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ARTICLE

AFRICAN LAND MAMMAL AGES

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ABSTRACT—We define 17 African land mammal ages, or AFLMAs, covering the Cenozoic record of the Afro-arabian continent, the planet's second largest land mass. While fossiliferous deposits are absent on the eroded plateau of the continent's interior, almost 800 fossil genera from over 350 locations have now been identified in coastal deposits, karst caves, and in the Neogene rift valleys. Given a well-developed geochronologic framework, together with continuing revision to the fossil record—both stimulated by the story of human evolution in Africa—and also to compensate for the variation in fossil ecosystems across such great distances, the AFLMAs are biochronological units defined by type localities, and not biozones to be recognized by the occurrence of certain genera. Disparities are notable: Africa is the highest of all continents, but almost every Paleogene locality was formed at sea level; the fossil record of its great rainforest ecosystem remains virtually unknown; and the Paleogene fauna is relatively isolated, whereas the Neogene begins with open exchange with Laurasia following the Tauride collision, with a simultaneous opening of the East African rift valleys in which the newly revolutionized fauna is abundantly preserved. Notably, the continent-wide and comprehensive documentation of the African mammalian record reveals an unparalleled rate of transformation in the hominin lineage, unmatched by any other group, in response to the Neogene expansion of the open-country ecosystem.

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INTRODUCTION

This paper presents a comprehensive Cenozoic LMA (land mammal age) model for Afro-arabia, for a record that may be the most complete of any Gondwana fragment. Even though Cenozoic deposits are absent on the elevated peneplain that extends over most of the continent, discoveries that began more than 150 years ago, with finds of extinct species of elephant, baboon, hippopotamus, equid, antelope, and buffalo uncovered in water-main excavations on the Mansourah plateau above Constantine, Algeria, reported by C. E. Bayle (1854), followed by a report of fossil bones in 'alluvial strata' of the Zambesi delta noted by the explorer John Kirk (1864), have resulted in a generous, if still notably partial, record in which it is clear that a significant percentage of the modern African fauna is descended from deeply rooted endemic lineages in a history of alternating exchange and isolation.

To many observers, the outstanding feature of African vertebrate paleontology is the fossil record of endemic higher primates leading to genus *Homo.* Hardly less interesting, however, is the progress of the endemic supergroup Afrotheria (chrysochlorids, tenrecids, tubulidentates, macroscelidids, hyracoids, sirenians, and proboscideans), not to mention other groups with a unique African presence such as anomalurid and hystricognath rodents, hippopotamids, bovids, giraffids, and the extinct anthracotheres and hyaenodonts. The brief appearance or total absence of otherwise globally successful marsupials, procyonids, and cervids is also a distinctive feature. In all, we hope that the consolidation of the Afro-arabian Cenozoic record in a usefully standardized pan-continental framework will enhance communication and understanding as research continues.

ORGANIZATION OF THE AFRICAN LAND MAMMAL RECORD

The outline of the AFLMA system (Fig. 1) was first published in 'Encylopedia of Human Evolution and Prehistory' (Tattersall et al., 1988:xxiv), with an updated version in the second edition (Delson et al., 2000), and occasionally elsewhere as the study continued to be upgraded to the level presented here.

The AFLMAs are what might be called bio-chronostratigraphic time units, calibrated to the age of type localities that function as boundary-stratotypes anchoring an isochronous lower boundary of each unit, and with the upper boundary defined by the base of the next succeeding unit according to the principle of 'base defines boundary' (NACSN, 2005). The distances and differences across the Afro-arabian region, the never-ending discovery of new fossil material, and the continuing advances in the state of radiochronometric, tephrochronological, and magnetostratigraphic dating, all favor this simple and stable method of coordinating the fossil record. Similar arguments are cited by Schmidt-Kittler (1987) and Fahlbusch (1991) in regard to defining the MP and MN divisions of the Cenozoic mammal record in Europe, and by Agustí et al. (2001) in designating

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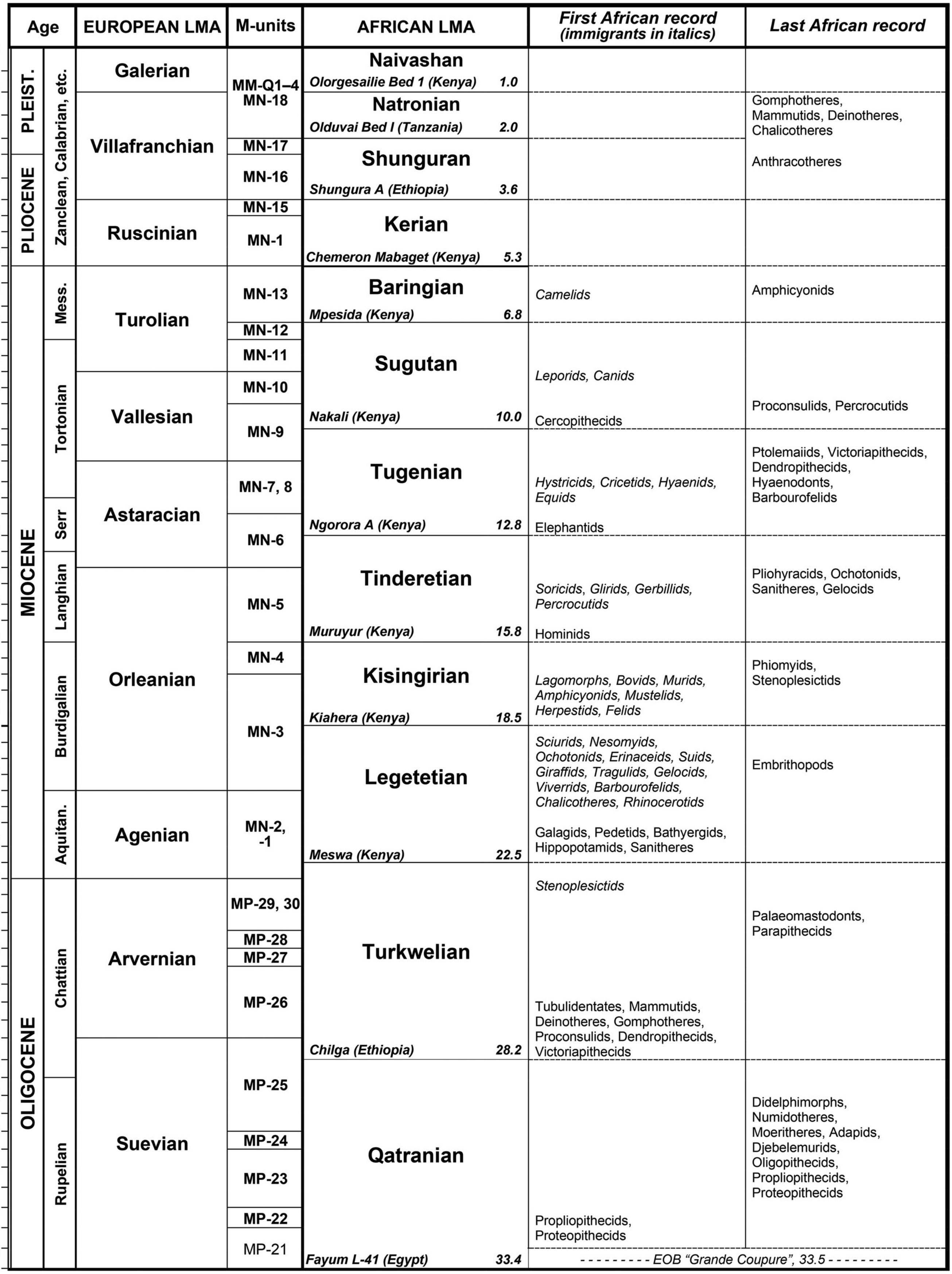

AFRICAN LMA			First African record (immigrants in italics)	Last African record
Naivashan	***Olorgesailie Bed 1 (Kenya)***	***1.0***		
Natronian	***Olduvai Bed I (Tanzania)***	***2.0***		Gomphotheres, Mammutids, Deinotheres, Chalicotheres
Shunguran	***Shungura A (Ethiopia)***	***3.6***		Anthracotheres
Kerian	***Chemeron Mabaget (Kenya)***	***5.3***		
Baringian	***Mpesida (Kenya)***	***6.8***	*Camelids*	Amphicyonids
Sugutan	***Nakali (Kenya)***	***10.0***	*Leporids, Canids* Cercopithecids	Proconsulids, Percrocutids
Tugenian	***Ngorora A (Kenya)***	***12.8***	*Hystricids, Cricetids, Hyaenids, Equids* Elephantids	Ptolemaiids, Victoriapithecids, Dendropithecids, Hyaenodonts, Barbourofelids
Tinderetian	***Muruyur (Kenya)***	***15.8***	*Soricids, Glirids, Gerbillids, Percrocutids* Hominids	Pliohyracids, Ochotonids, Sanitheres, Gelocids
Kisingirian	***Kiahera (Kenya)***	***18.5***	*Lagomorphs, Bovids, Murids, Amphicyonids, Mustelids, Herpestids, Felids*	Phiomyids, Stenoplesictids
Legetetian	***Meswa (Kenya)***	***22.5***	*Sciurids, Nesomyids, Ochotonids, Erinaceids, Suids, Giraffids, Tragulids, Gelocids, Viverrids, Barbourofelids, Chalicotheres, Rhinocerotids* Galagids, Pedetids, Bathyergids, Hippopotamids, Sanitheres	Embrithopods
Turkwelian	***Chilga (Ethiopia)***	***28.2***	*Stenoplesictids* Tubulidentates, Mammutids, Deinotheres, Gomphotheres, Proconsulids, Dendropithecids, Victoriapithecids	Palaeomastodonts, Parapithecids
Qatranian	***Fayum L-41 (Egypt)***	***33.4***	Propliopithecids, Proteopithecids	Didelphimorphs, Numidotheres, Moeritheres, Adapids, Djebelemurids, Oligopithecids, Propliopithecids, Proteopithecids

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FIGURE 1. Correlation of AFLMAs to the European ELMAs (Fahlbusch, 1976) and component MN and MP (Neogene and Paleogene) mammalian interval-zones (Mein, 1990; Steininger et al., 1996; Agusti et al., 2001; Domingo et al., 2007). The indicated ranges of suprageneric groups in the African record are based on the presently known occurrence of member genera. **Abbreviations**: **Aquitan.**, Aquitanian; **Mess.**, Messinian; **Pleist.**, Pleistocene; **Serr.**, Serravalian.

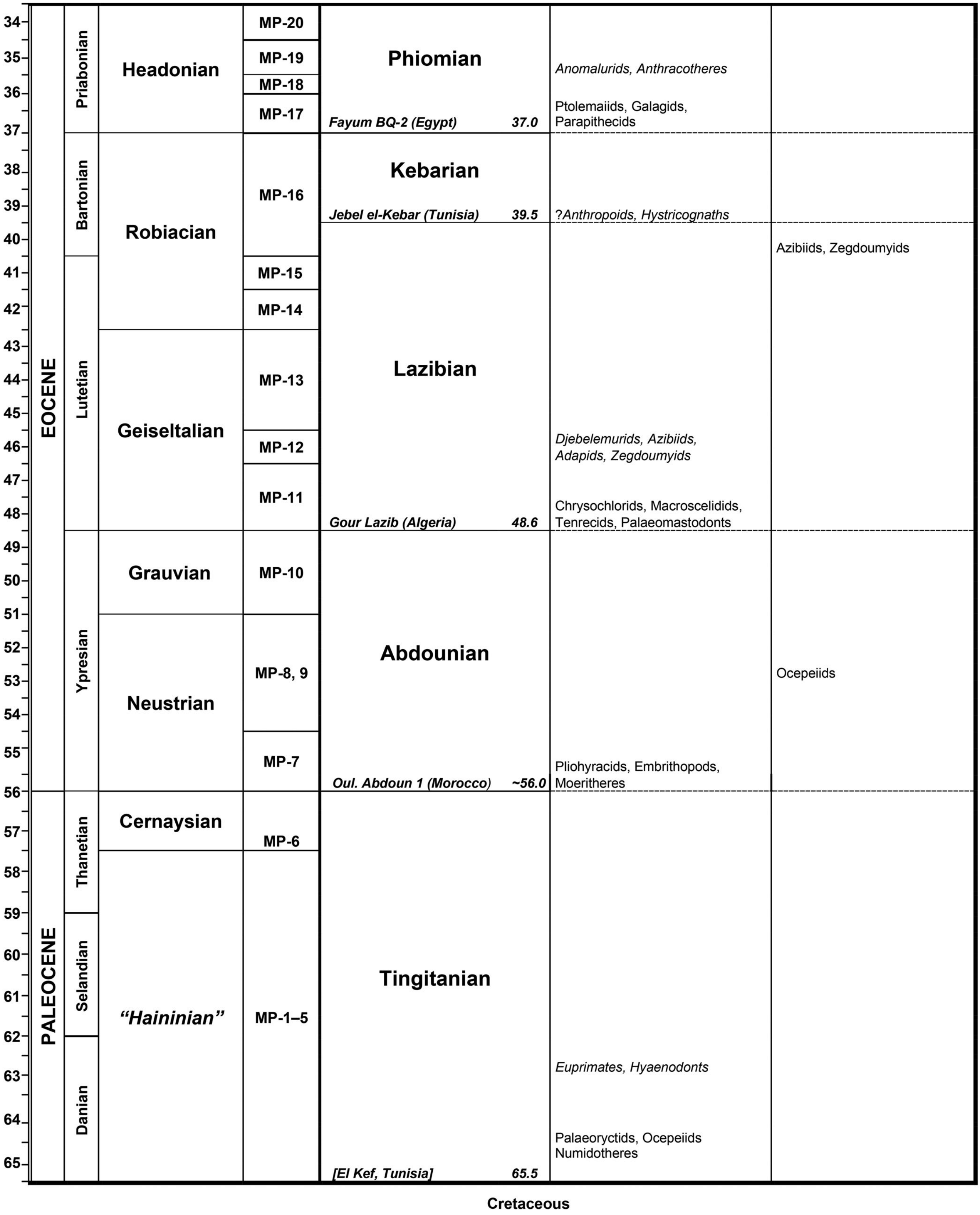


FIGURE 1. Continued

stratigraphically fixed boundary points for the continental Cenozoic of Spain. In most continental systems, however, biozonal concepts remain the norm in defining broad 'land mammal ages' (e.g., Wood et al., 1941; Steininger, 1999; Woodburne, 2007), such that age calibration becomes a secondary and constantly revised and debated value (cf. Marshall et al., 1983; Flynn and Swisher, 1995; Missiaen, 2011; Woodburne et al., 2014). The chronostratigraphic structure of the LMAs proposed here allows newly discovered sites and assemblages to be incorporated either by faunal correlation or relevant dating without disrupting boundaries, creating a stable pan-continental framework that permits patterns of faunal change such as those discussed near the end of this paper to be accurately analyzed. With LMA sequences presently defined for all other continents, this rounds out the global system and facilitates intercontinental correlation.

Previous African Schema

A number of researchers have previously defined subdivisions of the Afro-arabian mammalian record. A few of these schema were continent-wide, but none covered the entire Cenozoic. In

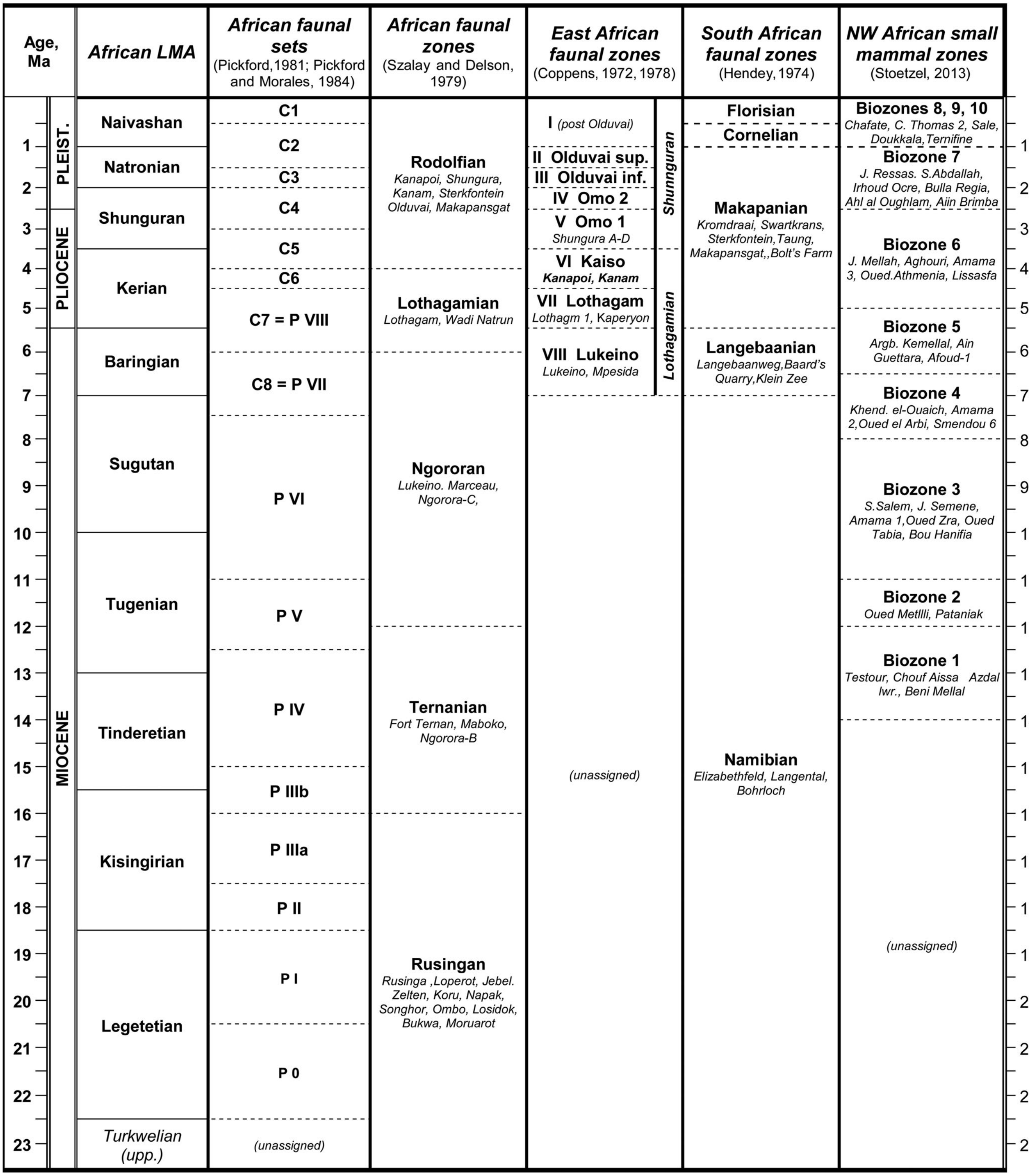


FIGURE 2. Previous African land mammal zonation schema. Stoetzel (2013) calibration is corrected to place Lisassfa in Zone 4 at 5.35 Ma. **Abbreviations: Pleist.**, Pleistocene.

Figure 2, a selection of these systems is correlated to the Neogene AFLMAs as an aid to interpreting the literature.

The most often-cited previous system is the sequence of 'faunal sets' created by Pickford (1981) for the Miocene of East Africa, subsequently extended to the Recent with comparisons to the Neogene fauna of Spain (Pickford and Morales, 1994; see also Pickford and Senut, 2003). In this system, Venn diagrams are used to group local faunas into sets according to the statistics of shared taxa, with dating and stratigraphic relationships that are noted within the sets providing age calibration. Correlation with the East African sets was found in Miocene faunas of North Africa (Pickford et al., 2001) and Namibia (Pickford and Senut, 2003). It remains the case, however, that here as in other fossil-defined units, recognition is subject to the presence of characterizing taxa or assemblages, and long-distance correlation is fundamentally less exact for this reason. In addition, dissimilarities may reflect differences in environment more than time (see 'Kisingirian').

The first pan-African scheme was put forward by Szalay and Delson (1979), who assigned 40 or so pre-Pleistocene primate-bearing localities across Africa to late Paleogene and Neogene time intervals that were named after their most prominent localities, with arbitrary chronological boundaries. Delson (1984) expanded the later Neogene part to document the relative age of more than 30 fossil cercopithecid species from 62 horizons in 25 Pliocene to Middle Pleistocene collecting areas from East Africa and South Africa, calibrated to the re-evaluated paleomagnetic and radiometric dating of the East African sequence by Cerling and Brown (1982).

A concurrent-range zonation of later Neogene faunas was proposed by Coppens (1972), according to changes over time in the assemblage of 14 large-mammal genera (primarily equids and proboscideans but also hominins), beginning in the Late Miocene at ca. 6.5 Ma. Eight units identified by Roman numerals were recognized in East Africa, together with three independently dated zones in South Africa, another three (not coeval) in North Africa, and two in the Albertine Rift. Coppens later (1978) referred to these units in proposing two inclusive 'continental stages,' Lothagamian and Shungurian, but apart from Savage and Russell (1983) referring to Lothagamian as a pan-African unit, these have seldom been used. In addition, a different 'Lothagamian' was almost simultaneously proposed by Szalay and Delson (1979; see above).

In South Africa, Hendey (1974; see also Klein, 1984) formalized the earlier 'faunal spans' erected by Cooke (1967) in a biozonation based on core groups of local faunas, much as in Europe (Fahlbusch, 1991). The ages of localities assigned to Florisian and Cornelian cover much of the same time span as our Naivashan, with the oldest Cornelian at Elandsfontein between 1.0 and 0.7 Ma (Klein et al., 2007; Braun et al., 2013). The present dating of the sites that were assigned to Makapanian age (Table 1) extend the base of this zone significantly beyond its original 3 Ma. The Langebaanian has been confirmed to lie within the early Pliocene (Roberts et al., 2011), while the Namibian age, based on the local faunas in the Sperrgebiet were simply assigned to a general Miocene age. In this sense the more recently discovered pre-Pliocene sites (cf. Pickford and Senut, 1997, 2003, 2008) would also belong to the Namibian.

In North Africa, Stoetzel (2013) defined 10 assemblage zones from mid-Miocene to Pleistocene, based on some 90 species of small mammals from over 100 individually dated Maghrebian localities, building on previous biochronological schemes for the later Neogene (Jaeger, 1977; Coiffat and Coiffat, 1991) that were revised by Benammi et al., (1996) and Benammi and Jaeger (2001), with paleomagnetic calibration of a number of key sites.

None of these zonal sequences, however, have physically defined chronostratigraphic boundaries, and aside from the specified index taxa of the Geraads zones (below), they are essentially groups of sites based on faunal similarity, with abstract calibration.

Other Land Mammal Zonation—Geraads (2002, 2010a) also described a concurrent-range sequence in the Pliocene and Pleistocene record of Morocco, according to the overlapping ranges of 14 large mammal and 8 small mammal genera, with calibration afforded by five dated sites.

