape was being utilized by ca. 1.6 Ma than had been the case before. In a number of instances, the source rocks are located many kilometers from the Acheulean archaeological sites. Controversial studies may document controlled fire by 1.4 Ma.

Middle Pleistocene fossils of early (i.e., “archaic”) *Homo sapiens* are known from such sites as Bodo (Ethiopia), Kabwe (Zambia), Ndutu (Tanzania), and Saldanha (South Africa). Moroccan specimens from Salé, Thomas Quarries, and Sidi Abderrahman probably also represent a similar population, and some have suggested that Tighenif is an early member as well. Most of these fossils probably date between 700 and 400 Ka. Moreover, it has been argued that somewhat younger specimens from Rabat (Morocco), Lake Eyasi (Tanzania), the Kapthurin Beds at Baringo (Kenya), and possibly the Cave of Hearths (South Africa) are referable to early *H. sapiens*. For the most part, these fossils are associated with Acheulean artifacts, with some indications of the use of the Levallois or a comparable technique of prepared-core flaking. In sub-Saharan Africa, industries of Acheulean or other

Mode 2 type are generally termed Early Stone Age, with local variants common in South and East Africa. For example, the Sangoan (ca. 300–200 Ka) includes finely made handaxes, prepared-core technology, and, in some cases, large blades struck from prismatic cores, foreshadowing Mode 4 assemblages. Dates for the youngest Acheulean/Mode 2 industries appear to span the period 200–150 Ka, as is also the case in Europe (although there the Micoquian may extend into the last interglacial).

By the Middle Paleolithic, regional differentiation becomes important in African archaeology and human paleontology. South of the Sahara, such specimens as those from Florisbad (South Africa) and Ngaloba at Lactoli (Tanzania) probably date to ca. 275–125 Ka. They may represent examples of a transition from “archaic” to the earliest “anatomically modern” *Homo sapiens*. Archaeological tool kits of this age are mainly of Mode 3 form and are broadly classed as Middle Stone Age (MSA). The earliest examples of MSA appear to date older (at ca. 250 Ka in South Africa, Zambia, Ethiopia, and perhaps Kenya) than the youngest Acheulean (ca. 250–175 Ka in South Africa, Tanzania, and Kenya), suggesting temporal overlap related to cultural differentiation and mosaic evolution of modern morphology.

Such South African MSA industries as the Pietersburg and Orangian typically include discoidal and Levallois-like cores, producing convergent flakes with faceted striking platforms, as well as flake blades, points, and side scrapers. Lupemban and Fauresmith assemblages also incorporate large bifacial tools, such as handaxes and picks, in some cases perhaps related to a woodworking, forest-dwelling adaptation. One of the most intriguing MSA variants is the South African Howieson’s Poort, dated mainly between 80 and 65 Ka, which includes small blades struck from prismatic cores, similar to younger Mode 5 assemblages. In Zaire, a broadly contemporary industry at Katanda included barbed bone points (hatpoons?), similar to those of the European Magdalenian at 15–10 Ka. Microlithic Mode 4–5 industries in Zaire and Tanzania also presage later European Upper Paleolithic developments. MSA industries continue until ca. 30 Ka, but they document a broader economic base (hunting of large game, fishing and shellfish collection, plant foods prepared with grindstones) than is common in the Eurasian Middle Paleolithic.

The earliest known representatives of “anatomically modern” *Homo sapiens* have been recovered from the Omo Kibish Formation (Ethiopia) and Klasies River Mouth Cave (South Africa). No tools were associated with the fossils in the former region, although a questionable date of 120 Ka was reported from levels older than the human remains. At Klasies (and the nearby Nelson Bay Cave, as well as Die Kelders [South Africa] and other sites), fragmentary human fossils are associated with MSA artifacts and dated to the Eemian (ca. 125–90 Ka) by geological inference. The Border Cave site in southern Africa has yielded a partial cranium and other remains of apparently African (rather than Eurasian or indeterminate) morphology, but the suggested age of 90 Ka has been questioned. Taken together, however, the southern African evidence is a strong indicator of the presence of anatomically modern humans by 100 Ka. It is tempting to

suggest a relationship with the Howieson’s Poort industry and similar “precursors” of Mode 4 technology, but associations are unclear. As with the emergence of the genus *Homo*, southern Africa probably saw the origin of modern humans and some contemporaneous technological and economic advancements. In North Africa, Middle Paleolithic (Mode 3) Levallois-Mousterian and Aterian industries are known before, during, and after the Eemian interglacial. It does not appear that Neanderthals of European or Southwest Asian type ever occurred south of the Mediterranean, but human fossils older than 100 Ka are rare. Archaic varieties of “anatomically modern” *Homo sapiens* occur in northern Africa during the Weichselian, at such sites as Jebel Irhoud, Temara, and Mugharet el ‘Aliya (Morocco), Haua Fteah (Libya), Singa (Sudan), and Diré-Dawa (Ethiopia). They are morphologically less comparable with the Neanderthals than with Levantine “archaic moderns” from Skhūl and Jebel Qafzeh.