Howell (1980) was the first to extend the European MN-zonation to Africa, with rough groupings of the known local faunas of Mio-Pliocene age. In this arrangement, Khendek-el-Ouaich, Sahabi and Wadi Natrun in North Africa, together with Lukeino, Lothagam-1, Mpesida in East Africa and Klein Zee and Langebaanweg in South Africa, were all correlated to lower MN-13 of western Europe, approximately equivalent to Baringian (Fig. 1). According to Howell, MN-14 or lower Pliocene was 'unknown in Africa' except for Hamada Damous, while taxa of later Pliocene age, characteristic of MN-15, were found only at Garet Ichkeul and Kanapoi. These latter three sites are all presently included, together with 24 other local faunas, in the Kerian LMA (Table 1), which is coeval with MN-14/15.

In the same year as Coppens, Maglio (1972) published four Plio-Pleistocene index zones for the newly discovered East Rudolf localities, which he defined by the presence of *Notochoerus capensis* in the Kubi Algi l.f. at ca. 4.6 Ma (corrected to 3.3 Ma by Brown and Cerling, 1982), *Mesochoerus limnetes* in the beds below the KBS tuff at 1.89 Ma, *Metridiochoerus andrewsi* above this horizon, and the extant *Loxodonta africana* in the uppermost Koobi Fora sequence. This zonation continued to be used in general discussion of the East African record (e.g., Boaz et al., 1982; Clark et al., 1984). A similar carefully documented phylostratigraphy of suids (Harris and White, 1979) also provided a reliable indicator of relative age.

A pan-African biochronology was presented by Savage and Russell (1983), who listed all taxa that had thereto been identified in the major Neogene localities across the continent and grouped them in the Rusingan, Ternanian and Ngororan of Szalay and Delson (1979), the Lothagamian of Coppens (1972) and the Laangebaanian and Makapanian of Hendy (1974). This arrangement was apparently too broad and loosely defined to be attractive in the field and has not been widely followed.

Climatostratigraphic Units—In early days, for lack of any other calibration, the climate-related units Kageran, Kamasian, Kanjeran, and Gamblian (in ascending stratigraphic order), based initially on the beach and terrace levels in the East African lake basins, were used to calibrate the sequence of upper Neogene archeological-paleontological sites of East Africa (Wayland, 1926; Leakey and Solomon, 1929). African continental environments unquestionably reflect the increasingly intense cycles of global climate in the late Cenozoic (DeMenocal, 2004; Maslin and Christensen, 2007) but the correlation has only recently been confirmed (see 'Natronian').

The prolific Pleistocene sites of the Casablanca region, where fossil mammals were first discovered in Africa, were formerly assigned to a sequence of glacio-eustatic stages (i.e., Amirian, Maarifian, Tensiftian, Anfatian, Soltanian, Ouljian, Rharbian) according to the succession of coastal terraces in the region (Biberson, 1971). Subsequent research (Lefevre and Raynal, 2002) presents a more complicated stratigraphic picture, and these units are no longer considered coherent and useful (see 'Naivashan').

Scope and Standards of the Study

This study is restricted to mainland Africa, Arabia, and the Levant, a contiguous paleogeographic entity with a characteristic fauna and flora in which long-established lineages have

TABLE 1. Sample localities and key genera of the African Land Mammal Ages. 'Kenya' is the default country. Two-letter codes (e.g., KV:, CH:) indicate locality groups, defined at the end of this table. In the case of localities with significant duration, only the basal age is cited here for consistent positioning.

Key genera	EQUATORIAL AFRICA	Ma	OTHER AFRO-ARABIA	Ma
NAIVASHAN (<1.0)				
(◆) *Megaceroides, Rusingoryx* (↗) *Nesokia, Saidomys, Sus* (↙) *Metridiochoerus, Afrochoerus, Sivatherium, Pelorovis, Megalotragus, Numidocapra, Ursus, Homotherium*	Olduvai Naisiusiu (Tanzania)	~0.02	CH: Gladysvale Cave .	0.04
	Mumba Cave-V (Tanzania)	~0.02	Melkbos; Swartklip (S. Afr.)	~0.06
	KV: Karungu Kisaaka	0.045	Casablanca Soltanian (Morocco)	0.07
	ET: Galana Boi	~0.08	Al Wusta (Saudi Arabia)	0.09
	AW: Melka Kunture 5; Herto Bouri (up.)	0.16	Klasies R.; Equus Cave (S. Afr.)	0.12
	OM: Omo Kibish I	0.195	Singa; Abu Hugar (Sudan)	0.13
	Olduv. Ndutu Beds (up.) (Tanzania)	~0.25	Rabat; Salé (Morocco)	0.14
	Laetoli Ngaloba (Tanzania)	~0.25	Groot Kloof T2, Florisbad (S. Afr.)	0.25
	AW: Herto Bouri (lwr.)	0.26	Jebel Irhoud J (Morocco)	0.32
(Late Naivashan NV2, <0.35)	Olorgesailie-Otuleilei	0.32	CH: Rising Star - Naledi	0.34
	Olduv. Ndutu Beds (lw.) (Tanzania)	0.37	Chrafate; Sidi Abderr. (Morocco)	~0.4
(◆) *Trischizolagus, Mascaromys, Nitidarcus, Bouria* (↗) *Dendrohyrax, Bathyergus, Parotomys, Afrochoerus, Connochaetes, Capra Archaepotamus, Menelikia, Parmularius, Eurygnathohippus*	Lainyamok	0.4	Tihodaine (Algeria)	~0.4
	Isimila (Tanzania)	~0.5	Florisbad P (lwr.) (S. Afr.)	0.48
	BA: Kapthurin K3, K4	0.55	Kabwe (Broken Hill) (Zambia)	~0.5
	AW: Asbole; Bodo Dawaitoli	0.55	Thomas 1, O. Hamida (Morocco)	0.5
	AW: Melka Kunture	1.0	Gesher Benot Ya'akov (Israel)	0.78
	Olduvai Masek; Peninj (up.) (Tanzania)	1.0	Tighennif - Ternifine (Algeria)	0.8
	Kariandusi; Isinya	1.0	Thomas L, S. Abdallah (Morocco)	~1.0
	Aalat Buia (Eritrea)	1.0	Elandsfont. - Saldanha (S. Afr.)	1.0
	< Olorgesailie 1-4	1.0	Cornelia-Uitzhoek (S. Afr.)	1.0
NATRONIAN (<2.0)				
(◆) *Prodontomys, Dinopithecus, Gorgopithecus, Parameriones* (↗) *Chrysospalax, Bunolagus, Heliosciurus, Meriones, Taurotragus, Bos, Ourebia, Neotragus, Alcelaphus, Sigmocerus* (↙) *Gigantohyrax, Deinotherium, Mammuthus, Anancus, Mammut, Australopithecus, Paranthropus, Cercopithecoides, Rhinocolobus, Parapapio, Protalactaga, Notochoerus, Hexaprotodon, Damalavus, Leptobos, Makapania, Chasmaporthetes, Dinofelis, Parahyena, Ancylotherium*	KV: Kanam East	1.1	CH: Bolt's Farm (up.)	1.2
	OM: Shungura L, ET: Chari	1.38	Jebel Irhoud Ocre (Morocco)	1.2
	Olduvai Bed III - IV (Tanzania)	1.4	Bochianga; Yayo (Chad)	~1.5
	KV: Kanjera North	1.4	Humpata Cangalongue (Angola)	~1.5
	AW: Melka Kunture1-2	1.5	CH Cooper's Cave D	1.5
	WR: Nyabusosi	1.5	'Ubeidiya (Israel)	1.6
	AW: Barogali (Djibouti)	1.5	Djebel Ressas (lwr.) (Tunisia)	1.6
	ET: Ileret	1.53	Mansourah; A. Kemellal (Algeria)	~1.6
	OM: Shungura K; ET: Okote	1.56	Aigamas; Uisib; Rietfont. (Namibia)	~1.6
	Peninj Humbu (Tanzania)	1.7	CH: Gladysvale	~1.7
	AW: Busidima, Konso-Gardula	1.73	CH: Sterkfontein 5	1.7
	ET: Fejej FJ-5	1.75	CH: Gondolin; Luleche	~1.8
	BA: Chesowanja - Chemoigut	~1.8	Bulla Regia (Tunisia)	~1.8
	WT: Kaitio; Nato'o	1.87	CH: Kromdraai A	1.8
	OM: Shungura H-J; ET: KBS	1.87	CH: Bolt's Farm (main)	2.0
	ET: Fejej FJ-1	1.9	Ain Hanech; El-Kherba (Algeria)	2.0
	ET: Marsabit - Chalbi	1.9	CH: Malapa, Drimolen	2.0
	AW: Anabo Koma, Gobaad	1.9	CH: Swartkrans 1	2.0
	<Olduvai Bed I-II (Tanzania)	2.0		
SHUNGURAN (<3.6)				
(◆) *Paleothentoides, Kenyanthropus, Procercocebus, Soromandrillus, Awashia, Pliocrocuta, Pseudocivetta,Therailurus* (↗) *Macroscelides, Procavia, Otolemur, Paranthropus, Homo, Rhinocolobus, Papio, Arvicanthus, Zelotomys, Jaculus, Gerbillus, Erinaceus, Silvisorex, Phacochoerus, Pelorovis, Antidorcas, Canis, Ursus, Otocyon, Lycaon, Atilax, Crossarchus, Proteles, Suricata, Caracal, Equus* (↙) *Primelephas, Paracolobus, Prolagus, Xenohystrix, Prototomys, Nyanzachoerus, Libycosaurus, Ugandax, Damalborea, Budorcas, Megaviverra, Percrocuta, Ikelohyaena, Hyaenictis, Hyaenictitherium*	OM: Shungura E-G; ET: Burgi (up.)	2.2	Ain Brimba (Tunisia)	~2.3
	WR: Semliki Lusso; Kaiso	2.2	Ain Boucherit, Ain Jourdel (Algeria)	2.32
	KV: Kanjera South, K. East	2.3	CH: Sterkfontein 4; Kromdraai B	2.4
	WT: Kalochoro; Lokalalei	2.33	Chiwondo Mwimbi (Malawi)	2.4
	AW: Matabaietu	2.5	Zarqa Valley (Jordan)	2.48
	OM: Shung. D; ET: Burgi (lwr.)	2.52	Ahl al Oughlam (Morocco)	2.5
	Laetoli Ndolanya (Tanzania)	2.66	Humpata Leba - Tchiua (Angola)	~2.5
	OM: Shungura C	2.7	Jagersquelle; Friesenb. (Namibia)	~2.5
	AW: Lee Adoyta - Busidima (bas.)	2.93	Taung; Buxton Limewks (S. Afr.)	2.7
	BA: Chemeron JM 90	~3.2	Chiwondo (mid) (Malawi)	2.7
	AW: Denen Dora, Kada Hadar	3.24	O. Fouarat; O. Akrech (Morocco)	?3.0
	WT: Lomekwi 1-3	3.35	Bethlehem (Israel)	~3.0
	OM: Shung. B; ET: Tulu Bor	3.42	Hondekklip 30m (S. Afr.)	~3.0
	AW: Hadar S. Hakoma, Dikika	3.44	Oued Smendou (Algeria)	~3.0
	Nairobi Kantis	3.45	CH: Makapansgat; Hoogland	3.2
	ET: Lokochot	3.6	!Nqumtsa Bone Cave (Botswana)	~3.5
	<OM: Shungura A	3.6	Arghoub (A. Kandoula) (Morocco)	~3.5
KERIAN (<5.3)				
(◆) *Stegodibelodon, Laetolia, Boltimys, Pliopapio, Kuseracolobus, Euryotomys, Brabovis, Praedamalis, Saotherium*	Laetoli (up.) (Tanzania)	3.85	Koro Toro; O. Derdemi (Chad)	3.65
	AW: Hadar Basal Mbr	3.9	Lac Ichkeul - J. Mellah (Tunisia)	~3.7
	WT: Kaiyumung; Kataboi	3.9	CH: Sterkfontein 2; Matjhabeng	3.7

(*Continued*)

TABLE 1. Continued.

Key genera	EAST AFRICA	Ma	OTHER AFRO-ARABIA	Ma
(↗) *Chlorotalpa, Elephantulus, Australopithecus, Colobus, Theropithecus, Thryonomys, Desmodillus, Praeomys, Mus, Apodemus, Mastomys, Gerbilliscus, Suncus, Notochoerus, Stylochoerus, Camelus, Syncerus, Beatragus, Antilope, Oryx, Oreotragus, Redunca, Connochaetes, Lutra, Mungos, Cynictis, Crocuta, Homotherium, Panthera, Acinonyx, Diceros* (↙) *Stegodon, Ardipithecus, Progonomys, Paracamelus,Tragoportax, Miotragocerus, Brachypotherium, Agriotherium, Hippotherium*	WR: Warwire; Nyamavi	~3.9	Chiwondo (up.) 3A (Malawi)	3.76
	ET: Lonyumun; Moiti; Allia Bay	4.1	Sais (Morocco)	~4.0
	WT: Kanapoi; Ekora	4.17	Amama-3 - El Eulma (Algeria)	~4.0
	OM: Mursi	~4.2	Vaal R. (Old Terrace) (S. Afr.)	?4.0
	Aterir; Karmosit	~4.2	Kollé; Toungour (Chad)	4.2
	AW: Sagantole As Aela	4.2	Kolinga (Chad)	4.5
	ET: Fejej FJ-3, AW: Aramis	4.42	CH: Bolt's Farm Waypoint 160	~4.5
	Laetoli (lwr.) (Tanzania)	4.4	Douaria (Tunisia)	~4.5
	BA: Chemeron - Tabarin	4.5	Hamada Damous (Morocco)	~4.5
	AW: Galili	4.5	Langebaan, Baards Qy. (S.Afr.)	5.15
	AW: Sagantole Segou Noum.	4.6	Ain Guettara (Morocco)	~5.3
	WT: Lothagam Apak	5.0	Chiwondo (lwr.) (Malawi)	~5.3
	AW: Sagantole As Duma	5.2	Lisassfa (Morocco)	5.3
	Manonga Ibole;Tinde (Tanzania)	~5.3	Afoud-8; Azib (Morocco)	5.3
	<BA: Chemeron - Mabaget	5.3		
	BARINGIAN (<6.8)			
(◆) *Sahelanthropus, Orrorin, Libypithecus* (↗) *Mammuthus, Mammut, Elephas, Ardipithecus, Macaca, Paracolobus, Lepus, Cricetus, Paracamelus, Kolpochoerus, Sivatherium, Giraffa, Tragelaphus, Madoqua, Kobus, Raphicerus, Mellivora, Megaviverra, Civettictis, Hyaena* (↙) *Prodeinotherium, Myocricetodon, Paraphiomys, Palaeotragus, Plesiogulo*	WR: Nkondo Nyawiege; Nyaburogo	~5.5	Wadi Natrun (Egypt)	~5.5
	AW: Adu-Asa (up.), Kuseralee	5.60	Wanou - A. Kandoula (Morocco)	5.5
	WR: Oluka (up.); Nkondo	~6.0	Kossom Bougoudi (Chad)	5.5
	WR: Sinda Ongoliba	~6.0	Afoud-1, 2 (Morocco)	6.2
	Lemudong'o	6.1	Argoub Kemmelal-1 (Algeria)	6.0
	BA: Lukeino	6.1	Afoud-5 (Morocco)	6.5
	WT: Lothagam Nawata (up.)	6.40	Sahabi (Libya)	~6.5
	AW: Adu-Asa (lwr.)	6.50	Hondeklip 50m, Kl. Zee (S. Afr.)	~6.5
	<BA: Mpesida	6.8		
	SUGUTAN (<10)			
(◆) *Samburupithecus, Chororapithecus, Nakalipithecus, Nakalimys, Kenyatherium* (↗) *Stegodon, Loxodonta, Primelephas, Cercopithecoides, Petromus, Hystrix, Paraxerus,Saccostomus, Paraethomys, Hexaprotodon, Archaepotamus, Hippopotamus, Aepyceros, Vulpes, Viverra, Galerella, Dinofelis, Felis, Eurygnathohippus* (↙) *Tetralophodon, Choerolophodon, Zygolophodon, Paraulacodus, Paranomalurus, Megapedetes, Proheliophobus*	WT: Lothagam Nawata (lwr.)	7.4	Tizi N'Tadourt (Morocco)	?7
	AW: Chorora (up.)	7.6	Tor. Menalla, Bochianga (Chad)	7.4
	AW: Chorora Beticha	8.1	Menacer, K. el-Ouaich (Algeria)	7.4
	AW: Chorora; Gololcha	8.5	Baynunah (Abu Dhabi)	~7.5
	Namurungule	~8.5	Amama-2, Smendou 6 (Algeria)	7.6
	BA: Ngeringerowa	~9.0	Amama-1, Tafna 2 (Algeria)	8.8
	<BA: Nakali	10.0	Dj. Krechem (Tunisia)	~9.0
			Berg Aukas 3 (Namibia)	~9.5
			Harasib (Botswana)	~9.5
			Oued Zra, Afoud 6 (Morocco)	10
	TUGENIAN (<12.8)			
(◆) *Otavipithecus, Giraffokeryx, Sivoreas* (↗) *Heterohyrax,Tetralophodon, Deinotherium, Galago, Dendromus, Progonomys, Crocidura,Nyanzachoerus, Miotragocerus, Damalavus, Hippotherium, Ceratotherium* (↙) *Victoriapithecus, Democricetodon, Listriodon, Morotochoerus, Dorcatherium, Canthumeryx, Hypsodontus, Protarsomys*	BA: Ngorora D-E	~11	Jebel Hamrin (Iraq)	~10.5
	WR: Kisegi	~12.5	Farafra - Sh. Abdallah (Egypt)	~11
	<BA: Ngorora A-C, Kabarsero	12.8	Beglia; Jebel Semene (Tunisia)	~11
			Rooilepel (mid.) (Namibia)	~11
			Od.Tabia - Ait Kandoula (Morocco)	~11
			Bir el Ater 2, 3; Oued Mya (Algeria)	~12
			Sahabi (lwr.) (Libya)	~12
			Berg Aukas (main) (Namibia)	~12
			Bou Hanifia 1-3 (Algeria).	12.2
	TINDERETIAN (<15.8)			
(◆) *Mabokopithecus, Equatorius, Kenyapithecus, Megalochoerus, Paradiceros* (↗) *Anancus, Pedetes, Gazella, Genetta, Herpestes, Percrocuta, Proticitherium* (↙) *Afrohyrax, Archaebelodon, Gomphotherium, Eozygodon, Afropithecus, Diamantomys, Kenyasus, Notocricetodon, Amphechinus, Eotragus, Walangania, Anasinopa, Hyainailourus,Amphicyon, Martes*	BA: Alengerr	13	Cherichera (Tunisia)	?13
	WT: Esha; Atirrir; Napudet	~13	Pataniak-6 - J. Irhoud (Morocco)	~13
	KV: Fort Ternan	13.8	Azdal 1 - Ait Kandoula (Morocco)	13.5
	Nachola, Nyakach, Kirimun	15	Beni Mellal (Morocco)	13.5
	KV: Maboko, Kaloma, Majiwa	15.3	Testour (Tunisia)	~13.5
	<BA: Muruyur Kipsaramon	15.8	Rooilepel (lwr.) (Namibia)	~14
			Hofuf (Saudi Arabia)	~15
			Jebel Zelten (up.) (Libya)	~15.5
	KISINGIRIAN (<18.5)			
(◆) *Prohyrax, Platybelodon, Turkanapithecus, Ekembo, Heliopithecus, Parapedetes* (↗) *Orycteropus, Choerolophodon, Martes Protalactaga, Democricetodon, Kenyapotamus, Amphicyon, Victoriapithecus* (↙) *Pachyhyrax, Dendropithecus, Phiomys Pterodon, Mioprionodon*	KV: Ombo; Mariwa; Rus. Kulu	~16	Ryskop; Hondeklip 90m (S. Afr.)	~16
	ET: Buluk	17.2	Arrisdrift (Namibia)	~16
	WT: Muruarot; Kalodirr	17.5	As Sarrar; Ad Dabt. (Saudi Arabia)	~16
	WT: Loperot; Locherangan	17.6	Ghaba - Huqf (Oman)	~16
	KV: Karungu	~18.3	Jebel Zelten, Reguba (Libya)	~16
	KV: Rus. Hiwegi, Mfwangano	18.3	Wadi Moghra (Egypt)	~18
	<KV: Rusinga Kiahera	18.5	Sperrgebiet; Auchas (Namibia)	~18

(*Continued*)

TABLE 1. Continued.

Key genera	EAST AFRICA	Ma	OTHER AFRO-ARABIA	Ma
	LEGETETIAN (<22.5)			
(◆) *Proconsul, Alophe, Legetetia*	Bukwa; Moroto (Uganda)	19.3	J. Midrash Shamali (Saudi Arabia)	?20
(↗) *Progalago, Zygolophodon, Afropithecus,*	Napak (Uganda)	20.1	Oued Bazina (up.) (Tunisia)	?20
Nyanzapithecus, Megapedetes, Proheliophobus,	KV: Songhor; Koru; Chamtwara.	20.3	Jebel Zelten (lwr.) (Libya)	~20
Amphechinus, Morotochoerus	ET: Kajong - Mwiti	20.3		
Dorcatherium, Palaeotragus, Walangania	WT: Nakwai	22.5		
(↙) *Thyrohyrax, Brachyodus*	< KV: Meswa Bridge	~22.5		
	TURKWELIAN (<28.2)			
(◆) *Kamoyapithecus, Rukwapithecus,*	Mai Gobro (Eritrea)	~23	Wadi Sabyah (Saudi Arabia)	?23
Lokonepithecus, Nsungwepithecus, Saadanius	WT: Erageleit	23.9	Silica N-S; Eocliff, Eoridge (Namibia)	?25
(↗) *Afrohyrax, Archaebelodon,*	Rukwa - Nsungwe (Tanzania)	25.2,	Harrat al Ujayfa (Saudi Arabia)	~28
Prodeinotherium, Gomphotherium,	WT: Losodok, Lokone	~26		
Dendropithecus,	Dogali (Eritrea)	26.8		
(↙) *Ptolemaia, Megalohyrax, Bunohyrax,*	< Chilga (Ethiopia)	28.2		
Paleomastodon, Metaphiomys				
	QATRANIAN <33.4			
(◆) *Wadilemur, Proteopithecus, Serapia,*	(None)		Gebel Qatrani A-E (Egypt)	30.7
Parapithecus, Oligopithecus, Propliopithecus,			Zallah (Libya)	~31
Dakhlamys, Qatraniodon			Thaytiniti; Taqah (Oman)	~33-31
(↗) *Pachyhyrax, Paraphiomys, Anasinopa*			Dakhla C2 (Morocco)	33.4
(↙) *Titanohyrax, Protophiomys, Afrotarsius*			< Gebel Qatrani L-41 (Egypt)	33.4
	PHIOMIAN (<37.0)		Qasr el-Sagha (Egypt)	35
(◆) *Nosmips, Masradapis, Saharagalago,*	(None)		Bir el-Ater - Nementcha (Algeria)	~35
Biretia, Talahpithecus, Nementchamys			Aydim (Oman)	~36
(↗) *Ptolemaia, Thyrohyrax, Afrotarsius,*			Dur al Talha; J. Hashawq (Libya)	~36
(↙) *Barytherium*			< Birqet Qarun BQ-2 (Egypt)	37
	KEBARIAN (<39.5)			
(◆) *Amamria*	(None)		Aydim lwr. - Salalah (Oman)	38.5
(↗) *Arsinoitherium, Protophiomys*			Bir Om Ali (Tunisia)	?39
			< Djebel el-Kebar (Tunisia)	39.5
	LAZIBIAN (<48.6)			
(◆) *Chambius, Notnamaia, Djebelemur,*	Mahenge (Tanzania)	45.6	Aznag - Ouarzazate (Morocco)	45
Azibius, Namadapis, Algeripithecus,			Taiba N'Diaye (Senegal)	45
Namatherium, Glibia, Zegdoumys,			Black Crow (Namibia)	~47
(↗) *Bunohyrax, Paleomastodon, Pterodon*			Chambi (Kasserine) (Tunisia)	~48
(↙) *Furodon*			< Gour Lazib, Gl. Zegdou (Algeria)	48.6
	ABDOUNIAN (<~56)			
(◆) *Seggeurius, Stylolophus, Koholia*	(None)		El Kohol (Algeria)	51
(↗) *Titanohyrax, Furodon*			N'Tagourt 2 - Ouarzazate (Morocco)	~52
(↙) *Todralestes, Ocepeia, Phosphatherium,*			Tamaguelelt (Mali)	?52
Afrodon, Garatherium, Palaeoryctes			< Ouled Abdoun 1 (Morocco)	~56
	TINGITANIAN (<66.5)			
(◆) *Cimolestes, Eritherium, Adapisoriculus,*	(None)		Ad. Mgorn 2 - Ourazazate (Morocco)	~58
Abdounodus,Tinerhodon, Lahimia,			< O. Abdoun 2; Chennane (Morocco)	~60
Altiatlasius				
(↗) *Afrodon, Garatherium,Todralestes,*				
Ocepeia, Phosphatherium, Palaeoryctes				

Key to symbols	Locality groups
(◆) Only appearance	AW: Awash (eastern Ethiopian Rift)
(↗) First appearance	BA: Baringo (Baringo basin, Tugen Hills)
(↙) Last appearance	CH: Cradle of Humanity (NE Gauteng)
? Uncertain date	ET: East Turkana (east side L. Turkana)
~ Approximate date	KV: Kavirondo Rift (SW Kenya)
< Defining level	OM: Omo River basin (NE extension Turkana)
	WR: Western Rift (L. Albert, L. Edward)
	WT: West Turkana (west side L. Turkana)

retained an influential role. The fossil record of Madagascar is virtually unknown, and in any case would be only distantly relevant. We also have not included the record of peripheral microplates within the Tethys, such as the Apulian microplate that carries the peninsula of Italy (Channel et al., 1979) or the Betic, Dinaric, Rhodopean, Anatolian, and Iranian blocks (Dercourt et al., 1986). One or more of these must have been involved in the limited exchanges between Eurasia and Africa in the late Cretaceous and early Paleogene (Gheerbrant and Rage, 2006), but that is also outside the focus of the present study.

Latitudinal Realms and Sample Bias—The latitudinal position of Afro-arabia changed relatively little during the Cenozoic, so that a broad division into three realms – northern, equatorial, and southern – was relevant to some extent throughout the period of this study (Fig. 3). As it happens, the present 15°N parallel falls between the equatorial region with its Rift Valley sites and the fossil-bearing region to the north in the Maghreb, Libya, Egypt, the Levant, and the Arabian peninsula. In turn, the 15°S parallel today coincides very well with the southern terminus of the East African Rift in the Zambesi Valley, and also with the northeastern tip of the fossiliferous paleokarst belt that extends across Africa from Malawi to Angola (Pickford et al., 1990, 1994). This convenient latitudinal symmetry is therefore used to define the boundaries of the three geographical realms incorporated in the AFLMA (Fig. 4), with a minor exception for the sites in the Chad basin, just south of the 15°N parallel, which we consider as being essentially 'north' in their paleogeographic character.

In regard to the mammalian record, the three realms have distinctive sampling biases (see 'Observations'). Fossils in the northern realm are almost entirely from low-elevation and coastal deposits with relatively few from cave karst, while Plio-Pleistocene sites in the southern realm are preponderantly from karst with relatively few sites in alluvial and coastal beds, even as earlier sites are almost wholly coastal as in the north. On the other hand, the paleontology of the rifted terrain in the equatorial realm, which is the basic framework for the Neogene ages, consists almost entirely of material from impounded, heavily mineralized waters in rift and perivolcanic depressions associated with alkaline volcanics, that create a sedimentary environment emulating the taphonomic conditions of desert playas (Harris and Van Couvering, 1995). Notably, the same scenario of volcanically mineralized ponds is also responsible for the exceptional Paleogene local faunas of Namibia (Pickford, 2015). Even with such exceptions, the distinctive geographic and geologic context of samples from the three realms justifies their specification in the occurrence data compiled in Appendix 1.

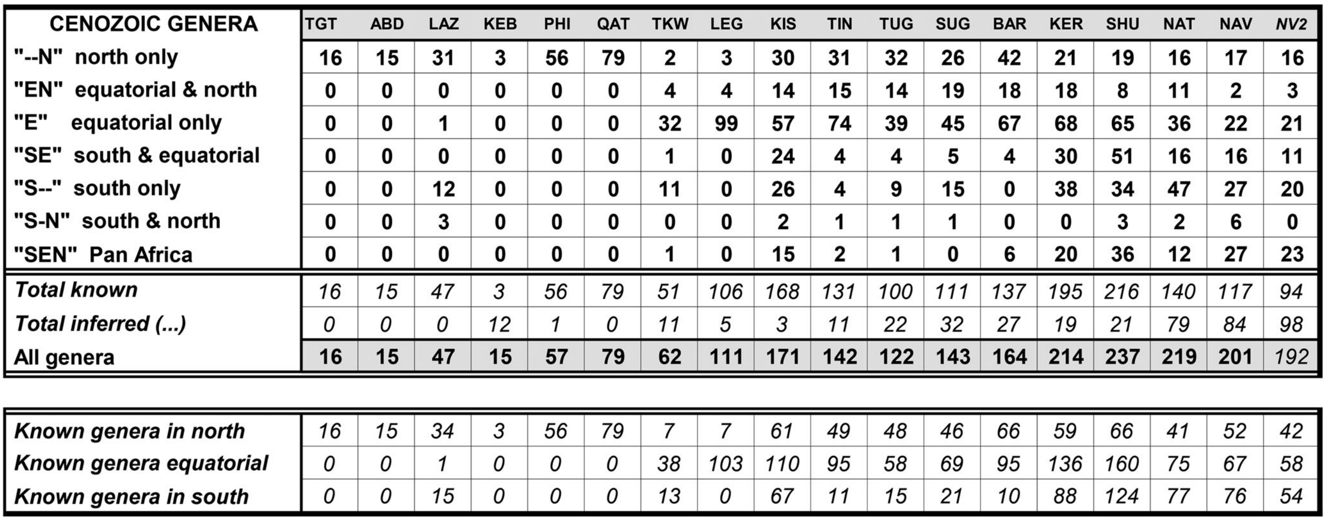
Aside from the absence of specimens from the interior highlands during the Paleogene (Table 1; Fig. 3), the most conspicuous gap in the record is that of the closed-canopy forest of equatorial West Africa. It is notable that the sites in the Albertine or western rift, which are on the margin of the modern equatorial forest (Pickford et al., 1993), have a fossil fauna that is not significantly different from that of the eastern segment of the rift.

Finally, there is a time-dependent bias. Beginning in the Early Miocene but increasing from later Miocene onwards, the mammalian communities became more localized through the effects of ocean cooling. The increasing latitudinal gradient and seasonality favored the expansion of grasslands, brushlands and (eventually) deserts, replacing open forests and woodlands over great areas (Retallack, 2001; DeMenocal, 2004; Bobe, 2006; Senut et al., 2009; Levin, 2015). This shift in the habitat is reflected in a major Mio-Pliocene overturn (see 'Observations'), as distinguished from the simple improvement of the record in younger deposits.

Limits of Documentation—For practical reasons, the references that are cited herein with regard to the paleontology and age of specified localities are intentionally limited to recent literature. Citations to earlier sources may be found in these works, as well as in the bibliography of the fossil mammals of Africa from 1950 to 1972 (Cross and Maglio, 1975). For systematics and taxonomy, we have generally followed the authors in Werdelin and Sanders (2010), with some adjustments according to more recent work (cf. Appendix 1). In the case of complex localities with individually named collecting sites and/or several fossil-bearing levels in the same stratigraphic unit, such details are subsumed in a single locality name to reflect a composite local fauna. The list of localities in Table 1 does not include many of the localities whose limited sample is duplicated in major sites of the same region, or which yield less significant samples. Finally, in order to place relatively poorly dated localities in the AFLMA system, it has been necessary in some cases to estimate their age from the available information, while recognizing that initial rough estimates are almost always inconsistent with new data. In any case, and with the sole exception of the Early Eocene Abdounian, no localities with such estimated age values are used to define the AFLMA units.

Principles of Definition—The assignment of localities to LMA units is determined by their measured or inferred ages, as shown in Table 1, and the genera identified in these localities are thereby assigned to LMA as shown in Appendix 1. In the briefer LMAs, and with the more rarely found genera, it is strongly probable that further studies will expand generic ranges into the adjoining units. Allowing for such imprecision, the overall groupings of genera in the LMAs nonetheless provide informative and relatively stable evidence of the development of the Afro-arabian land mammal community over the past 65.5 million years (see 'Observations'). As localities and specimens become more rare and the record less detailed with increasing antiquity (Table 1; Fig. 3), the older mammal ages necessarily extend over longer intervals.

The reference localities that define the bases of the LMAs were selected, as far as possible, with regard to important



CENOZOIC GENERA	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NAV	*NV2*
"--N" north only	**16**	**15**	**31**	**3**	**56**	**79**	**2**	**3**	**30**	**31**	**32**	**26**	**42**	**21**	**19**	**16**	**17**	**16**
"EN" equatorial & north	**0**	**0**	**0**	**0**	**0**	**0**	**4**	**4**	**14**	**15**	**14**	**19**	**18**	**18**	**8**	**11**	**2**	**3**
"E" equatorial only	**0**	**0**	**1**	**0**	**0**	**0**	**32**	**99**	**57**	**74**	**39**	**45**	**67**	**68**	**65**	**36**	**22**	**21**
"SE" south & equatorial	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**24**	**4**	**4**	**5**	**4**	**30**	**51**	**16**	**16**	**11**
"S--" south only	**0**	**0**	**12**	**0**	**0**	**0**	**11**	**0**	**26**	**4**	**9**	**15**	**0**	**38**	**34**	**47**	**27**	**20**
"S-N" south & north	**0**	**0**	**3**	**0**	**0**	**0**	**0**	**0**	**2**	**1**	**1**	**1**	**0**	**0**	**3**	**2**	**6**	**0**
"SEN" Pan Africa	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**15**	**2**	**1**	**0**	**6**	**20**	**36**	**12**	**27**	**23**
Total known	*16*	*15*	*47*	*3*	*56*	*79*	*51*	*106*	*168*	*131*	*100*	*111*	*137*	*195*	*216*	*140*	*117*	*94*
Total inferred (...)	*0*	*0*	*0*	*12*	*1*	*0*	*11*	*5*	*3*	*11*	*22*	*32*	*27*	*19*	*21*	*79*	*84*	*98*
All genera	**16**	**15**	**47**	**15**	**57**	**79**	**62**	**111**	**171**	**142**	**122**	**143**	**164**	**214**	**237**	**219**	**201**	*192*

Known genera in north	*16*	*15*	*34*	*3*	*56*	*79*	*7*	*7*	*61*	*49*	*48*	*46*	*66*	*59*	*66*	*41*	*52*	*42*
Known genera equatorial	*0*	*0*	*1*	*0*	*0*	*0*	*38*	*103*	*110*	*95*	*58*	*69*	*95*	*136*	*160*	*75*	*67*	*58*
Known genera in south	*0*	*0*	*15*	*0*	*0*	*0*	*13*	*0*	*67*	*11*	*15*	*21*	*10*	*88*	*124*	*77*	*76*	*54*

FIGURE 3. Distribution of African Cenozoic genera by realm. Strong differences are due to the incompleteness of the record. The more consistent count in the northern realm indicates a stable continent-wide ecosystem. **Abbreviations: ABD**, Abdounian; **BAR**, Baringian; **KEB**, Kebarian; **KER**, Kerian; **KIS**, Kisingirian; **LAZ**, Lazibian; **LEG**, Legetetian; **NAT**, Natronian; **NAV**, Naivashan; **PHI**, Phiomian; **QAT**, Qatranian; **SHU**, Shunguran; **SUG**, Sugutan; **TGT**, Tingitanian; **TKW**, Turkwelian; **TUG**, Tugenian.

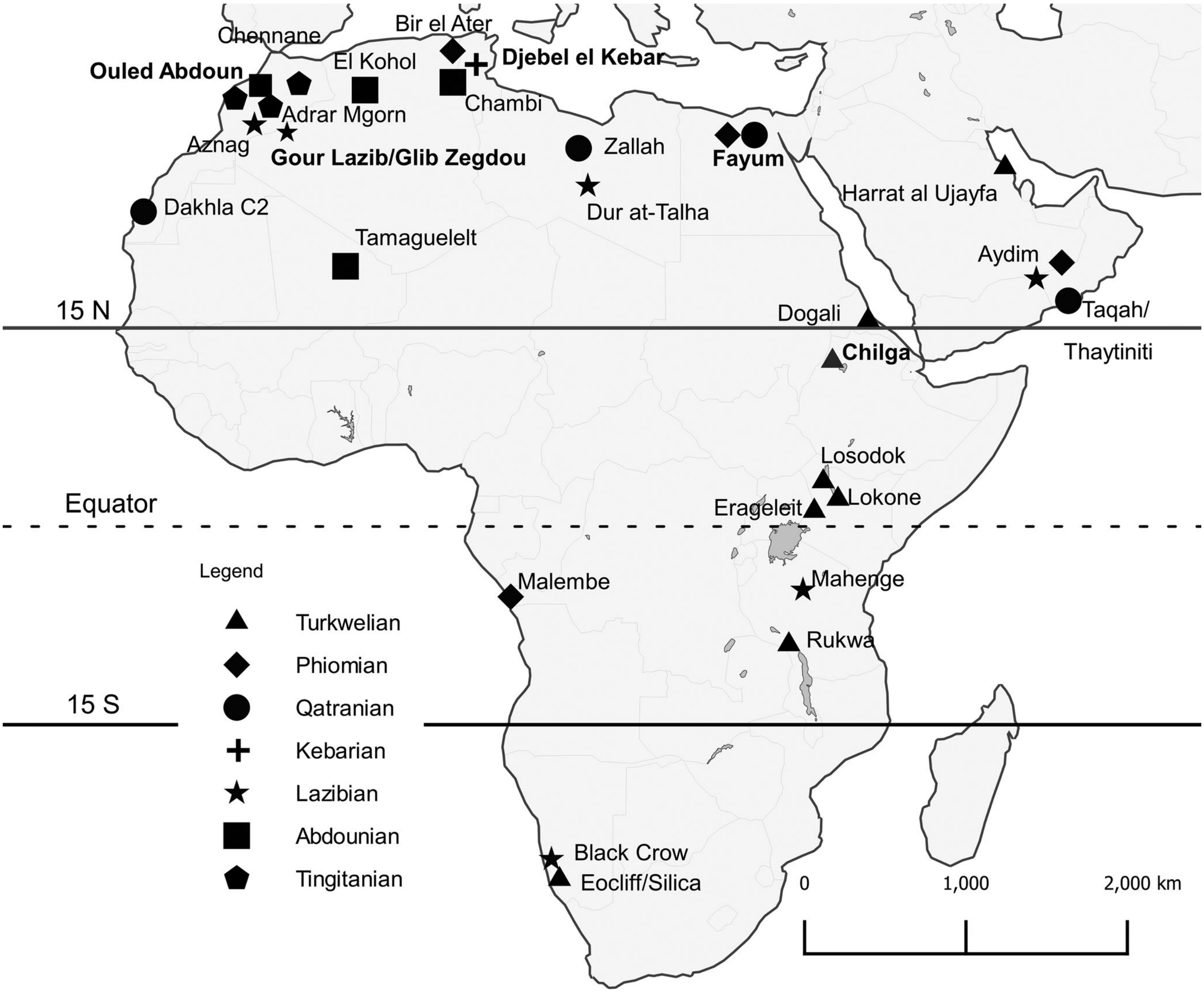


FIGURE 4. Principal Paleogene localities; emphasized names are the defining localities for the Paleogene LMAs (cf. Table 1). The northern, equatorial, and southern geographic realms are defined by the 15th parallels.

transitions, such as the lower limits of major fossiliferous sequences (Phiomian, Kisingirian, Tugenian, Shunguran, Natronian) or events that impacted the record, i.e., the opening of the Rift Valley and the initiation of open exchange with Laurasia at the beginning of the Neogene (Legetetian), the expansion of equatorial grasslands (Baringian), or the end of Mediterranean desiccation at the beginning of the Pliocene (Kerian). The Abdounian, Lazibian, and Kebarian ages are defined to recognize the better-documented intervals in the sparse early Paleogene record (Table 1). In all instances where features of the Afro-arabian record result in LMA boundaries that approximately coincide with European or global units (Fig. 1), this is not through primary intent. The LMAs are described below in stratigraphic order.

AFRICAN LAND MAMMAL AGES

Tingitanian

The Tingitanian age (65.5–56 Ma), defined by the Cretaceous–Paleocene boundary, is approximately coeval with the Paleocene epoch (Fig. 1). The name is taken from the Roman province of Tingitana, now Morocco, because this is the only known source of African fossil mammals of this age—the mid- and upper Paleocene strata of the Ouled Abdoun lagoonal phosphate deposit and the lower part of the Ourzazate foreland basin (Gheerbrant, 1995, 2009; Gheerbrant et al., 1998). These widely exposed shallow water deposits are relatively well dated through correlation of the associated marine biota (Tabuce et al., 2005), by paleomagnetic surveys in the Ourzazate basin (Gheerbrant et al., 1998), and by chemostratigraphy of the Ouled Abdoun phosphates (Yans et al., 2014) that places the Lower Bone Bed—the oldest known Cenozoic mammal locality in Africa—in the Middle Paleocene (upper Selandian), at ca. 60 Ma.

Despite their relative rarity, the 16 so far known genera of Tingitanian age suggest a complex biogeographic picture at the beginning of the Cenozoic. The distinctive Afrotheria, in what may be a uniquely African clade (cf. Werdelin and Sanders, 2010), are represented by two early paenungulates and three proboscideans. The relationship of the listed Afroinsectiphilia to Afrotheria is uncertain, and they may possibly be related to Laurasian forms (Gheerbrant, 1995; Seiffert, 2010). Other Tingitanian taxa so far described belong to clades (Adapisoriculida, Primates, Hyaenodonta) that are also known in the Late Cretaceous and Paleocene of Laurasia, but not so far in the fossil record of other Gondwana land masses. The only evidence of a mammalian connection to other Gondwana continents, a connection that is made plain by the inherited ratites and varanids in Africa, are two Late Cretaceous gondwanatheres, one in Tanzania (Krause et al., 2003) and the other in Madagascar (Krause et al., 2014), that could have common ancestry with forms in South America and India (cf. Goswami et al., 2011). The presence of hyracoid afrotheres (Benoit et al., 2016) in the early Abdounian would suggest that this group, not to mention other lineages that first appear in the African Eocene, may yet be traced into the poorly sampled Tingitanian Paleocene.

Abdounian

The Abdounian Age (56–48.6 Ma), named for the widely fossiliferous Ouled Abdoun phosphate basin in the coastal Atlas of northwestern Morocco, is defined by the Ouled Abdoun-1 site in the Grand Douari quarries that expose the upper part of this thick deposit (Gheerbrant et al., 2003). As in most African Paleogene localities, the known Abdounian land mammals are from localities in coastal deposits, in this instance associated with shallow-marine fossils that provide correlation to the Lower Eocene Ypresian stage (Fig. 1). In addition to the type sequence, the other principal sites are the middle Abdounian El Kohol section near Brezina, Algeria (Mahboubi et al., 1986) with two closely spaced fossil beds in the lower C23n2 chronozone at 51.6 Ma (Coster et al., 2012b). Less diverse assemblages come from N'Tagourt in the Ourzazate Basin (Hartenberger et al., 2002), while an unidentified hyracoid and a questionable *Moeritherium* are described from provisionally dated phosphates in Tamaguélelt, Mali (O'Leary et al., 2006).

Although only 16 Abdounian genera are presently known, we find representatives of all Tingitanian lineages, with an increased diversity of endemic afrotheres and primitive placentals, as well as the Cretaceo-Paleocene immigrants such as primates and hyaenodontids (cf. Appendix 1).

Lazibian

The Middle Eocene Lazibian (48.6–39.6 Ma) is essentially equivalent to the Lutetian of Europe (Fig. 1). Its defining locality is the site HGL49, the lowermost of several in the Hammada du Dra Formation, a shallow lacustrine and coastal floodplain sequence in the Atlas foredeep of northwestern Algeria that is well exposed in the mesa of Gour Lazib and its Glib Zegdou outlier (Adaci et al., 2016). The Hammada du Dra beds have a magnetostratigraphic signature (Coster et al., 2012a) that could be either upper C22n (base Lutetian, 48.6 Ma) or upper C21n (mid-Lutetian, 45.0 Ma); the former is preferred, in view of the wide consensus (cf. Solé et al., 2016) that Gour Lazib is close to the transition between Early and Middle Eocene.

Some 41 genera of Lazibian age are presently known, including a significant portion from the Black Crow deposit in Namibia (Fig. 4). Black Crow is the oldest of several volcanic pond deposits in the northern Sperrgebiet (see also 'Turkwelian'), in which reactive ash and hydrothermal activity created strongly cemented beds that are now erosion-resistant white hillocks that yield abundant fossilized owl pellets and occasional large mammals (Pickford 2008b; Pickford et al., 2014). So far, aside from Mahenge with a single chiropteran (Gunnell et al., 2003), Black Crow is the only known source of early Paleogene mammals south of the equator.