No true Mode 4 (Late Paleolithic) industries are known well in west, central, or southern Africa, but they do appear after the Aterian in North Africa. At Haua Fteah, the Dabban is comparable with European blade-based industries of 40–20 Ka, and similar assemblages are known in Kenya, Ethiopia, and Somalia. The Ibero-Maurusian (or Oranian) occurs in western North Africa ca. 20–10 Ka, and the eastern Oranian of Libya is of similar age. Younger levels yield such industries as the Capsian in Tunisia. To the south, Later Stone Age (LSA) industries are characterized by microlithic technology and greater emphasis on fishing and hunting of large plains ungulates. The LSA begins before 40 Ka and continues into the Holocene, in some areas into the historic present.

See also Acheulean; Adapiformes; Afar Basin; Africa, East; Africa, North; Africa, Southern; Anthropoidea; Archaic *Homo sapiens*; Archaic Moderns; *Ardipithecus ramidus*; Asia, Western; Aterian; *Australopithecus*; *Australopithecus afarensis*; *Australopithecus africanus*; *Australopithecus bahrelghazali*; Bambata; Baringo Basin/Tugen Hills; Bone Tools; Border Cave; Bow and Arrow; Breccia Cave Formation; Broom, Robert; Catarrhini; Cave of Hearths; Cenozoic; Cercopithecidae; Cercopithecinae; Chiwondo Beds; Climate Change and Evolution; Colobinae; Dabban; “*Dendropithecus*-Group”; Early Paleolithic; Early Stone Age; Economy, Prehistoric; Eocene; Epipaleolithic; Fayum; Fire; First Intermediate; Florisbad; Haua Fteah; Hominidae; Homininae; Hominoidea; *Homo*; *Homo erectus*; *Homo ergaster*; *Homo habilis*; *Homo rudolfensis*; *Homo sapiens*; Howieson’s Poort; Jebel Irhoud; Kabwe; Kalambo Falls; Karari; Kenyapithecinae; Klasies River Mouth; Kromdraai; Late Paleolithic; Later Stone Age; Lithic Use-Wear; Lupemban; Makapansgat; Man-Land Relationships; Mesolithic; Middle Awash; Middle Paleolithic; Middle Stone Age; Miocene; Modern Human Origins; Mousterian; Natron-Eyasi Basin; Oldowan; Olduvai Gorge; Oligocene; Oligopithecidae; Orangian; Paleoenvironment; Paleolithic; Paleolithic Lifeways; Paleomagnetism; *Paranthropus*; *Paranthropus aethiopicus*; *Paranthropus boisei*; *Paranthropus robustus*; Parapithecidae; Pietersburg; Plate Tectonics; Pleistocene; Pliocene; Pre-Aurignacian; Prepared-Core; Proconsulidae; Propithecidae; Raw Materials; Rift

Valley; Saldanha; Sangoan; Second Intermediate; Senga-5; Smithfield; Spear; Sterkfontein; Stillbay; Stone-Tool Making; Swartkrans; Taphonomy; Taung; Tshitolian; Turkana Basin; Victoriapithecinae; Western Rift; Wilton. [J.A.V.C., E.D., J.G.F., F.E.G., A.S.B.]

Further Readings

- Fleagle, J.G., and Kay, R.F., eds. (1994) *Anthropoid Origins*. New York: Plenum.
- Howell, F.C. (1978) Hominidae. In V.J. Maglio and H.B.S. Cooke (eds.): *Evolution of African Mammals*. Cambridge, Mass.: Harvard University Press, pp. 149–258.
- Phillipson, D.W. (1993) *African Archaeology*, 2nd ed. Cambridge: Cambridge University Press.
- Pickford, M. (1986) The geochronology of Miocene higher primate faunas of East Africa. In J.G. Else and P.C. Lee (eds.): *Primate Evolution*. Cambridge: Cambridge University Press, pp. 19–33.
- Suwa, G., White, T.D., and Howell, F.C. (1996) Mandibular postcanine dentition from the Shungura Formation, Ethiopia: Crown morphology, taxonomic allocation, and Plio-Pleistocene hominid evolution. *Am. J. Phys. Anthropol.* 101:247–282.
- Szalay, F.S., and Delson, E. (1979) *Evolutionary History of the Primates*. New York: Academic Press.
- Vrba, E.S., Denton, G.H., Partridge, T.C., and Burckle, L.H., eds. (1995) *Paleoclimate and Evolution, with Emphasis on Human Origins*. New Haven: Yale University Press.
- Wood, B.A. (1991). *Koobi Fora Research Project, Vol. 4: Hominid Cranial Remains*. Oxford: Oxford University Press.

By: John A. Van Couvering, Eric Delson, John G. Fleagle,
Frederick E. Grine and Alison S. Brooks