In the northern realm, the Chambi 1 and 2 (formerly Kasserine) sites of Tunisia are located in prolific lacustrine deposits (Hartenberger et al., 2002; Solé et al., 2016) like those of the type locality in Algeria, while the upper Ourzazate beds at Aznag in Morocco (Tabuce et al., 2005) are shallow marine and estuarine sequences The early mid-Eocene Taiba N'Diaye seaside phosphate quarry in Senegal, rich in marine mammals, has recently yielded a proboscidean as well (Tabuce et al., 2019). No Lazibian localities younger than Aznag have been reported, and the later part of the Lazibian age is a 5-Myr gap in the Afro-arabian record (Table 1).

A filtered exchange with southeastern Laurasia prior to the Lazibian is clearly indicated by the occurrence of at least two invasive groups: basal strepsirrhines (*Djebelemur* from Chambi; *Algeripithecus* and *Azibius* from Gour Lazib) and primitive zegdoumyid rodents in both northern and southern realms (Gheerbrant and Hartenberger, 1999; Tabuce et al., 2004, 2009; Marivaux et al., 2013; Pickford, 2018).

Kebarian

The late Middle Eocene (late Bartonian) Kebarian LMA (39.6–37.5 Ma) corresponds to the later Robiacian mammal age of Europe (Fig. 1). It is defined by the KEB-1 locality at Soug-Jedid in the foothills of the Jebel el-Kébar, central Tunisia, in lagoonal beds with abundant selachian remains (Marivaux et al., 2014a, 2014b). This is the first adequately dated (and apparently the first known) Afro-arabian locality above the 45 Ma Aznag level in the early Lazibian, following a 5-Myr gap in the record. The Kebarian sites (Table 1) have yielded only a few identified land mammals, such as the embrithopod *Arsinoitherium* from Bir om Ali of Tunisia and the lower Aydim Formation of Oman (Al-Sayigh et al., 2008). Remains of *Protophiomys*, the earliest known hystricognath rodent in Africa, together with the indeterminate primate *Amamria*, are described from the type locality (Marivaux et al., 2014a, 2014b).

The newly confirmed timing of ca. 40 Ma for the intercontinental transfer of basal hystricognaths and anthropoids from southeast Asia to South America, via Africa together with boas and cichlid fish (Bond et al., 2015; Coster et al., 2015; Seiffert et al., 2020) is strengthened by the occurrence of *Protophiomys* in the Kebarian (Marivaux and Boivin, 2019). Even if *Amamria* is probably not an anthropoid (Jaeger et al., 2019), the evidence from the two end points (SE Asia and South America) leaves little room to doubt that primitive anthropoids were present in the poorly sampled Kebarian fauna. This moment of connection across two oceans also coincides with wide turnover in the mammal record of North America and Eurasia (Prothero, 1994) when many archaic lineages were replaced.

Phiomian and Qatranian

The Phiomian (37.0–33.4 Ma) and Qatranian (33.4–28.2 Ma) LMA are based on the prolific fossil sites in the Fayum depression southwest of Cairo, where mid-Cenozoic shallow marine and coastal-plain deposits, succeeded by sheets of late Oligocene basalt, are exposed by wind erosion. In this area, over 600 m of vertebrate-bearing sediments spanning some 10 million years are divided into four formations, named (in ascending order) for (1) Gehannam district southwest of the Fayum agricultural area, (2) Birket Qarun basin in the center of the depression; (3) Qasr el-Sagha badlands north of the basin; and (4) Gebel Qatrani, or 'tar hill,' the escarpment further north with its cap of black lava (Bown and Kraus, 1988; Gingerich, 1993). The two mammal ages, while divided into late Eocene and early Oligocene units, are treated together here because of their geographic, stratigraphic, and paleontologic contiguity. We have named the earlier age according to the classic term for 'Fayum' and the later age after Gebel Qatrani.

Local dating is based on magnetostratigraphy (Kappelman et al., 1992; Rasmussen et al., 1992; Seiffert, 2006, 2010), in a profile that is further calibrated with the late mid to upper Eocene (Bartonian-Priabonian) marine microfauna in the three lower formations, as summarized by Strougo et al. (2013), and by late Oligocene radiometric dates of 23.6 Ma on the overlying Widan al-Faras basalts (Kappelman et al., 1992). In all current interpretations, the oldest continental local fauna, sampled in locality BQ-2 near the base of the Birqet Qarun section, is dated to early Priabonian (ca. 37 Ma), while the youngest localities are dated to Chron C11n, corresponding to later Rupelian age at ca. 30 Ma (Seiffert, 2010).

The Eocene–Oligocene boundary (EOB) is in middle Chron C13r at 33.9 Ma (Walker et al., 2013), which Seiffert (2006, 2010) correlated with the reversed-polarity interval of the lower Gebel Qatrani just below Locality L-41. Support for this calibration was found in the species level correlation between the middle Gebel Qatrani sites and the Thaytiniti and Taqah local faunas in Oman that occur within a mid- to upper-Rupelian marine sequence (Roger et al., 1993; Thomas et al., 1999) with an abbreviated paleomagnetic zonation that is consistent with that of the mid-Gebel Qatrani (Seiffert 2006, 2010).

On the other hand, Gingerich (1993) proposed that L-41 and thus the entire Gebel Qatrani Formation is probably of Rupelian age, noting that the major ‘Type 1’ drop in sea level when the Antarctic ice cap began to form at the EOB (see also Katz et al., 2008; Miller et al., 2020) must have caused a prolonged interval of erosion and nondeposition in the Fayum basin, which he identified with a basin-wide disconformity between the marine Qasr el-Sagha and the continental Gebel Qatrani Formations. Reasoning that the EOB regression would produce a depositional gap of some 1.5 Myr, Gingerich noted that this could mean that the reversed polarity of the uppermost Qasr el-Sagha and that of the lowermost Gebel Qatrani (Rasmussen et al., 1992) could be a composite of the C15r reversal below and the C13r reversal above the Eocene-Oligocene boundary. This is still consistent with the preferred correlation of the middle Qatranian fauna to mid-Rupelian time (Seiffert, 2006), but it shifts L-41, just above the boundary disconformity, from late Priabonian to early Rupelian age. Pending further study, this is the calibration adopted here, with L-41 as the defining basal locality for the Oligocene Qatranian.

The estuarine section exposed in coastal bluffs south of Dakhla on the Atlantic coast of Morocco (Fig. 4) includes a number of newly discovered sites that have yielded abundant marine vertebrates, including at least five species of archaeocetes. Most Dakhla sites are of mid to late Eocene (Phiomian) age, but the uppermost C2 level, which has yielded a wide diversity of rodents (Marivaux et al., 2017a, 2017b) and other small mammals, has been dated by Benammi et al. (2019) to a level just above the Oi-1 thermal low at the C13r/n transition, and thus closely coeval to L-41. Other Phiomian localities include the isolated Malembe coastal site in Angola (Pickford, 1987), the lower Nementcha level of the Bir el-Ater Formation in Algeria (Mahboubi, 2003), numerous sites in the widely exposed Idam Member of the Dur at-Talah escarpment in Libya (Jaeger et al., 2010; Coster et al., 2015) and the shallow marine beds of the upper Aydim locality in westernmost Oman (Al-Sayigh et al., 2008). Qatranian sites outside the Fayum include Minqar Tibaghbagh in the Qattara Depression to the west (Van Vliet et al., 2017), the prolific Zallah Oasis locality in Libya (Coster et al., 2012b), and the Thaytiniti and Taqah localities in Oman (Table 1).

The sudden sea level drop at the end of the Eocene (Miller et al., 2011) led to the dramatic ‘Grande Coupure’ overturn in European mammal faunas that Hooker et al. (2009) dated to the 33.5-Ma acme of the EOB glacial advance. Land bridges exposed in the new sea level led to an incursion into western Europe from Asia of cricetids, lagomorphs, rhinoceroses, and carnivores, well after they entered North America during the Late Eocene (Prothero, 1994; Hooker et al., 2009). With no lagomorphs, rhinocerotids, or carnivora known in Africa prior to the latest Oligocene (cf. Appendix 1), there is no evidence for a major ‘Grande Coupure’ invasion of Africa at the EOB, contra Gheerbrant and Rage (2006). On the other hand, the brief and only Afro-arabian occurrence of a marsupial (*Peratherium*) is in the early Oligocene, in the Fayum (Simons and Bown, 1984) and in Oman (Taqah), with a possible but also temporary cricetid in the latter fauna (Thomas et al., 1999), which suggests that there may have been a limited exchange at this time.

Turkwelian

The record of Afro-arabian land mammals during the Late Oligocene Turkwelian LMA (28.2–22.5 Ma) is known primarily from the earliest deposits in the East African Rift System (Table 1), and is named for the district in northern Kenya where the Turkwel River cuts across the Rift Valley floor to the south end of Lake Turkana. This is where fossils were discovered at Losodok by Camille Arambourg (1933), as he passed through on his way to the Omo Basin to rediscover the sites noted half a century earlier during Count Teleki’s elephant-hunting ‘expeditions.’ It took yet another half century before the specimens from this site and adjoining localities in the Turkwel drainage became recognized as the first known Late Oligocene assemblages in Africa (Boschetto et al., 1992). Additional discoveries of Late Oligocene mammals in the Turkana basin followed at Lokone Hill in the Lokichar half-graben south of the Turkwel River (Ducrocq et al., 2010; Leakey et al., 2011; Marivaux et al., 2012), as well as in the Rukwa basin of Tanzania (Stevens et al., 2004, 2013) and in the Ethiopian coastlands at Chilga (Sanders et al., 2004) and at Dogali (Shoshani et al., 2006) and Mai Gobro (Abbate et al., 2014) in Eritrea. The Chilga site, which defines the beginning of the Turkwelian, is only slightly younger than the uppermost levels in the Fayum (Seiffert, 2006, 2009) and is close to the beginning of the marine Chattian Stage at 28.1 Ma (Walker et al., 2013). Evidence from other deposits of Turkwelian age comes from Saudi Arabia, on the Red Sea coast at Wadi Sabyah (Madden et al., 1982) and a major new locality at Harrat al Ujayfa near Jiddah (Zalmout et al., 2010).

In the coastal Sperrgebiet of Namibia, prolific small mammal remains from the mineralized pond deposits of Eocliff, Eoridge, Silica North, and Silica South have been difficult to correlate. The absence of any members of several rodent families that are abundant in the Phiomian–Qatranian, together with the presence of other groups not known in the Lazibian, supports the opinion of Pickford (2015, 2018) that this almost totally endemic assemblage should be assigned to the upper Eocene (i.e., Kebarian). On the other hand, detailed Bayesian tip-dating analysis of material from three ‘Eo-Silica’ species (Sallam and Seiffert, 2019; E. R. Seiffert, pers. comm.) points to an early Miocene age. Given its clear difference from the Early Miocene (Kisingirian) fauna of the Sperrgebiet, and in particular the absence of any of its Laurasian immigrants, we have compromised with a tentative Turkwelian age (Table 1) for this problematic assemblage. It may be significant that the hystricognath *Turkanamys* from Lokone preserves a number of primitive phiomyid features (Marivaux et al., 2012) that are found in the Namibian assemblage.

The Turkwelian fauna, while less diverse than in the preceding or following ages, clearly reflects the continued if not complete isolation of Afro-arabia during this time. With the sole exception of the stenoplesictid *Mioprionodon* in the late Turkwelian—the first true carnivoran in Africa—all Turkwelian genera so far known have African Paleogene ancestry (Leakey et al., 2011). On the other hand, major changes are seen in the record of these endemic groups, most clearly in the sweeping replacement of all earlier families of proboscideans and haplorhine primates by families that subsequently flourished in the Early Miocene.

The broad transformation seen in the Turkwelian fauna may be due in part to the nearly total shift in the sample from coastal to upland localities at this time (Fig. 3), but a relatively high peak in global warmth in the early Turkwelian, ca. 25 Ma (Miller et al., 2020), may also have influenced the apparent overturn.

Legetetian

The basal Miocene Legetetian LMA (22.5–18.5 Ma) is named for Legetet Hill, an eroded carbonatite cinder cone near Koru in the upper Kavirondo rift valley of western Kenya (Fig. 5), where the calcified tuffs that were mined here as limestone yielded the first described pre-Quaternary fossil mammals in sub-Saharan Africa in 1909 (Wayland, 1926), and in 1926 the first fossil 'apes' in all of Africa (Hopwood, 1933). Over the years more than 10,000 specimens, mostly mammals, have been collected from the Koru area with as many more from nearby alkaline volcaniclastics at Songhor and the LMA-defining site at Meswa Bridge (Andrews et al., 1981a; Pickford, 1986). Important collections have also come from northeastern Uganda in the Moroto and Napak eruptive centers (Bishop, 1962, 1964; MacLatchy et al., 2006). More recently, material of this age, as yet relatively sparse, has been recovered at Kajong in the lower Mwiti sequence east of Lake Turkana (Brown et al., 2016) as well as in the Nakwai sequence in West Turkana, initially correlated on faunal grounds to upper Oligocene (Rasmussen et al., 2019). The relatively minor sites of upper Oued Bazina in Tunisia (Jeddi et al., 1991) and Jabal Midra ash-Shamali in Saudi Arabia (Hamilton et al., 1978) are the only other local faunas of Legetetian age (Fig. 6), which is thus almost exclusively represented by collections from the developing Rift Valley system in East Africa.

Bukwa on Mount Elgon, initially dated to ca. 23 Ma (Walker, 1969), yields an assemblage that Pickford (1986) correlated to his Set II (i.e., early Kisingirian, ca. 18 Ma; Fig. 2), while placing the local fauna from sites on the nearby Moroto volcano in Set III, equivalent to late Kisingirian, ca. 16 Ma (Pickford and Mein, 2006), again despite a previous dating to an earlier age (20.7 Ma per Gebo et al., 1997). The recent re-dating of the Bukwa l.f. to an age of 19.3–19.0 Ma by Cote et al. (2018), or latest Legetetian, would make it only slightly older than Pickford's estimate. As for Moroto, the corrected age of 19.2 Ma (MacLatchy et al., 2006) also shifts this local fauna to later Legetetian age, such that *Morotochoerus*, the most primitive known hippopotamid (Orliac et al., 2010) is reasonably placed earlier than the more advanced genera in the Kisingirian. Likewise, the type specimen of the Moroto hominoid originally named *Morotopithecus*, and now commonly synonymized with *Afropithecus* (Harrison, 2010) is placed with other examples of this genus in the Miocene (Appendix 1).

Legetetian faunas document the beginning of open Afro-Laurasian exchange, due to the initial temporary exposures of the rising Tauride land bridge during the eustatic lowstands Mi 1 and Mi 1aa, at 21.0 and 20.2 Ma (Pekar and DeConto, 2006), some 2 Myr before the next exposure at the beginning of the Kisingirian (q.v.). This 'first wave' exchange is clearly seen in the simultaneous appearance of genera from at least 14 Eurasian families: ochotonids, sciurids, nesomyids, erinaceids, sanitheriids, suids, tragulids, gelocids, giraffids, barbourofelids, viverrids, herpestids, chalicotheriids, and rhinocerotids (Appendix 1). At the same time, African endemics appear in Laurasia in what has been called the 'Proboscidean Datum Event' (Madden and Van Couvering, 1976; Tassy, 1990; Barry et al., 2005). In Africa, the 'first wave' coincides with rapid diversification of the anthropoid groups that appeared in the Turkwelian and final extinction of parapithecids, proteopithecids, and oligopithecids. Ten new families appeared in other endemic lineages, of which only tubulidentates, pedetids, and bathyergids survived past the middle Miocene (Appendix 1).

Kisingirian

The Kisingirian LMA (18.5–15.8 Ma) is named for the Kisingiri volcano in the failed Kavirondo Rift of westernmost Kenya, where highly fossiliferous deposits accumulated in the peripheral depression created by the rapidly growing mountain. Kisingirian sites are numerous on Rusinga and neighboring Mfwangano Island, and in the mainland areas of Nyakongo-Uyoma and Karungu (Table 1), the latter being one of the earliest reported Cenozoic localities of sub-Saharan Africa (Oswald, 1914). The sites on Rusinga, first described by Wayland (1931) on a visit in company with the young Louis Leakey to follow up on a report of proboscidean fossils in limeworks at Hiwegi, have been extensively investigated due to the abundance of hominoid material (i.e., Le Gros Clark and Leakey, 1951; Andrews, 1970; Drake et al., 1988; Peppe et al., 2016) among as many as 78 mammal genera (Van Couvering and Van Couvering, 1976).

Pickford (1986) assigned the fossil assemblages of the Kisingiri region to his Set 2, or P II, biozone, while assigning Early Miocene assemblages in the northern Rift Valley (cf. Savage and Williamson, 1978) to the younger set P IIIa (Fig. 2), noting that there were fewer than 50% of shared genera. The difference, however, is apparently due more to habitat than age, with the Kavirondo sites formed in the interior highlands (Maxbauer et al., 2013), while the main Rift Valley sites were at or near sea level, as evidenced by a fossil whale (Mead, 1975; Wichura et al., 2015) at Loperot, west of Lake Turkana (Harris and Watkins, 1974; Grossman et al., 2014). Other West Turkana sites include Muruarot (formerly Ferguson's Gulf), Naserte and Kalodirr in the southwest corner of the basin (Leakey and Leakey, 1987; Adrian et al., 2018) and the Locherangan site to the north, together with Buluk in the Lake Stephanie or Chew Bahir basin (Leakey and Walker, 1985). The faunas from these sites have similarity coefficients verging on unity (Pickford, 1986), with assigned ages ranging from 19 to 17.5 Ma (McDougall and Watkins, 1985; Brown and McDougall, 2011), i.e., little if at all different from the Kisingiri sites (Table 1).

Other Kisingirian assemblages (Table 1; Fig. 6) are found in northern coastal deposits across the broad Sirtean plain, from Jebel Mrhila (Biely et al., l972), Reguba (Pickford, 2009), and Jebel Zelten (Savage and Hamilton, 1973; Wessels et al., 2003) to the Egyptian sites at Wadi Moghra (Miller, 1999), Siwa Oasis (Hamilton, 1973a) and Wadi Faregh (Hamilton, 1973b). On the Arabian peninsula, the Saudi 'early Miocene' Hadrukh (Jabal Midrah as-Shamali) locality is older than the prolific Al Sarrar–Ad Dabtiyah sites and the Ghaba localty of Oman (Whybrow and Clements, 1999a). These northern assemblages, mainly large mammals, comprise a uniform regional fauna that is well correlated to that of the Turkana Basin (Tchernov et al., 1987). In addition, Zelten has a small-mammal assemblage (Fejfar and Horacek, 2006) that shares a majority of species with the Negev sites (Tchernov et al., 1987) and Al-Sarrar (Thomas et al., 1982).

A third major source of Early Miocene mammals (Fig. 7) was discovered in 1910 almost simultaneously with the Legetetian finds in western Kenya, as a result of the great diamond rush on the southern coast of Deutsche Südwest-Afrika, now Namibia, when excavation of the diamondiferous beach terraces uncovered several Miocene paleo-estuaries (Hamilton and Van Couvering, 1977; Pickford, 2008) in the region subsequently named Sperrgebiet ('forbidden district') after it was fenced off. Fossils of similar age were later found in the Ryskop coastal terrace of Namaqualand to the south, with a diverse, younger local fauna in the Arrisdrift sites in the lower Oranje River valley (Pickford and Senut, 2003). Pickford (2008a) considered

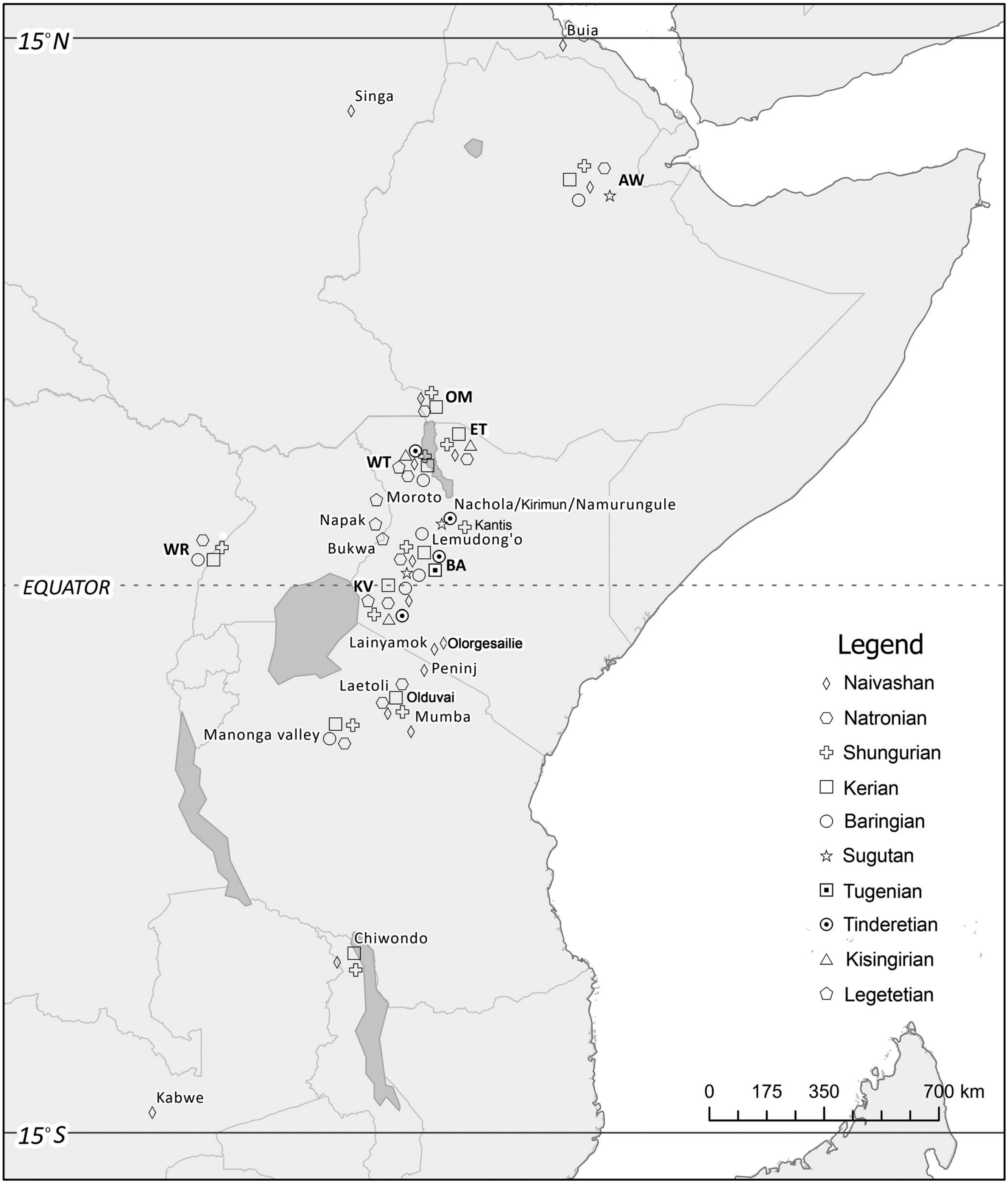


FIGURE 5. Principal Neogene localities and locality groups in the equatorial realm; emphasized names are the defining localities for the Neogene LMAs. Locality group acronyms (AW, BA, ET, KV, OM, WR and WT) are identified in Table 1.

the Sperrgebiet Miocene localities to be equivalent to the Kenya sites of Legetetian age, noting that of 19 taxa also found in East Africa, there were fewer in common with his faunal set 2 than were shared with faunal sets 0 and 1 (Fig. 2). Further collecting, however, has brought the count of genera shared with East Africa to 41 out of a total of 67 (Fig. 3; Appendix 1), with

100% of these in the Kisingirian of the equatorial realm, including representatives of nearly every immigrant family from the post-Legetetian 'second wave' (see below).

Paleoceanography suggests that the Kisingirian coastal assemblages were preserved in one of two stages in relatively prolonged eustatic cycles: first, in the initial progradation wedge or backfill of continental deposits, that accumulated on the downcut shorelines when sea level began to rise; and secondly, in the shallow marine deposits that flooded the coastal plain during the highstand climax. This sequence model agrees with the sea level curve for the Early Miocene (Pekar and Deconto, 2006; Miller et al., 2011), in which the third-order steep decline in late Burdigalian (lowstands Mi 1ab and Mi 1b, at 18.4 and 17.7 Ma) were followed by a slow, second-order recovery (cf. Posamentier et al., 1988) that reached a highstand only in the early Langhian at ca.16 Ma. The highstand facies was not preserved in the Turkana basin or in the Sperrgebiet, but may be seen in the Ryskop terrace, the high-water backfill of Arrisdrift, and the onlapping shallow-marine Marada Formation in North Africa (Tchernov et al., 1987; El-Hawat, 2008), specifically the upper levels of the Zelten sequence (Fejfar and Horáček, 2006), and the equivalent upper Dam Formation on the Arabian coast at As-Sarrar and Ghaba (Thomas et al., 1999).

A direct consequence of the major eustatic lowstand in the early Kisingirian was a 'second wave' of trans-Tethyan exchange, the reality of which is made plain by the fact that, in the 11 Eurasian families that make their first appearance in the Kisingirian, 21 of the 27 genera, including every member of Muridae, Dipodidae, Deomyidae, Spalacidae, Felidae, Hyaenidae, and Ursidae, and all but one of four Amphicyonidae, are known so far only from the coastal faunas of West Turkana and the continental periphery (Appendix 1), in stark contrast to the composition of abundant samples from the upland sites of southern Kenya. The effect of this paleogeographic segregation of new lineages with regard to the early Miocene 'Tauride overturn' (see 'Observations') is yet to be evaluated.

Tinderetian

The early Middle Miocene Tinderetian LMA (15.8–12.8 Ma) takes its name from Tinderet in western Kenya, the eroded remnant of one of several Middle Miocene nephelinite-phonolite volcanos at the head of the failed Kavirondo Rift. Here, as elsewhere in East Africa, the alkaline chemistry of rift vulcanism favored fossilization in the associated sediments (Andrews and Van Couvering, 1975; Harris and Van Couvering, 1995; Winkler, 2002). With only some 20% fewer recorded genera than in the Kisingirian (Fig. 3), Tinderetian history convincingly shows a sharp reduction in the rate of change in higher-order levels, compared to the major changes at the beginning of the Miocene (Appendix 1). The appearance of immigrant Soricidae, Gerbillidae, and Gliridae in coastal sites documents the full establishment of the Tauride land bridge, after a new drop in eustatic sea level beginning in the early Tinderetian at ca. 15 Ma (Pekar and DeConto, 2006; Miller et al., 2011).

The age of the Tinderetian is set by the Kipsaramon Level 1 site in the Muruyur Beds (Behrensmeyer et al., 2002; Gilbert et al., 2010), the oldest of many fossiliferous levels in the Tugen Hills fault block on the west side of the Baringo rift basin, and which is virtually coeval with the beginning of the middle Miocene, defined by the Langhian stage at 16.0 Ma (Walker et al., 2013).

The early Tinderetian is well documented in the Kavirondo Gulf, on Maboko Island (Andrews et al., 1981b; Benefit and McCrossin, 1997), and in the stratigraphically correlative mainland sites of Majiwa and Kaloma (Pickford, 1982). In these localities as well as the slightly younger sites of Nachola in the Samburu Hills (Ishida et al., 1999) and Nyakach in the Sondu area, southeast of Kisumu (Pickford, 1986a), at least nine genera of anthropoid primates have been recorded (Harrison, 2010; Appendix 1). The upper Tinderetian beds at Fort Ternan, located on the slopes of the Tinderet volcano itself, is the most prolific of this age (Leakey, 1968; Andrews, 1970; Pickford, 1986a, 1986b; Tong and Jaeger, 1993) and is further notable as the type locality of *Kenyapithecus wickeri* (Leakey, 1962), considered by many to be the earliest representative of the modern large-bodied hominoids, or Hominidae. Interestingly, the first appearance of *Kenyapithecus* in the later Tinderetian follows a sharp decline from the early Tinderetian diversity in proconsulids, dendropithecids and other stem catarrhines, in an evolutionary transition that coincides with an environmental shift to a more open habitat evidenced by heavily grazed, short grass mollisols at Maboko, Nyakach and Fort Ternan (Cerling et al., 1997; Wynn and Retallack, 2001; Retallack et al., 2002). Recent finds at Napudet in the Turkana basin (Boisserie et al., 2017), provisionally dated to 13 Ma (Brown and McDougall, 2011), further document the shift to a new Middle Miocene fauna in the equatorial realm.

Material in the northern realm comes from shallow marine and lagoonal sequences in Libya in the upper Jebel Zelten sequence (Savage and Hamilton, 1973; Wessels et al., 2003; Fejfar and Horáček, 2006); in Tunisia from Testour (Robinson and Black, 1973) and the proboscidean site of Cherichera first reported in 1887 by De la Croix (cf. Pickford, 2007); in Morocco at Azdal, Beni Mellal and Pataniak (Benammi et al., 1995; Benammi and Jaeger, 2001); and in several rich localities of the Hofuf beds of southern Saudi Arabia (Thomas et al., 1978). Only scattered remains are known from the southern realm, in the lower aeolianite of the Rooilepel sequence of coastal Namibia (Senut and Pickford, 1995).

Turnover in the Tinderetian was moderate, with relatively high extinction vs low origination rates (see Observations). Among the various families of rodents that had entered Afro-arabia during the Early Miocene, only Nesomyidae showed significant expansion into the East African interior, while the others continued to be represented with only one or two genera limited to coastal sites. As shown in Appendix 1, most of the other Eurasian families that were introduced during the Early Miocene show no more than moderate increase in diversity, while genera of endemic hystricognaths and hyaenodonts were sharply reduced in number.

Tugenian

The Tugenian LMA (12.8–10.0 Ma) is based on the late Middle Miocene Ngorora Formation in the Tugen Hills escarpment, part of a 3,000-m sequence of interbedded sediments and volcanics dating from early Miocene to Pleistocene, exposed by subsidence of the adjoining Lake Baringo block in the axis of the rift valley. Aside from a few poorly dated large mammals from Kisegi in the Albertine Rift (Pickford et al., 1992; Pickford, 1997), only the Ngorora beds, divided into members A through E (Bishop and Pickford, 1975; Hill et al., 1986) provide the fossil record for this age in equatorial Africa, and with only half as many genera as in the Kisingirian. The Tugenian record from the southern part of the continent is even poorer, with the only known source being karstic limestone debris in the mine dump at Berg Aukas (Conroy et al., 1992) and the middle aeolianite of the Rooilepel basin in Namibia (Pickford and Senut, 2010). Numerous productive localities in northern Africa, however, provide a good record during this time, with abundant small mammals from Sheikh Abdallah travertines in Egypt (Mein and Pickford, 2010), bovid-rich lake beds in the Beglia Formation of Tunisia (Robinson, 1986) and a number of estuarine and coastal terrace sites in Algeria and Morocco (Lihoreau et al., 2015a), some of which have magnetostratigraphic calibration (Mahboubi et al., 2015). At the furthest extremity of Afro-arabia in northern Iraq, 'Vallesian' fossils are reported from the fluvial Agha Jari Formation at Jebel Hamrin (Thomas et al., 1980).

The late Tugenian is marked by the first appearance of equids at Oued el Hammam (Arambourg, 1951), at a level now known as Bou Hanifia 5 (Ameur et al., 1976; Sen, 1990) at 10.9 Ma, and in the upper level of the Ngorora sequence (Pickford, 2001) at ca. 10.5 Ma. This is essentially coincident with the spread of equids throughout Eurasia in the event widely known as the 'Hipparion Datum' (i.e., Sen, 1990; Woodburne, 2007), although the pioneering genus itself is not recognized in Africa. The immigrant equids were accompanied by the earliest known canids and cricetids. In the endemic fauna, the transformation of Anthropoidea that began with the first hominid in late Tinderetian was completed in the early Tugenian. *Otavipithecus* in Namibia (Conroy et al., 1992) is one of the last proconsulids, while the last known victoriapithecid and the first known cercopithecid are reported from the basal Tugenian at Kabarsero (Hill et al., 2002; Rossie et al., 2013). In addition, Hyaenodontidae and Climacoceratidae appear to come to an end during the Tugenian, without leaving any successors.

The Tugenian record is unusually selective, in that there is, as yet, no sign of nine Tinderetian families that re-appear in subsequent ages and whose presence is therefore inferred in Appendix 1. The gap in the record of Hominidae, Spalacidae, Anomaluridae, Bathyergidae, Mustelidae, and Herpestidae is limited to the Tugenian, while species of Chrysochloridae, Dipodidae, and Erinaceidae do not reappear for one or more additional ages. On the other hand, the numbers of recorded genera of Muridae, Nesomyidae, and Bovidae sharply increase in the Tugenian. In addition, it would also appear that by the end of the Tugenian, all of the numerous genera of Suidae in the Early Miocene become extinct except for *Nyanzachoerus*, which then (presumably) gives rise to all subsequent African lineages (not immigrant *Sus*).

Sugutan

The Sugutan LMA (10.0–6.8 Ma) takes its name from the Suguta Valley, between the Turkana and Baringo basins in the northern Kenya Rift, where prolific fossil beds at Nakali and Namurungule are found in fault escarpments rising above the valley floor (Aguirre and Leakey, 1974; Nakaya et al., 1984; Kunimatsu et al., 2007). The other East African localities of Sugutan age (Table 1) are likewise found in fault blocks of rift-floor strata, notably in the lower levels at Lothagam (Leakey and Harris, 2003) on the western side of Lake Turkana, but also Ch'orora in the Awash rift basin, which was for many years assumed to be coeval with older levels in the Ngorora sequence before being re-dated (Suwa et al., 2015; Katoh et al., 2016). As in the preceding Tugenian, a relatively large proportion of Sugutan genera are reported from sites outside the rift valleys. In the Maghreb, a number of productive sequences rich in small mammals are confirmed to be of Sugutan age according to magnetostratigraphic dating in the Tafna basin of Algeria (Mahboubi et al., 2015) and the Ait Kandoula basin of Morocco (Benammi et al., 1996), as well as faunally correlated localities at Djebel Krechem in Tunisia (Geraads, 1989, 2002), Toros Menalla in the Chad paleolake basin (Vignaud et al., 2002), Baynunah in the Persian Gulf coastal plain of Abu Dhabi (Whybrow and Clements, 1999b; Gilbert et al., 2014), and localities in the karstic terrain of Namibia and Botswana (Pickford and Senut, 2010).

Whereas Sugutan has almost as few land mammal genera as Tugenian, the assemblage is distinctly more modern (Table 1; Appendix 1). The earliest known African leporids as well as a diversity of hominids appear at the beginning of this age (Nakaya et al., 1984), together with the earliest record of *Loxodonta*, *Hystrix*, *Vulpes*, *Viverra*, *Gallerella*, *Panthera*, and *Hippopotamus* among other extant genera. The putative hominid *Samburupithecus* from Namurungule (Begun, 2015) appears instead to be the last surviving proconsulid (but Kunimatsu et al., 2016, suggest another might occur at Nakali). *Microcolobus* from Nakali and Namurungule is the first crown cercopithecid (subfamily Colobinae, see Nakatsukasa, 2010), while a single tooth from Baynunah documents the earliest known member of the cercopithecid tribe Cercopithecini (guenons), which implies the as yet unknown presence of the widespread and successful Papionini (baboons, macaques and relatives) elsewhere on the continent (Gilbert et al., 2010). The apparent extinction of hyaenodonts in the Tugenian was followed by proliferation of large carnivores (mainly immigrants) in the Sugutan. Among endemic groups, deomyid and sciurid rodents also show significant diversification, accompanied by the 'hippopotamine event' (Boisserie et al., 2011, 2017), in which the fully terrestrial *Kenyapotamus* was suddenly replaced in the late Sugutan by large populations of at least five wetland genera including the living *Hippopotamus*.

Despite its relatively limited sample, the Sugutan clearly shows a sharp shift towards the modern African ecostructure in open-country mammals, coincident with renewed global cooling after a mid-Miocene pause, with a decrease in CO_2 and a new increase in seasonality (Zachos et al., 2001). In the wide areas dominated by monsoonal climate, the increasing duration and intensity of the dry season favored expansion of fire-tolerant grasses and shrubs, mostly with the C4 metabolism that provides energy for rapid seasonal growth at lower CO_2 levels (Lattanzi, 2010; Levin, 2015). The effects on mammals of the accelerated expansion of grasslands at the expense of open nondeciduous forest plants with C3 metabolism is traced by carbon isotopes in the teeth of East African large herbivores, which show a shift from C3 to C4 forage in equids at ca. 9.9 Ma, followed by rhinocerotids at 9.6 Ma, while some bovid species (but not all) were consuming mainly C4 vegetation by 7.4 Ma (Uno et al., 2011; Feakins et al., 2013). The same timing is seen in all Proboscidea but *Loxodonta*, which only switched to grass and shrubs at about 5 Ma (Cerling et al., 1999).

Baringian

The terminal Miocene Baringian LMA (6.8–5.3 Ma) is identified by the 'Mpesida beds' as defined by Pickford (1975), a term for sedimentary packets within the Kabarnet Trachyte in the Tugen Hills fault-block west of Lake Baringo. The fossiliferous beds are pond deposits that accumulated in depressions on the upper surfaces of successive flows and are a chronostratigraphically (if not physically) coherent element of this formation (Kingston et al., 2002).

The fossil record of this age is better known (Appendix 1) than that of the preceding Sugutan. In the Eastern Rift, the abundant material from Mpesida and the overlying Lukeino beds (Mein and Pickford, 2006) in the Tugen Hills is complemented by highly fossiliferous sequences in the Turkana basin in the upper Nawata Member at Lothagam (Leakey and Harris, 2003) and in the Awash basin, where the Adu-Asa sequence occurs across a wide area in Mpesida-like packets intercalated between flows in two main horizons (Haile-Selassie et al., 2004; Kleinsasser et al., 2008). A diverse local fauna is described from southern Kenya at Lemudong'o (Ambrose et al., 2003). Sparse large mammal assemblages of this age have been collected in the Albertine Rift along the Uganda shore of Lake Albert at Oluka and Nkondo (Pickford et al., 1992, 1993), as well as in the 'Ongoliba Bone Bed' of the Sinda-Mohari region, originally thought to be earlier Miocene but now estimated to date ca. 7–5 Ma (Werdelin 2010).

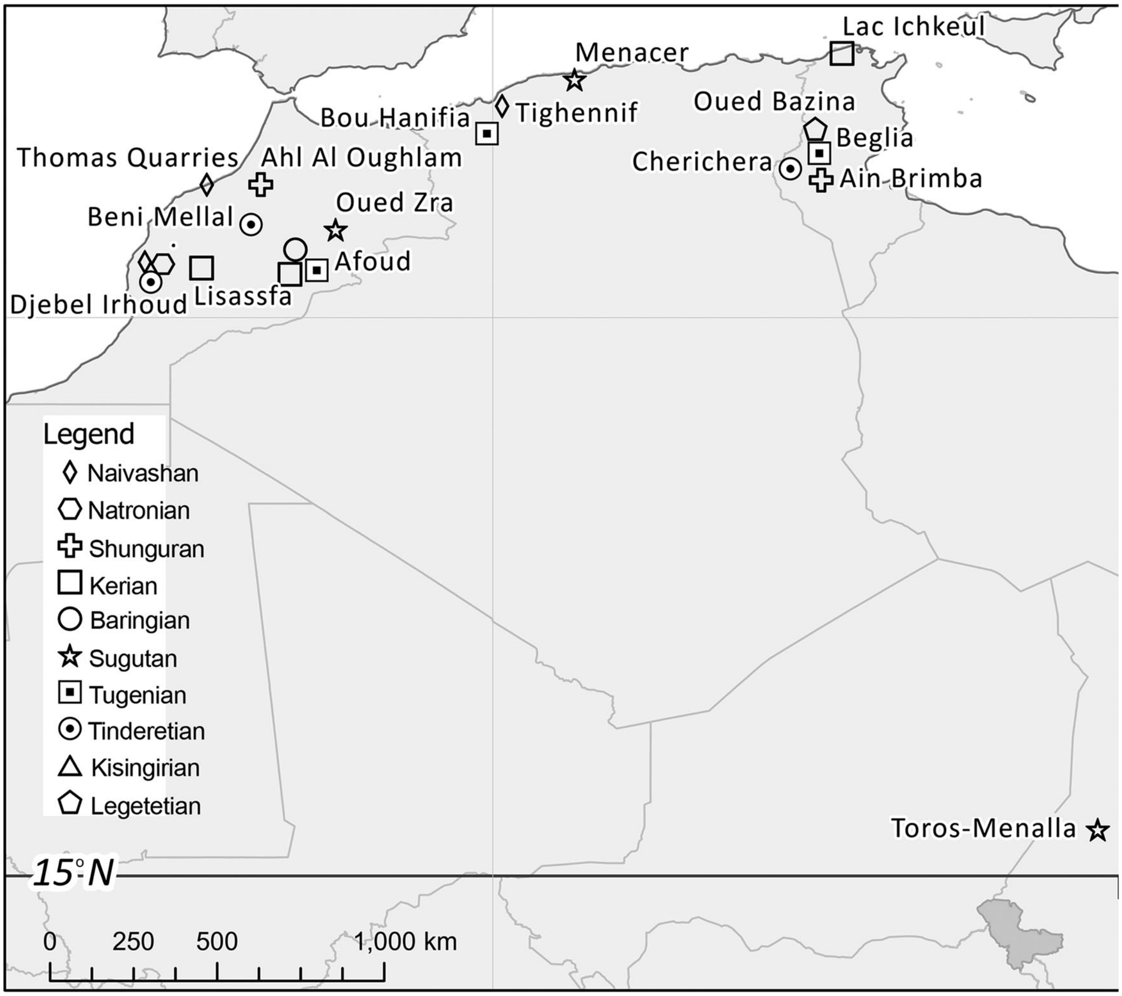


FIGURE 6. Principal Neogene localities in the northern realm (cf. Table 1).

Coastal sites are relatively rare, but are moderately prolific at Sahabi in Libya (Boaz et al., 1987; El-Shawaidi et al., 2016), Wadi Natrun in Egypt (Andrews, 1902; cf. Werdelin and Sanders, 2010) and more notably in the Ait Kandoula basin of Morocco (Benammi et al., 1995, 1996). Menacer (formerly Marceau) in Algeria was originally thought contemporary with Bou Hanifia (Oued el Hammam) by Arambourg (1959), but later workers demonstrated stratigraphically and faunally that it is much younger, perhaps best dated between 7 and 5.5 Ma (see Choubert and Faure-Muret, 1961; Thomas and Petter, 1986; Werdelin, 2010), and most likely Baringian. The Kossom Bougoudi localities in the Chad Basin provide an informative sample from the northern interior (Brunet et al., 2000; Lebatard et al., 2010). In the south, the fauna from coastal Namaqualand in the Hondeklip 50 m terrace and in the Klein-Zee paleoestuary (Pickford and Senut, 1997) is limited to a few genera of large mammals.

The global climate event that led to the Miocene-Pliocene transition is reflected in the Baringian mammal fauna of the Mediterranean coast. The glacially generated drop in eustatic sea level at 5.9 Ma (Miller et al., 2020) had the effect of closing the already shallowed ocean connections between the converging Maghrebian and Iberian promontories, leading to the 'Messinian desiccation event' and the exposure of a Betic land bridge. Relatively open exchange between northern Africa and southern Spain during this period of low sea level is evidenced by the presence in the Andalucian Late Miocene of genera known from Lukeino, Lothagam-1, Sahabi, and Wadi Natrun (Brandy and Jaeger, 1980; Geraads, 2010b; Gibert et al., 2013). These included *Macaca*, hippopotamids, and most notably the proboscidean assemblage found in the Arenas del Rey above Granada (Alberdi and Boné, 1978). While some African lineages, such as macaques and hippopotamids are found as survivors (or immigrants) in southern Europe during the Pliocene, the opening of the Gibraltar straits effectively removed Andalucia from Africa to Europe, in an example of Malcolm McKenna's 'Beached Viking Funeral Ship' (Jacobs et al., 2011).

The Baringian, and the following Kerian, have the highest apparent origination rates of any of the Neogene LMAs (see 'Observations'), at the beginning of a significant diversification among Bovidae (Appendix 1), together with increases in leporids, chrysochlorids, murids, giraffids, and small carnivores. On the other hand, almost all recorded Sugutan genera persisted into the Baringian, and it is necessary to acknowledge that more

FIGURE 6. Continued

than a few Baringian 'first appearances' are genera that would have been first seen in a more complete Sugutan record.

Kerian

The Kerian age (5.3–3.6 Ma) is defined in the Chemeron Formation, exposed in the Tugen Hills fault block on the west side of the upper Kerio rift valley in west-central Kenya (Hill et al., 1986). The base of the Chemeron sequence, dated to 5.3 Ma (Deino et al., 2002), is closely coincident with the base of the Pliocene (Fig. 1) marked by the refilling of the near-desiccated Mediterranean at 5.33 Ma (Garcia Castellanos et al., 2009). The re-submergence of the Mediterranean margin led to a basal Kerian episode of backfilling and fossilization along this part of the Afro-arabian coastline, in which a number of stranded European 'tourist genera' were preserved (Geraads, 1998, 2002; Gibert et al., 2013). The reappearance of the Mediterranean Sea had little apparent effect on the Afro-arabian climate compared to the intensifying seasonality caused by global cooling and the consequent expansion of drought-tolerant grasslands and open woodlands (DeMenocal, 2004; Levin, 2015). On the other hand Morales et al. (2005) describe a wave of extinction among carnivores at the end of the Miocene that appears to have extended from Africa to Eurasia and North America.

Most Kerian fossil material comes from the East African rift system. In Kenya, the lower Chemeron correlates to sites in the Lake Turkana basin, including the upper Nawata levels at Lothagam (Leakey and Harris, 2003; Brown et al., 2013), the group of localities at Kanapoi, Ekora and Allia Bay at the southern end of the lake (Leakey et al., 1996; Feibel, 2003), the sequence at Fejej to the northeast (Asfaw et al., 1991; Kappelman et al., 1996), and the isolated Mursi beds in the Omo River trough (Drapeau et al., 2014). More importantly, the Kerian includes many sites in highly prolific exposures in Ethiopia (Table 1), mainly in the Awash basin (Haileab and Brown, 1992; Renne et al., 1999; Deino et al., 2010; Beyene et al., 2013) but also at Galili on the southeastern Red Sea coast (Kullmer et al., 2008).

Along the rift to the south, important local faunas of Kerian age are described from Tanzania in the sequence at Laetoli (Harrison, 2011) and at several levels in the inter-rift Manonga basin (Harrison, 1997), as well as the lower Chiwondo level in the Malawi rift valley (Sandrock et al., 2007). In the Lake Albert basin of the Western Rift, local faunas of this age are known from the upper Nyawiega Member of the Nkondo Formation and in the Warwire Formation (Pickford et al., 1993).

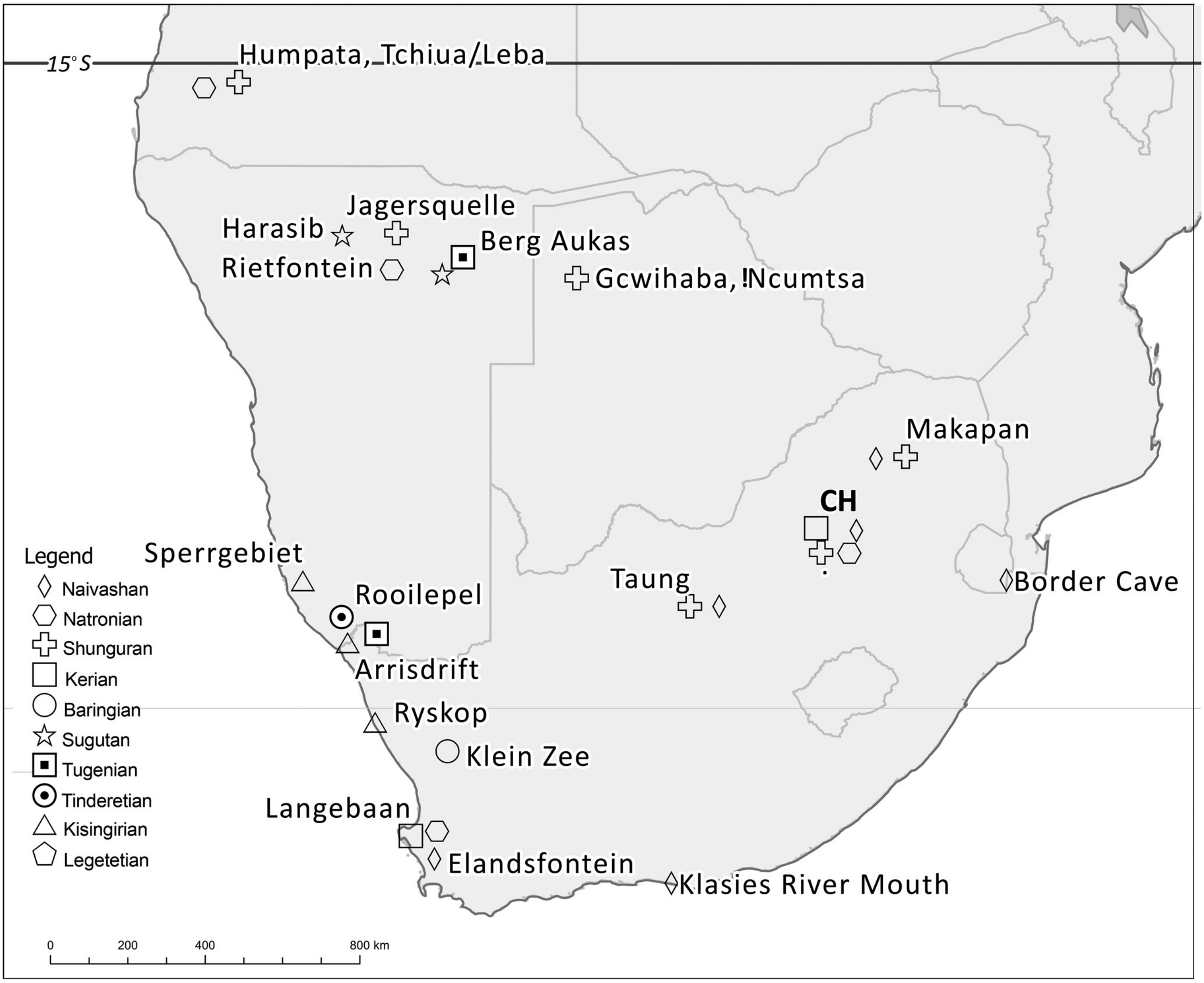


FIGURE 7. Principal Neogene localities and CH (Cradle of Humankind) locality group in the southern realm (cf. Table 1).

Outside of the equatorial region, Kerian faunas are described from the upper levels of the Chad Basin sequence (Viriot et al., 2008: Lebatard et al., 2010; cf. Table 1). The basal-Pliocene inundation of the North African coast is well documented at Lissasfa, in the oldest of the coastal terraces above Casablanca that formed after Messinian erosion (Gibert et al., 2013). In this terrace, and others dated to 5.3 Ma (Geraads, 2002, 2010a; Stoetzel, 2013), a number of otherwise Eurasian genera, including the murids *Mus*, *Praomys*, and *Golunda* and the carnivores *Lutra* and *Mungos* (Appendix 1) support the scenario of latest Miocene exchange across a Betic land bridge.

South African Kerian sites include the prolific phosphate quarries at Langebaanweg (Hendey, 1981) with a paleomagnetically correlated age of 5.15 Ma (Roberts et al., 2011), the earliest cave breccias in the dumps at Bolts Farm (Thackeray et al., 2008), and century-old excavations in diamondiferous alluvium along the Vaal River (Helgren, 1977). The late Kerian Matjhabeng excavations (De Ruiter et al., 2010) are provisionally dated to be coincident with the most recent age given to the highly fossiliferous Member 2 at Sterkfontein (Granger et al., 2015).

The end-Miocene Baringian peak in generic turnover with resulting higher diversity among bovids and carnivores continued into the Kerian, with the tripling of cercopithecid genera and a significant rise in myomorph rodents, that essentially brings the Afro-arabian open-country fauna to its present adaptive structure, aside from the forthcoming decline in megaherbivore diversity (see Observations).

Shunguran

The Late Pliocene-Early Pleistocene Shunguran LMA (3.6–2.0 Ma) is calibrated to the base of the highly productive and virtually continuous Shungura sequence in the Omo rift valley of southern Ethiopia (Brown and McDougall, 2011), whose 'petrifactions' were the first mammal fossils to be collected, if not described, from sub-Saharan Africa (cf. Arambourg, 1933). In the Shunguran, as well as in the preceding Kerian and following Natronian, the alternating volcanogenic and fluviolacustrine beds in the northern Rift are linked in a regional tephrochronology (Fig. 8) that extends from the Afar depression (Quade and Wynn, 2008; Brown and McDougall, 2011) to the Turkana basin, including the Omo valley (McDougall et al., 2012) and the main depression centered on Lake Turkana (Harris et al., 1988; Brown and Feibel, 1991). This body of strata is notable for its exceptionally abundant and diverse fossil content, including the most complete record of early humans now known (MacLatchy et al., 2010; Leakey et al., 2012), with as many as five genera of hominins described from the Shunguran alone (Appendix 1). This includes what is presently the oldest known specimen identified as genus *Homo*, reported from Lee Adoyta at 2.75 Ma in the basal Busidima Formation of the Ledi-Geraru research area (diMaggio et al., 2015; Villmoare et al., 2015), together with the oldest known examples of flaked tools at Lomekwi, dated to 3.35 Ma (Harmand et al., 2015) and what are debatably the earliest cut-marked bones, in the Sidi Hakoma beds at Dikika, dated to 3.42 Ma (McPherron et al., 2010; but see Dominguez-Rodrigo and Alcalá, 2016).

Other equatorial African localities of this age in the Eastern Rift are the main (upper) levels of the Chemeron series (Hill et al., 1992; Deino et al., 2006) of the Baringo basin, the upper Ndolayna levels at Laetoli in Tanzania (Harrison, 2011) and Lothagam Apak in the Turkana basin (Brown et al., 2013). The lower units in the Kanam complex of Homa Mountain in the Kavirondo lateral rift are also of comparable age on both faunal and paleomagnetic grounds (Ditchfield et al., 1999), and an abundant assemblage including *Australopithecus* is newly reported (Mbua et al., 2016) from long-known but unstudied bone beds in Kantis creek outside of Nairobi. In the Western Rift, the lower Kaiso Village (Hohwa) beds in the Albert basin (Pickford et al., 1993) and the well-dated Lusso beds in the Semliki basin (Boaz et al., 1992) are essentially coeval with Shungura F-G.

Localities of Shunguran age in the Maghreb are reviewed in the regional biochronologies of Geraads (2010a, 2010b) and Stoetzel (2013). One of Africa's most prolific sites, most notable for its 25 carnivore genera, is the fissure-fill of Ahl al Oughlam outside of Casablanca (Geraads, 2002), in a quarry that is unfortunately now a garbage dump. The Algerian localities of this interval are further described by Sahnouni et al. (2011) and Parés et al. (2014), while the classic Tunisian localities of Ain Brimba and Garaet Ichkeul were faunally correlated to Shungura C by Aguirre et al. (1997). The Oldowan tools found in the upper Shunguran sequence of Zarqa Valley in Jordan (Scardia et al., 2019) document the presence of hominins in northernmost Afro-arabia prior to their first appearance outside of Africa at the 1.8 Ma Dmanisi site in the southern Caucasus.

The Shunguran is very well documented in southern Africa, with 128 known or inferred genera (Fig. 3). The material from the Chiwondo sequence in northern Malawi is both geographically and faunally transitional to the open habitats of the East African region (Bromage et al., 1995; Sandrock et al., 2007), with its most prolific main localities of Shunguran age. Further to the south, cave deposits in the arc of karstified Paleozoic carbonates stretching from northern South Africa through Botswana and northern Namibia into Angola (cf. Pickford and Senut, 2010) have preserved abundant remains of this age; these include stratified cave deposits at Makapansgat, and at Sterkfontein and Hoogland in the 'Cradle of Humankind' (McFadden and Brock, 1984; Adams et al., 2010; Reynolds and Kibii, 2014; Bruxelles et al., 2017); the historic quarry at Taung (McKee, 1993); partially exposed cave deposits in the Gcwihaba and !Ncumtsa (Koanaka) hills of Botswana (Pickford and Mein, 1988; Pickford et al., 1994; Williams et al., 2012); and younger Berg Aukas breccias and exposed cave deposits at Jägersquelle and other Plio-Pleistocene localities in Namibia (Pickford and Senut, 2010) as well as on the Humpata plateau in Angola (Pickford et al., 1990, 1994). Shunguran local faunas are also well represented in capping sediments on the SW-African 30 m coastal terrace at Hondeklip Bay on the Namaqua coast and further north at Kaukasib in Namibia (Pickford, 1998, 2000).

During Shunguran time intensifying precession-driven global climate cycles that affected monsoonal precipitation, as recorded in the Chemeron basin (Deino et al., 2006a), had an impact on the African ecosystem outside of the tropical forest zone. The cyclic climate patterns became more extreme just before the beginning of the Pleistocene, ca. 2.8 Ma (DeMenocal, 2004), coincidentally contemporaneous with the presently accepted appearance of genus *Homo* in the East African fauna (see above). At present, there is no evidence of *Homo* until the early Natronian, more than three-quarters of a million years later, in either southern Africa (Dusseldorf et al., 2013) or northern Africa (Geraads et al., 2004) despite the abundant later Shunguran record in both realms that includes numerous remains of other hominins. The apparent long delay in the geographic expansion of *Homo* would suggest a dependence on some particular characteristics of the eastern equatorial savanna habitat (Domínguez-Rodrigo, 2014), where the genus evolved.

Natronian

The Early Pleistocene Natronian age (2.0–1.0 Ma) takes its name from the Lake Natron rift basin on the Tanzania-Kenya border, in which the intensively studied sequence of Olduvai Beds I–IV in the southern end of the basin has been scrupulously dated (Tamrat et al., 1995; Deino, 2012; McHenry, 2012). Regrettably, the name 'Olduwan' is pre-empted by archaeologists (as Oldowan), thanks to the early discoveries of stone tools and eventually the remains of their human makers at Olduvai Gorge (Leakey, 1936; Leakey et al., 1964). It is also inconvenient that the base of the Olduvai paleomagnetic subchron at 1.95 Ma is not quite correlative to the base of Bed I at 2.0 Ma (McHenry, 2012). The Peninj sequence, now re-dated to Natronian age (Deino et al., 2006b) is also located in the same segment of the Eastern Rift. With regard to the succession of high water 'pluvial stages' in East African basins (Cole, 1954; Behrensmeyer et al., 1995), improved faunal correlation and dating now equate the Kanjeran pluvial to the highstand seen in Olduvai Bed I rather than Bed IV (Ditchfield et al., 1999; Plummer and Finestone, 2018), making the Bed IV highstand part of the Gamblian pluvial and the Kamasian pluvial, formerly identified with Bed I, an earlier event.

In the northern rift, more than a hundred individual collecting sites have been found in the prolific localities of the main Turkana basin (Harris et al., 1988; McDougall and Brown, 2006), the Omo river valley (McDougall et al., 2012), the Awash depression of southeastern Ethiopia (Haileb and Brown, 1992; Beyene et al., 2013; Gallotti and Mussi, 2017a, 2017b), and Djibouti (De Bonis et al., 1988). Other sites to the east of the main rift, in the upper Fejej of southernmost Ethiopia (Chapon et al., 2011) and in the long-ignored Marsabit site in the Chalbi basin southeast of Lake Turkana (Ferraro et al., 2013) also yield significant fauna. The important Nyabusosi locality in the Albertine rift basin (Pickford et al., 1993; Texier, 1995) is also of Natronian age.

The later Early Pleistocene of Afro-arabia yields fluviolacustrine sites in Israel at 'Ubediya (Martinez-Navarro et al., 2012) and the Chad basin (Viriot et al., 2008). In the Maghreb, among the numerous small-mammal localities of this age that are listed by Stoetzel (2013), large mammals are also abundant at the classic shallow-marine site of Mansourah (Chaïd-Saoudi et al., 2006) in Algeria, discovered in the 1850s, and in travertine accumulations at Ain Hanech (Sahnouni et al., 2011; Parés et al., 2014) and Djebel Ressas (Mein and Pickford, 1992). Newly discovered fossiliferous volcaniclastics at Sidi Younès near Oran sample yet another productive environment (Chaïd-Saoudi, 2010).

In South Africa's 'Cradle of Humankind,' intense anthropological interest has stimulated research on the complex stratigraphy of the episodically formed cave deposits across the karstified

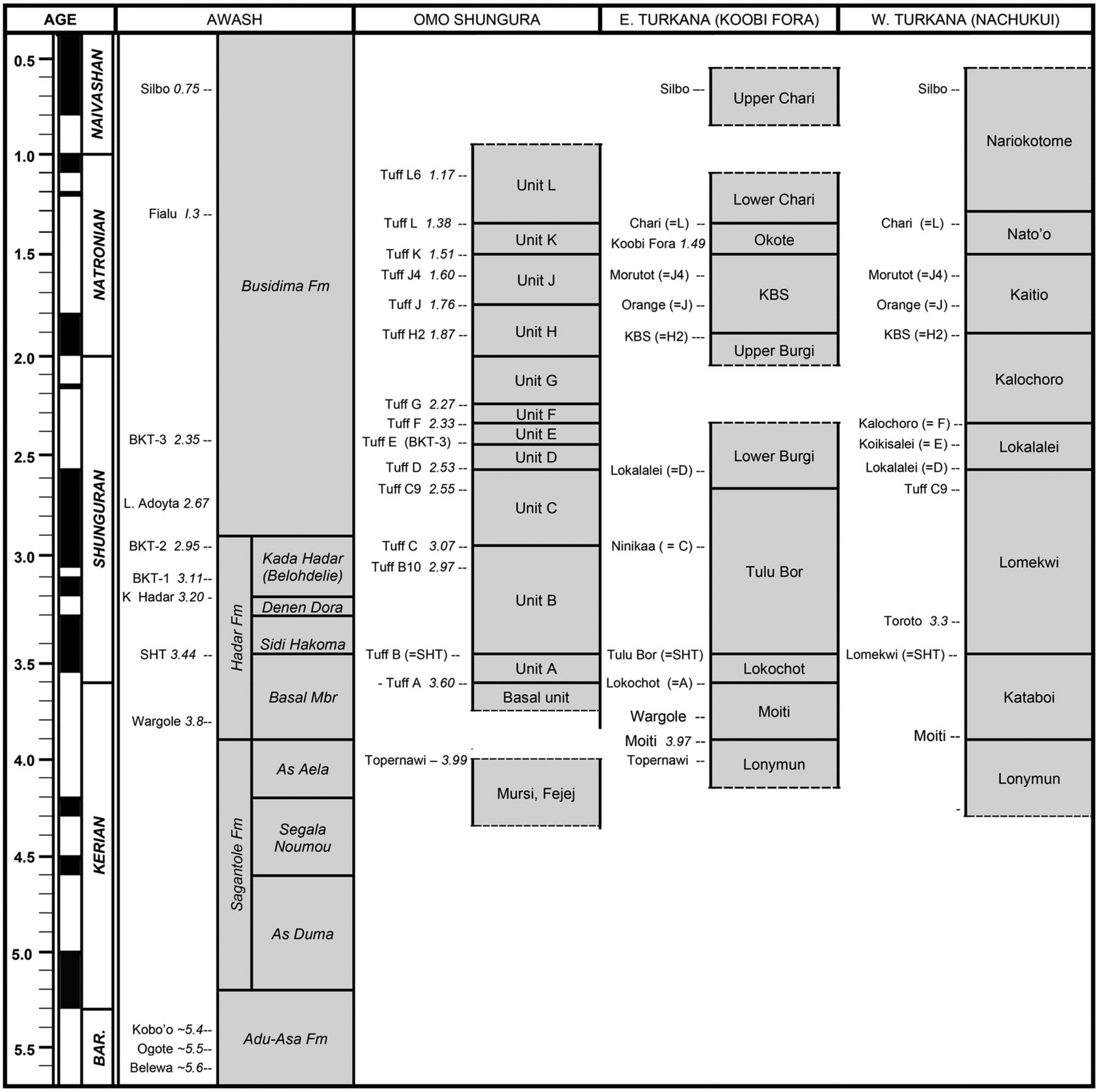


FIGURE 8. Correlation in the northern Rift between the Awash (Campisano and Feibel, 2008), and Omo and Turkana sequences (McDougall et al., 2012).

basement terrain that include the classic *Paranthropus* sites of Swartkrans and Kromdraai (Kuman, 1994; Thackeray et al., 2008; Pickering and Kramers, 2010; Herries, 2011; Adams et al., 2016) and also new discoveries at Gondolin (McKee et al., 1995; Herries et al., 2006), Luleche (Adams et al., 2007), and Malapa (Val et al., 2015). Paleokarst sites of Natronian age are also found in Angola and Namibia (Pickford et al., 1994; Senut et al., 1992).

The Natronian fauna has a very similar generic diversity, if a markedly reduced turnover rate (see 'Observations'), in comparison with the Pliocene Kerian and Shunguran, signifying relatively stable communities in the sampled open-forest and grassland habitats, even as oceans continued to cool and climate cycles intensified (Trauth et al., 2005; Maslin and Christensen, 2007).

Naivashan

The youngest of the African land mammal ages (1.0–0.0 Ma) is defined in the Lake Naivasha rift basin in southern Kenya, where the Kariandusi lake beds in the north and the Isinya and the basal Olorgesailie lake beds in the south were synchronously deposited at almost precisely 1 Ma, during the peak interval of annual monsoonal rainfall in the first of the intense eccentricity-driven climate cycles of the present day (Durkee and Brown, 2014).

The same deep-lake event is seen in localities of this age in the Natron, Turkana and Awash basins (Trauth et al., 2005; cf. Table 1), as well as at Kasibos in the upper Homa Mountain Kanam faunal sequence (Ditchfield et al., 1999).

Artefacts are abundant in fossil localities of Naivashan age, not to mention in the many purely archeological sites not included here. The lithic assemblages of the long-lived Acheulean or ESA (Early Stone Age) culture began to include more developed tools as early as 0.6 Ma, in what is known as the Fauresmith phase (Johnson and McBrearty, 2010; Herries, 2011; Ferraro et al., 2013), but it is the current consensus that the beginning of the MSA (Middle Stone Age) with a full array of new tool-making technology, more or less coincident with the earliest recognized *Homo sapiens*, is dated across the continent at or just older than 0.3 Ma, as documented in the prolific sequences at Kapthurin and in the Olorgesailie basin (Johnson and McBrearty, 2010; Deino et al., 2018), Florisbad (Dusseldorf et al., 2013), and Jebel Irhoud (Hublin et al., 2017). A major reorganization of the mammal fauna is roughly coincident with this event, but studies have yet to find evidence that human activity played a significant role (Faith et al., 2012, 2018; Potts et al., 2018; Smith et al., 2019). In consideration of this distinct change in the latest Pleistocene record, whatever its cause, an informal 'Late Naivashan' or NV2 interval is designated, beginning at 0.35 Ma.

In other important localities of the Eastern Rift, the Aalat sequence near Buia, Eritrea, yields abundant fauna, artifacts and a well-preserved *Homo* cranium (Abbate et al., 2014; Ghinassi et al., 2015; Hammond et al., 2018). Lainyamok (ca. 0.4 Ma) was previously seen as the oldest site with exclusively modern fauna, but at least one extinct taxon has now been reported there (Faith et al., 2012). The long-known sites at Isimila in southern Tanzania (Willoughby, 2012), and the prolific localities at Farre in the Chalbi dry lake of northeastern Kenya (Ferraro et al., 2013) and at Asbole in the Awash (Geraads et al., 2004), as well as Olorgesailie, are famous for vast numbers of Acheulean hand-axes and other large and small tools interred with the mammalian remains. The younger (Herto) levels at Bouri (Clark et al., 2003) and Melka Kunturé (Johnson and McBrearty, 2010) document the early MSA with relatively early *Homo sapiens* in a faunal context, while the Galana Boi 'Holocene' exemplifies the central African environment during the final pluvial (Ndiema et al., 2010). In the Kavirondo rift, later Pleistocene faunas are sampled in the Kanam sequence on Homa Mountain (Ditchfield et al., 1999, 2019) and in the Lake Victoria terraces of Karungu and Rusinga Island (Tryon et al., 2010, 2012).

The major sites of Naivashan age in the Maghreb, as reviewed by Geraads (2010a, 2010b) and Stoetzel (2013), include the often-cited transgressive-regressive sequences in Moroccan coastal terraces, provisionally identified by Biberson (1971) to correspond with glacial-interglacial sea level cycles over the past 1 Myr. These units have recently been drastically reorganized in terms of MIS (marine isotopic stages) to better date the prolific cave fillings, including the Thomas grottoes (Geraads et al., 2010) and the Sidi Abderrahmane quarry (Lefevre and Raynal, 2002) as well as the caves of nearby Rabat (Barton et al., 2009). Mammal-rich karstic sites have recently been found in the highlands of northern Morocco, at Chrafate and Ez Zarka (Ouahbi et al., 2003), and essentially modern faunas are also abundant in fluviolacustrine beds at Wadi Sarrat (El Kef) in Tunisia (Martinez-Navarro et al., 2014) and in the Blue Nile valley at Singa and Abu Hagar (Spoor et al., 1998). In the Nafed (Nafud) desert of Saudi Arabia, Groucutt et al. (2018) have reported a finger bone attributed to *Homo sapiens* in the Al Wusta site dated to 0.085 Ma.

According to current dating of the principal South African sites in the later Pleistocene, the Cornelian and Florisian ages (Fig. 2), with their earliest sites at Cornelia-Uitzoek and at Florisbad main (Beaumont and Vogel, 2006; Brink et al., 2012; Granger et al., 2015) very nearly coincide with the early and late divisions of the Naivashan. Recent discovery of deeper levels in Wonderwerk Cave (Brink et al., 2015) expand this long sequence down to earliest Naivashan age, while the new excavations along the Ghaap Escarpment at Groot Kloof and other sites produce a sequence of fauna and culture spanning the Pleistocene but mainly Naivashan (Doran et al., 2015). The widely discussed Rising Star site complex with its apparent grave-pit of otherwise unknown *Homo naledi* is now dated to ca. 0.3 Ma (Dirks et al., 2017), with the question of the culture (if any) and ancestry of this isolated human taxon yet to be resolved. The thousands of bones (including *Homo*) from the dune-base sands around Elandsfontein's former water hole can only be approximately dated older than 0.8 and younger than 1.1 Ma (Braun et al., 2013), or probably base Naivashan at ca. 1.0 Ma.

OBSERVATIONS

The fossil record of Afro-arabian mammals, while still incomplete and forever destined to remain so, has nevertheless reached a level that supports some realistic interpretations of the Cenozoic history of this community. For example, Kingdon (1997), in describing the living mammals of 'Africa' (i.e., excluding the Levant and Arabia but including the closed-canopy tropical forest), notes 275 genera of all kinds, or 224 genera excluding Chiroptera. This can be compared to 207 genera, or 188 sans bats, from the Naivashan sites that only sample the open-country environment of the same Africa. The particulars of intercontinental exchanges and environmental trends are noted in the descriptions of the individual LMAs, but overviews of the information assembled in the database of Appendix 1 also provide interesting general observations in this regard.

Differential Preservation

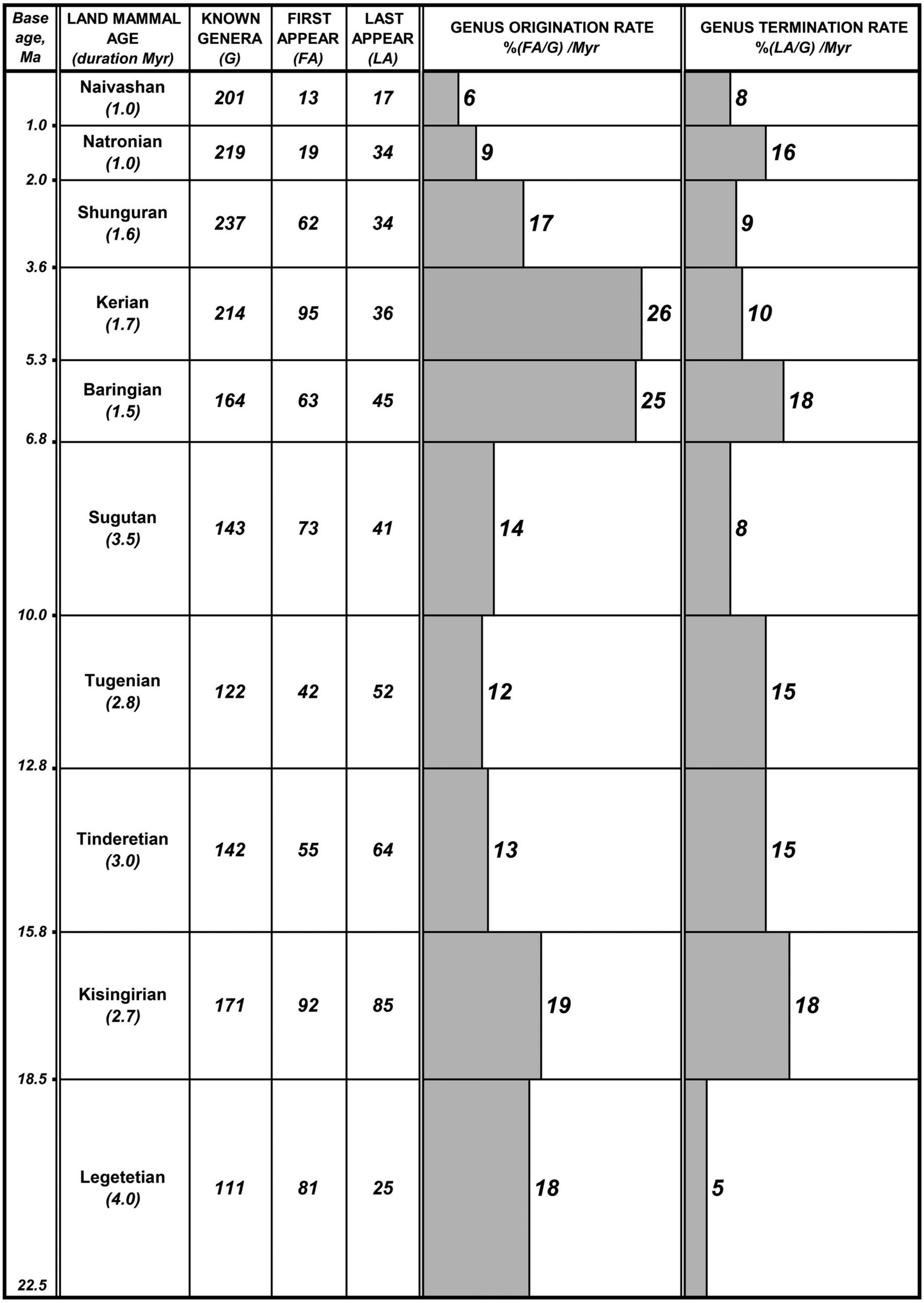
How meaningful is the record we refer to? For one thing, the attribution of African fossil genera to three latitudinal realms, each of which happens to have its own characteristic sample (described above) gives us a remarkably clear view of how the Afro-arabian fossil record has developed. The Eo-Oligocene, Miocene, and Plio-Pleistocene intervals summarized in Figure 3 each begin with improbably sharp, step-like increases in the total of fossil genera. That this is a matter of differential preservation in the three realms becomes plain when we note that the number of identified genera in the coastal sediments of North Africa (i.e., 'all known north' as the total of 'North,' 'North and Equatorial' and 'Pan Africa' in Fig. 3), unlike the other realms, shows no significant trend. This would be normal in coastlands, where the environment (including the taphonomic process) is essentially constant, and follows the principle of 'niche incumbency' (Alroy, 1996) that projects a relatively stable number of taxa in the fauna of an environmentally stable habitat regardless of successional turnover. On the other hand, by comparing the northern and equatorial numbers in Figure 3, we can be certain that the doubling of the average genus count in the Miocene, starting in the Legetetian, is not due to the invasion of Eurasian genera at that time, but must be due instead to the coincident addition of the second locus of preservation—the highland rift valleys of the equatorial realm. Similarly, the third increase in fossil abundance, which comes in the basal Pliocene Kerian, is clearly due to the new inclusion of material from karst deposits in the previously unsampled highlands of the southern realm.

Differential Diversity

Allowing for the progressive steps in preservation (see above), the observed history of diversity in various groups at the family and superfamily level, summarized in Fig. 9, show revealing inconsistency. In the most conspicuous example, the diversity in some groups rises sharply in the Kerian when the only significant increase in genera comes from the southern realm (Fig. 3). A

		TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NAV	*NV2*
	Total genera	**16**	**15**	**47**	**15**	**57**	**79**	**62**	**111**	**171**	**142**	**122**	**143**	**164**	**214**	**237**	**219**	**201**	**192**
MARSUPIALIA						1	1												
PLACENTALIA inc. sed.		3	2	2		1													
AFROINSECTIPHILIA		4	2	1															
AFROSORICIDA				4		1	4	3	4	**5**					3	3	3	3	3
TUBULIDENTATA									1	2	2	1	3		1	1	1	1	1
MACROSCELIDEA				1		2	2	1	2	**7**	2	3	1	1	4	**5**	4	4	4
PTOLEMAIIDA						1	3	1	1	1	1	1							
OCEPEIDA		2	1																
HYRACOIDEA			1	**5**	3	**6**	**10**	**10**	**6**	**5**	3	3	1	1	2	3	3	3	3
EMBRITHOPODA			1	1	1	1	1	1	1										
PROBOSCIDEA	NUMIDOTHERIIDAE	3	3	3	2	3	2												
	MOERITHER / PALEOMASTODON.		1	2	2	1	3	3											
	DEINOTHERIIDAE							2	1	1	1	2	2	2	1	1	1		
	MAMMUTIDAE							2	2	2	2	1	1	1	1	1	1		
	GOMPHOTHERIIDAE							2	3	**7**	**7**	4	3	2	1	1	1		
	ELEPHANTIDAE											1	**5**	**6**	**6**	4	3	2	1
EUPRIMATES inc. sed.		1			1	2	1												
STREPSIRRHINI				**5**		4	**6**	1	4	2	2	1	1	1	2	2	2	2	2
ANTHROPOIDEA	PROTEOPITHECIDAE					2													
	PARAPITHECIDAE					1	5	1											
	OLIGOPITH / PROPLIOPITHECIDAE					1	3												
	DENDROPITHECIDAE/ SAADANIIDAE							2	**8**	4	3	1							
	PROCONSULIDAE							1	**5**	**5**	**7**	1	1						
	HOMINIDAE										1		2	3	3	**5**	3	1	1
	VICTORIAPITH / CERCOPITHECIDAE							1	4	3	2	1	3	4	**10**	**13**	**11**	**6**	6
ANOMALUROMORPHA		1		**6**		4	**7**	2	4	**6**	**6**	**6**	**5**	4	3	3	3	3	3
HYSTRICOGNATHA					1	**9**	**13**	**10**	**14**	**20**	**12**	**9**	**9**	**9**	**11**	**10**	**7**	**10**	9
SCIUROMORPHA									1	1	**5**	**5**	**6**	**9**	**5**	**5**	**6**	**6**	6
MYOMORPHA	NESOMYIDAE								3	3	**7**	**9**	**6**	4	**5**	**5**	**5**	**5**	5
	DIPODIDAE									3	2	1	1	1	1	2	2	1	1
	CRICETIDAE											1	4	4	**5**	**6**	**5**	5	5
	MURIDAE									3	3	**7**	**11**	**10**	**23**	**22**	**19**	**18**	18
	GERBILLIDAE										2	3	3	2	3	**5**	**7**	**7**	**7**
	DEOMYIDAE									1	1	1	3	4	4	1	1	1	1
	SPALACIDAE									1	1	1	2	2	1	1	1	2	1
LAGOMORPHA									1	3	1		1	**5**	**5**	4	4	4	3
EULIPOTYPHLA									3	3	3	3	4	4	**5**	**7**	**7**	**7**	7
CHIROPTERA				**11**	1	**8**	**5**	4	4	**7**	**9**	**8**	**7**	**7**	**10**	**15**	**18**	**18**	18
TYLOPODA														1	2	1	1	1	1
SUOIDEA									4	**9**	**10**	4	1	4	**7**	**8**	**6**	**6**	6
WHIPPOMORPHA						2	2	4	**6**	**8**	3	3	6	4	4	4	3	2	1
RUMINANT.	TRAGULIDAE								3	2	2	1	1	1	1	1	1	1	1
	GELOCIDAE								2	6	3								
	GIRAFFIDAE								3	3	4	5	1	4	2	2	2	2	1
	BOVIDAE									4	**9**	**13**	**10**	**19**	**32**	**36**	**34**	**35**	33
PHOLIDOTA				1	1	1	1								2	3	3	3	3
HYAENODONTA		2	4	**5**	3	**6**	**10**	**10**	**11**	**12**	**5**	4							
CARNIVORA	AMPHICYONIDAE									4	3	1	2	2					
	URSIDAE									1		1	2	1	1	2	1	1	
	CANIDAE												1	2	3	**6**	**8**	**6**	6
	MUSTELIDAE									**5**	3	3	**7**	**6**	6	10	10	8	8
	VIVERRIDAE								2	4	3	2	2	**5**	4	**5**	3	3	3
	HERPESTIDAE (incl. *Nandinia*)									2	1	1	2	**5**	**7**	**10**	**10**	**10**	10
	STENOPLESICTIDAE / PERCROCUTIDAE							1	2	3	2	2	2						
	HYAENIDAE										1	2	**6**	**8**	**11**	**11**	**6**	4	4
	BARBOUROFELIDAE / FELIDAE								2	**6**	2	2	**7**	**6**	**9**	**8**	**8**	**6**	6
PERISSODACTYLA									4	**7**	**6**	4	**8**	**10**	**8**	**5**	**5**	4	4

FIGURE 9. Generic diversity in the AFLMAs.



Base age, Ma	**LAND MAMMAL AGE** *(duration Myr)*	**KNOWN GENERA** *(G)*	**FIRST APPEAR** *(FA)*	**LAST APPEAR** *(LA)*	**GENUS ORIGINATION RATE** *%(FA/G) /Myr*	**GENUS TERMINATION RATE** *%(LA/G) /Myr*
1.0	**Naivashan** *(1.0)*	*201*	*13*	*17*	*6*	*8*
2.0	**Natronian** *(1.0)*	*219*	*19*	*34*	*9*	*16*
3.6	**Shunguran** *(1.6)*	*237*	*62*	*34*	*17*	*9*
5.3	**Kerian** *(1.7)*	*214*	*95*	*36*	*26*	*10*
6.8	**Baringian** *(1.5)*	*164*	*63*	*45*	*25*	*18*
10.0	**Sugutan** *(3.5)*	*143*	*73*	*41*	*14*	*8*
12.8	**Tugenian** *(2.8)*	*122*	*42*	*52*	*12*	*15*
15.8	**Tinderetian** *(3.0)*	*142*	*55*	*64*	*13*	*15*
18.5	**Kisingirian** *(2.7)*	*171*	*92*	*85*	*19*	*18*
22.5	**Legetetian** *(4.0)*	*111*	*81*	*25*	*18*	*5*

FIGURE 10. Origination and termination rates in Neogene AFLMAs. Rate values are rounded to reflect the fact that the FA (first appearance) and LA (last appearance) of Neogene genera are only minimal approximations. Occurrences that are restricted to a single age are counted as both first and last appearance.

feasible explanation for the relatively unchanged count of hystricognath rodents, mustelids, hyaenids and perissodactyls in the Pliocene may be that these groups are not as commonly found in cave deposits. As noted above, the relatively stable records of the northern and equatorial realms during this increase (Fig. 3) make it probable that the overall diversity in African faunas remained essentially constant as the Pliocene opened.

An increase in recorded generic diversity of several groups that are now presently associated with open woodlands and grasslands, including elephantids, myomorphs, bovids, hyaenids, and felids, is seen in the later Miocene Sugutan and Baringian. This increase, without any major change in preservation circumstances, again contrasts with the lack of significant variation in other groups, but here it would appear to reflect a real increase in generic diversity stimulated by the opening of new niche opportunities for 'pre-adapted' clades, as the climate became more seasonal and new associations of drought-adapted vegetation evolved over wide areas (Uno et al., 2011). A corresponding increase of the species diversity in the noted groups has been described in some detail from the northern rift basins of Kenya and Ethiopia (Vrba, 2005; Bobe, 2006; Bobe et al., 2007), although in this case the increase in diversity of species is dated only to later Baringian at about 6 Ma.

A synchronous decline in diversity is seen in three groups of open-country megaherbivores, which go from five or more genera in Late Miocene and Early Pliocene to two genera by Late Pleistocene and then to a single genus in the present day open-country ecofauna of Afro-arabia. These are Proboscidea, with *Loxodonta* outlasting *Elephas*; Whippomorpha, with *Hippopotamus* outlasting *Archaeopotamus* and *Hexaprotodon* retreating to tropical forest in the Pleistocene; and Giraffidae, with *Giraffa* outlasting *Sivatherium*. In each instance the surviving genus is not a dwindling relic but is highly successful and abundant across the continent's open-country terrain. In that the Hominidae show a very similar decline in diversity, going from five genera to one monospecific genus over the last 3 Myr, this strangely synchronous feature of Afro-arabian diversity may demonstrate a general principle.

As Faith et al. (2018) point out (see also Bobe and Carvalho, 2018), the widely accepted consensus that the megaherbivore clades were adapting to increasingly efficient human predation is not well supported. For one thing, the decline in megaherbivore diversity must have begun in the Kerian age prior to 3.6 Ma to cause the diminished numbers in the Shunguran, and this would be long before hominin tools had developed beyond the simple choppers and scrapers presumably used in scavenging carcasses (Dominguez-Rodrigo and Alcalá, 2016). The only other continent-wide influence, if we set aside hominin predation, is the increasing impact of stronger and more sustained climate extremes during the Plio-Pleistocene (DeMenocal, 2004). Such an unprecedented, super-cyclic environment may well have had equally unprecedented effects, one of which could be pressure to select uniquely competent forms that could cope with these extreme changes.

Differential Turnover

The rates of origination and extinction, or more precisely, the percentage of first and last occurrences in the recorded fauna of the individual AFLMA (Fig. 10) indicate two Miocene turnover events, as well as a moderate pulse of extinction and a striking decline of origination in the Pleistocene.

The Early Miocene turnover is a simultaneous increase of origination and extinction of genera in the Kisingirian, coincident with the first waves of Eurasian exchange. Extinction rates continued higher than origination for the next 5 Myr, reflecting a decline among endemic genera (cf. Fig. 9), and suggesting a slow takeover of niches by more successful genera.

The terminal Miocene turnover begins in the Baringian, at ca. 6.5 Ma, with a notably strong synchronous pulse in origination and extinction, after which origination rates decline only slightly in the Pliocene even as extinctions immediately return to average levels. This differential relationship is the opposite of that seen in the Early Miocene, and would logically suggest that after the initial Baringian turnover, more genera continued to be added without significantly replacing pre-existing ones, as an indication of new niches in the expanding and climatically adapting grasslands habitat. The record of genus origination, however, is inconsistent with that of species, as reported by Behrensmeyer et al. (1997), DeMenocal (2004), and Vrba (2005) who describe a much later species origination pulse in the late Pliocene between 3.0 Ma and 2.5 Ma, followed by a decline in diversity that reached a minimum in early Naivashan.

The sampled faunas of Natronian and Naivashan age show the lowest genus origination rates of the Neogene, suggesting that the lowered diversity of megaherbivores and hominids, as noted above, was part of a broader loss of variance. As noted elsewhere, this steady decline in origination has not been credibly attributed to human activity and reinforces the possibility that the increasingly wide swings in global climate may inhibit, rather than stimulate variation.

A singular outlier to the general trends in the Neogene, however, is the (apparently) precipitous overturn in Homininae (Van Couvering, 2017; cf. Appendix 1), in which only six of 12 genera endured for more than one age, and not one hominin genus identified in Kerian (early Pliocene) localities survived past the Natronian into the Middle Pleistocene, a rapidity of development which, if not a self-centered exaggeration of otherwise modest changes, exceeds that of any other group. The closest comparison is the record of the open-country Suidae, which like Homininae is unusual in that none of its six Early Pliocene genera are now extant, but which today includes not one but three genera that arose in the Pleistocene. The 'dash to *Homo*' would imply that the combination of derived primate features in hominins (e.g., manipulative forelimbs, optional bipedality, binocular vision, omnivory) was uniquely advantageous for a great ape in the new open-country habitat.

CONCLUSIONS

The land mammal ages established in this work are designed to integrate the history of Cenozoic land mammals across the entire Afro-arabian continent. The relatively solid structure and broad scope of this record at the genus level provides the clearest possible recognition of basic trends, in a stable framework that readily incorporates new information coming from the hard work of our colleagues. Above all, this finally brings Africa into the global LMA system, completing the basic web of intercontinental correlation in the history of land mammals.

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Dedication

Judith Anne Harris (1936–2019), Professor emerita, University of Colorado, Boulder, was the wife of the senior author when she prepared studies of the paleoecology of Afro-arabia for early drafts of the present paper. As time progressed, her work took on a life of its own, culminating in a major contribution, 'Principles of Continental Paleoecology' (Wiley), presently nearing completion by her co-author Kenneth Carpenter. We respectfully dedicate this paper to her, in recognition of the insight and inspiration that Judith provided to bring this concept into reality.

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APPENDIX 1. Genera of the African Land Mammal Ages. See 'Remarks' at end.

1

	PALEOGENE							MIOCENE						PLIO-PLEISTOCENE					R
	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
METATHERIA -- DIDELPHIMORPHIA - HERPETOTHERIIDAE																			
Peratherium > Qatranitherium					--N	--N													
EUTHERIA -- Placentalia indet.																			
Adapisoriculus	--N																		
Afrodon	--N	--N																	
Garatherium	--N	--N																	
Kasserinotherium			--N																
Namalestes			S--																
Ghamidatherium					--N														
AFROTHERIA																			
AFROINSECTIPHILIA -- order indet.																			
"Cimolestes"	--N																		
"Palaeoryctes"	--N	--N																	
"Aboletylestes"	--N																		
Todralestes	--N	--N																	
Chambilestes			--N																
TENRECOIDEA -- TENRECIDAI `																			
Namagale			S--																
Nanogale			S--																
Dilambdogale					--N														
Widanalfarasia						--N													
Jawharia						--N													
Qatranilestes						--N													
Arenagale							S--												
Sperrgale							S--												
Tenrecogale									S--										
Erythrozootes								E	E										
Protenrec								E	SE										
Parageogale								E	SE										
CHRYSOCHLORIDAE																			
Damachloris			S--																
Diamantochloris			S--																
Eochrysochloris						--N													
Namachloris							S--												
Prochrysochloris								E	SE										
Proamblysomus														S--	S--				
Amblysomus														S--	S--	...	...	*...*	>
Chlorotalpa														S--	...	S--	...	*...*	>
Chrysospalax																S--	...	*...*	>
TUBULIDENTATA -- ORYCTEROPIDAE																			
Myorycteropus								E	E	E									
Orycteropus									SE	...	EN	E	EN	SEN	SEN	...	E	*E*	>
Leptorycteropus												E							
Amphiorycteropus												--N	--N						
MACROSCELIDEA -- MACROSCELIDIDAE																			
Chambius			--N																
Eotmantsoius					--N														
Nementchatherium					--N														
Herodotius						--N													
Metoldobotes						--N													
Macroscelidid sp.							S--												
Myohyrax								E	SE	E									
Miorhynchocyon								E	E	E	E								
Brachyrhynchocyon									S--										

2	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
Hypsorhynchocyon									S--										
Hiwegicyon									E										
Miosengi									E										
Protypotheroides									S--										
Rhyncocyon											--N	...	...	...	E	...	...	...	>
Pronasilio											E								
Elephantulus														S--	SEN	S--	...	...	>
Macroscelides															S--	...	...	...	>
Palaeothentoides															S--				
Mylomygale															S--	S--			
PTOLEMAIIDA																			
Ptolemaia (Ptolemaiidae)					--N	--N	E												
Cleopatrodon						--N													
Qarunavus						--N													
Kelba (Kelbidae)								E	E	...	E								
PAENUNGULATA																			
OCEPEIDA - OCEPEIIDAE																			
Ocepeia	--N	--N																	
Abdounodus	--N																		
HYRACOIDEA																			
PLIOHYRACIDAE (s. l.)																			
Seggeurius		--N																	
Bunohyrax			S-N	...	--N	--N	EN												
Namahyrax			S--																
Dimaitherium					--N														
Geniohyus						--N	--N												
Pachyhyrax						--N	...	...	--N										
Brachyhyrax							E	E											
Megalohyrax		--N	--N	...	...	--N	--N												
Microhyrax			--N																
Saghatherium					--N	--N													
Selenohyrax						--N													
Thyrohyrax						--N	E	E											
Rupestrohyrax							S--												
Titanohyrax		--N	--N	...	...	--N													
Antilohyrax						--N													
Rukwalorax							E												
Afrohyrax							E	E	SEN	E									
Meroehyrax							E	E	E	E									
Prohyrax									SEN										
Regubahyrax									--N										
Parapliohyrax										EN	SE								
Pliohyrax											--N								
PROCAVIIDAE																			
Heterohyrax											S--	...	...	...	...	...	E	*E*	>
Gigantohyrax														S--	S--	S--			
Procavia															S--	S--	...	*S--*	>
Dendrohyrax																	E	*...*	>
EMBRITHOPODA - ARSINOITHERIIDAE																			
Stylolophus		--N																	
Namatherium			S--																
Arsinoitherium				--N	--N	--N	EN	E											
PROBOSCIDEA																			
NUMIDOTHERIIDAE																			
Eritherium	--N																		
Khamsaconus	--N																		
Phosphatherium	--N	--N																	
Daouitherium		--N																	

3	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	***NV2***	R
Numidotherium		--N	--N																
Saloumia			--N																
Arcanotherium			--N	...	--N														
Barytherium					--N	--N													
Omanitherium						--N													
MOERITHERIIDAE, PALAEOMASTODONTIDAE																			
Moeritherium		--N	--N	...	--N	--N													
Palaeomastodon			--N	...	--N	--N	EN												
Phiomia						--N	E												
Eritreum							E												
DEINOTHERIIDAE																			
Chilgatherium							E												
Prodeinotherium							E	E	SEN	E	EN	...	E						
Deinotherium											--N	EN	E	E	E	E			
MAMMUTIDAE																			
Losodokodon							E												
Eozygodon							E	E	SE	E									
Zygolophodon								EN	--N	EN	E	--N							
Mammut													--N	--N	--N	--N			
GOMPHOTHERIIDAE																			
Gomphotherium							EN	EN	SEN	--N									
Archaeobelodon							E	EN	EN	E									
Afrochoerodon								--N	...	SE	E								
Platybelodon									EN										
Progomphotherium									SE										
Afromastodon									SEN	E									
Choerolophodon									--N	E	...	E							
Protanancus										EN	E	E	E						
Anancus										E	E	EN	SEN	SEN	EN	EN			
ELEPHANTIDAE																			
Tetralophodon											EN	E							
Stegodon												EN	E	EN					
Stegotetrabelodon												EN	E						
Primelephas												EN	E	EN	--N				
Loxodonta												EN	SE	SEN	E	E	SEN	*SEN*	>
Elephas													E	SE	SE	EN	EN		
Mammuthus													SE	SEN	S-N	--N			
Selenotherium / Stegodibelodon														EN					
EUARCHONTOGLIRES																			
PRIMATES - **EUPRIMATES** (fam. incog,)																			
Altiatlasius	--N																		
Amamria				--N															
Nosmips					--N														
Afrotarsius					--N	--N													
STREPSIRRHINI - DJEBELEMURIDAE																			
Djebelemur			--N																
Notnamaia			S--																
"Anchomomys"						--N													
Omanodon						--N													
Shizarodon						--N													
AZIBIIDAE																			
Algeripithecus			--N																
Azibius > Tabelia; Dralestes			--N																
ADAPIDAE																			
Namadapis			S--																
Afradapis					--N														
Masradapis					--N														
Aframonius						--N													

4	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
LEMURILORIFORMES -- fam. incog.																			
Karanisia					--N														
Namaloris							S--												
GALAGIDAE																			
Saharagalago					--N														
Wadilemur						--N													
Mioeuoticus								E	E										
Progalago								E	E	E									
Komba								E	E	E									
Galago / Galagoides											--N	...	E	E	E	...	...	...	>
Laetolia														E					
Otolemur															E	...	...	...	>
PLESIOPITHECIDAE																			
Plesiopithecus						--N													
Propotto								E											
ANTHROPOIDEA -- *PARACATARRHINI*																			
PROTEOPITHECIDAE																			
Proteopithecus						--N													
Serapia						--N													
PARAPITHECIDAE																			
Biretia					--N														
Arsinoea						--N													
Abuqatrania						--N													
Qatrania						--N													
Apidium						--N													
Parapithecus > Simonsius						--N													
Lokonepithecus							E												
OLIGOPITHECIDAE																			
Talahpithecus					--N														
Catopithecus						--N													
Oligopithecus						--N													
EOCATARRHINI																			
PROPLIOPITHECIDAE																			
Propliopithecus > Aegyptopithecus						--N													
SAADANIIDAE																			
Saadanius							--N												
DENDROPITHECIDAE																			
Dendropithecus								E	E										
Micropithecus								E	E	E									
Simiolus									E	E	E								
Eocatarrhini fam. incog.																			
Kamoyapithecus							E												
Iriripithecus								E											
Lomorupithecus								E											
Kalepithecus								E											
Karamojapithecus								E											
Kogolepithecus								E											
Limnopithecus								E	E	E									
EUCATARRHINI																			
PROCONSULIDAE																			
Rukwapithecus							E												
Rangwapithecus								E	EN	E									
Nyanzapithecus								E	E	E									
Proconsul > Ugandapithecus								E											
Xenopithecus								E											
Afropithecus > Morotopithecus								E	EN	E									
Ekembo									E										

5	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	***NV2***	R
Turkanapithecus									E	E									
Heliopithecus										E									
Mabokopithecus										E									
Equatorius										E									
Nacholapithecus										E									
Otavipithecus											S--								
Samburupithecus												E							
HOMINIDAE																			
Kenyapithecus										E									
Chororapithecus												E							
Nakalipithecus												E							
Sahelanthropus													--N						
Orrorin													E						
Ardipithecus													E	E					
Australopithecus														E	SE	SE			
Kenyanthropus															E				
Paranthropus															SE	SE			
Homo															E	SEN	SEN	*SEN*	>
VICTORIAPITHECIDAE																			
Nsungwepithecus							E												
Alophe								E											
Prohylobates								--N											
Zaltanpithecus									--N										
Noropithecus									E	E									
Victoriapithecus								E	E	E	E								
CERCOPITHECIDAE																			
Microcolobus												E							
Libypithecus													--N						
Kuseracolobus														E					
Paracolobus														E	E				
Colobus / Procolobus														E	E	E	E	*SEN*	>
Cercopithecoides												--N	E	E	SE	SE			
Rhinocolobus															E	E			
Cercopithecus / Chlorocebus														E	E	...	E	*S--*	>
Nanopithecus														E	E				
Macaca													EN	--N	--N	...	--N	*--N*	>
Dinopithecus																S--			
Gorgopithecus																S--			
Parapapio												E	E	SE	SE	S--			
Cercocebus / Lophocebus															SE	SE	...	*E*	>
Pliopapio														E					
Procercocebus															S--				
Soromandrillus															SE				
Theropithecus														E	SEN	SEN	SEN	*E*	>
Papio															SE	SE	SE	*E*	>
GLIRES **-- RODENTIA**																			
PROTROGOMORPHA -- PARAMYIDAE																			
"Ischyromyid" indet.	--N																		
Namaparamys			S--																
ANOMALUROMORPHA																			
ZEGDOUMYIDAE																			
Zegdoumys			S-N																
Tsaukheabymys			S--																
Glibia			S-N																
Glibemys			--N																
Lazibemys			--N																

6	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	***NV2***	R
ANOMALURIDAE (s. l.)																			
Kabirmys					--N														
Nementchamys					--N														
Shazurus					--N	--N													
Argouburus						--N													
Oromys						--N													
Dakhlamys						--N													
Prozenkerella						--N	...												
Nonanomalurus						--N	...	E											
Paranomalurus						--N	E	E	E	E	...	E							
Zenkerella								E	...	...	...	...	...	...	...	...	...	...	>
Anomalurus										E	...	...	...	...	...	...	...	...	>
PEDETIDAE																			
Megapedetes								E	SEN	EN	--N								
Parapedetes									S--										
Propedetes									S--										
Rusingapedetes									E										
Oldrichpedetes										S--	S--	...	--N						
Pedetes										E	E	...	...	SE	SE	S--	S--	*E*	>
HYSTRICOGNATHA																			
THRYONOMYIDAE																			
Protophiomys				--N	--N	--N													
Waslamys					--N														
Monamys					--N														
Talahphiomys					--N	--N													
Paraphiomys						--N	...	E	SEN	EN	SE	E	E						
Acritophiomys						--N													
Kahawamys							E												
Silicamys							S--												
Namaphiomys							S--												
Apodecter								E	E	E									
Epiphiomys								E	SE										
Neosciuromys (Phthinylla)									S--										
Paraulacodus										E	E	E							
Petromus												S--	E	SE	S--	...	S--	...	>
Thryonomys														E	E	...	E	*E*	>
PHIOMYIDAE																			
Phiomys > Lavocatomys					--N	--N	...	EN	SE										
Phenacophiomys					--N	--N													
Birkamys					--N	--N													
Mubhammys					--N	--N													
Neophiomys					--N	--N													
Acritophiomys						--N													
Gharbalamys						--N													
Turkanamys							E												
Ugandamys								E											
Andrewsimys								E											
GAUDEAMURIDAE																			
Gaudeamus					--N	--N													
DIAMANTOMYIDAE																			
Metaphiomys					--N	--N	S-E												
Prepomonomys							S--												
Tufamys							S--												
Diamantomys							E	E	SE	E									
Pomonomys									S--										
MYOPHIOMYIDAE																			
Phiocricetomys					--N	--N													
Myophiomys								E	E	S-N									

7	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	NV2	R
Elmerimys								E	E	E									
Phiomyoides									S--										
KENYAMYIDAE																			
Kenyamys								E	E										
Simonimys								E	E										
BATHYERGIDAE																			
Bathyergoides								E	S--										
Proheliophobus								E	E	...	...	S--							
Renefossor								E	E										
Efeldomys									S--										
Geofossor									S--										
Microfossor									S--										
Richardus										E	...	...	...	E					
Cryptomys														S--	S--	S--	...	...	>
Heterocephalus														E	SE	...	E	...	>
Gypsorhychus														S--	S--	...	...	...	>
Georychus														S--	...	S--	...	S--	>
Bathyergus																	S--	S--	>
HYSTRICIDAE																			
Atherurus											--N	...	E	EN	...	...	...	...	>
Hystrix												E	E	SEN	SE	SE	S-N	...	>
Xenohystrix													E	SEN	SE				
CTENODACTYLIDAE																			
Sayimys									--N	--N	...	...	--N						
Africanomys										--N	--N	...	--N						
Metasayimys									--N	...	--N								
Irhoudia											--N	--N	...	--N	--N	--N	--N		
Testourimys										--N									
SCIUROMORPHA -- SCIURIDAE / GLIRIDAE / MYOXIDAE																			
Vulcanisciurus								E	SE	E	SE								
Atlantoxerus										--N	--N	--N	...	--N	--N	...	...	...	>
Heteroxerus										--N	...	S--							
Kubwaxerus												E	E						
Xerus												E	--N	EN	E	...	...	...	>
Sabara													--N						
Paraxerus												S--	E	E	E	...	...	...	>
Heliosciurus																E	...	...	>
Microdryomys										--N									
Dryomys										--N	--N								
Otaviglis												S--							
Eliomys													--N	...	...	...	--N	...	>
Graphiurus														S--	S--	S--	...	...	>
MYOMORPHA																			
NESOMYIDAE																			
Afrocricetodon								E	E	E									
Notocricetodon								E	E	E	S--								
Protarsomys								E	SE	S--	S--								
Mabokomys										E	E								
Ternania										SE	EN	--N							
Potwarmus										--N									
Mabokomys										E	E								
Senoussimys											--N								
Steatomys											S-N	S-N	E	...	SE	S--	SE	...	>
Dendromus											--N	SE	EN	SE	SE	S--	S--	...	>
Petromyscus											S--	S--	...	...	S--	...	...	...	>
Harimyscus												S--							
Saccostomus												E	E	E	E	S--	S--	E	>
Malacothrix														S--	S--	S--	...	...	>

8

	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
DIPODIDAE																			
Protalactaga									--N	--N	...	...	...	...	E	E			
Arabosminthus									--N										
Heterosminthus									--N	--N									
Jaculus															E	...	E	*E*	>
CRICETIDAE																			
Apocricetus											--N	...	--N						
Stenodontomys												S--	...	S--	S--				
Faraframys												--N							
Afaromys												SE							
Lophiomys													--N	...	--N	...	...	*...*	>
Cricetus													--N	...	...	--N	...	*...*	>
Protolophiomys															--N				
Mystromys														S--	SE	S--	...	*...*	>
Desmodillus														S--	S--	...	...	*...*	>
Proodontomys																S--			
Ellobius																		*--N*	>
MURIDAE																			
Shamalina									--N										
Mellalomys									--N										
Leakeymys									--N	E									
Zramys										--N	--N	--N							
Dakkamys										--N	E								
Ameuromys											--N								
Saharamys											--N								
Dakkamyoides											S--	S--							
Karnimata											S--	EN							
Progonomys											--N	--N	...	--N					
Paraethomys												--N	--N	--N	--N	--N	--N		
Preacomys												SE	E						
Micaelamys												S--							
Mioharimys												S--							
Otavimys												S--							
Parapelomys												E	--N	--N	...	...	--N		
Saidomys													EN	E	E				
Castillomys													--N						
Stephanomys													--N						
Anthracomys													--N						
Golunda														EN	E				
Mus														SEN	SEN	SEN	SEN	*EN*	>
Praomys														EN	SE	S-N	--N	*--N*	>
Apodemus														--N	...	--N	...	*--N*	>
Oenomys														E	E	...	...	*...*	>
Arvicanthus															EN	...	EN	*--N*	>
Aethomys														S--	SE	S--	SE	*...*	>
Boltimys														S--					
Pelomys														E	SE	...	...	*...*	>
Grammomys															SE	...	...	*...*	>
Otomys														S--	SE	S--	SE	*E*	>
Euryotomys														S--					
Palaeotomys														S--	SE	S--			
Prototomys														S--	SE				
Parotomys																	S--	*...*	>
Delanymys															E	...	...	*...*	>
Eulmus													--N	--N					
Abudhabia												E	EN						
Lukeinomys													EN						
Stenocephalomys																		*E*	>

9	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
Mastomys														E	E	S--	E	*E*	>
Thallomys														E	SE	...	SE	*S--*	>
Lemniscomys															SE	S--	--N	*--N*	>
Dasymys															S--	S--	...	*E*	>
Zelotomys															SE	...	...	*E*	>
Millardia														SE					
Rhabdomys														S--	SE	S--	...	*...*	>
Nesokia																		*--N*	>
GERBILLIDAE																			
Myocricetodon										EN	SEN	--N	--N						
Ameuromys										--N	--N								
Protatera											--N								
Debruijnomys												--N	--N						
Mioharimys												S--							
Gerbilliscus (=Tatera)														SE	SE	S--	E	*E*	>
Taterillus														S--	S--	...	...	*...*	>
Gerbillurus														S--	S--	...	...	*...*	>
Gerbillus															SE	--N	--N	*--N*	>
Desmodilliscus															SE	E	...	*...*	>
Parameriones																--N			
Meriones																--N	--N	*...*	>
Mascaramys																	--N		
DEOMYIDAE																			
Democricetodon									S-N	...	E								
Namibimys												S--							
Praecomys												SE	E						
Ruscinomys													--N	--N					
Tectonomys												E	E	E					
Acomys													E	SE	SE	S--	S--	*S--*	>
Uranomys														S--					
SPALACIDAE																			
Prokanisamys									--N										
Pronakalimys										E									
Nakalimys											E	SE							
Harasibomys												S--							
Kanisamys													E						
Tachyoryctes													E	E	...	...	E	*...*	>
Nannospalax																	--N	*--N*	>
LAGOMORPHA -- OCHOTONIDAE																			
Kenyalagomys								E	EN										
Alloptox									--N										
Australagomys									S--	S--									
LEPORIDAE																			
Alilepus												E	E	E					
Pronolagus													E	E	S--	...	...	*...*	>
Prolagus													--N	--N	--N				
Bunolagus																S--	...	*...*	>
Serengetilagus													EN	EN	...	S--			
Trischizolagus																	--N		
Lepus													E	EN	SE	S-N	S-N	*SEN*	>
LAURASIATHERIA																			
***EULIPOTYPHLA* -- ERINACEOMORPHA** ERINACEIDAE																			
Amphechinus								E	SE	SE									
Galerix								E	E										
Gymneurechinus								E	SE										
Protechinus										--N									
Schizogalerix												--N	--N						
Erinaceus															SE	...	...	*...*	>

10	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
SORICIDAE																			
Lartetium										--N	--N	...	...	--N					
Myosorex											--N	...	...	S--	SE	S--	...	*S--*	>
Crocidura											S--	...	...	...	SE	--N	--N	*--N*	>
Suncus														S--	SEN	S--	...	...	>
Diplomesodon														S--	S--	...	...	...	>
Sylvisorex															E	...	...	...	>
Asoriculus															--N	--N			
SCROTIFERA *CHIROPTERA*																			
Aegyptonycterus (*Aegyptonycteridae*)					--N														
Necromantis (Necromantidae)			--N																
Dizzya (Philisidae)			--N																
Witwatia			--N	...	--N														
Philisis > Vampyravus					--N	--N	...	...	...	...	...	...	...	...	...	...	...	...	>
Scotophilisis									--N										
Hipposideros (Hipposideridae)			..N	...	...	--N	...	E	...	...	...	...	...	--N	E	S--	...	*S--*	>
Palaeophyllophora			..N																
Asellia										--N	...	...	...	...	...	...	...	...	>
Tanzanicterys (Tanzanycteridae)			E																
Qarunycteris (Rhinopotamidae)					--N														
Rhinolophus (Rhinolophidae)									S--	--N	...	...	...	...	S-N	S--	S--	...	>
Phasmatonycteris (Myzopodidae)						--N													
Myzopoda															E	...	...	...	>
Khonsunycteris (Vespertilionidae					--N														
Chamtwaria								E											
Scotophilus															E	...	...	...	>
Myotis															SEN	...	...	...	>
Eptesicus															E	...	...	...	>
cf. Nycticeius															E	...	...	...	>
Pipistrellus															E	...	...	...	>
Vespertiliavus (Emballonuridae)			--N																
Pseudovespertiliavus			--N																
Dhofarella					--N	--N													
Saccolaimus (Pteropodidae)							E	...	E	...	...	...	...	...	E	...	...	...	>
Eidolon															E	...	...	...	>
Coleura															E	...	...	...	>
Taphozous																S--	...	...	>
Saharaderma (Megadermidae)					--N														
Afropterus									E	--N									
Megaderma										E	--N								
Cardioderma															E	...	...	...	>
Khoufechia (Nycteriidae)			--N																
Chibanycteris						--N	...	...	...	...	...	...	--N						
Nyctereis														S--	E	...	...	...	>
Miniopterus (Miniopteridae)															--N	E	...	*S--*	>
Tadarida (Molossidae)									E	--N	...	...	...	...	E	...	S--	...	>
Chambinycteris (fam. indet.)			--N																>
Draconycteris			--N																>
CETARTIODACTYLA																			
TYLOPODA - CAMELIDAE																			
Paracamelus													--N	--N					
Camelus														E	E	EN	--N	*--N*	>
SUOIDEA																			
SANITHERIIDAE																			
Sanitherium									EN	E									
Diamantohyus > Xenochoerus								E	SEN										

11

	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
SUIDAE																			
Nguruwe								E	SEN	E									
Namachoerus								E	SE	E									
Kenyasus > Nasus								E	SE	EN									
Libychochoerus									SEN	E									
Listriodon									--N	EN	E								
Lopholistriodon									E	SEN	E								
Mabokochoerus										E									
Barberahyus										E									
Albanohyus										E									
Megalochoerus										E									
Nyanzachoerus											EN	EN	SEN	SEN	SE				
Cainochoerus > "Pecarichoerus"													E	S--	...	S--			
Potamochoeroides													E	S--	S--				
Kolpochoerus													E	EN	EN	EN	SEN		
Metridiochoerus														E	SE	SE	SEN	*S--*	
Notochoerus														SE	SE	E			
Phacochoerus															SE	SE	E	*SEN*	>
Stylochoerus														E	SE	E	E		
Potamochoerus																	E	*SE*	>
Afrochoerus																	E	*E*	
Hylochoerus																		*E*	>
Sus																		*--N*	>
WHIPPOMORPHA																			
ANTHRACOTHERIIDAE																			
Bothriogenys					--N	--N	SEN	E	E										
Nabotherium					--N														
Qatraniodon						--N													
Epirigenys							E												
Brachyodus > Masritherium							E	E	SEN										
Afromeryx							E	E	--N	E									
Sivameryx > Hyoboops								E	EN										
Kulutherium								E	E										
Jaggermeryx									--N										
Libycosaurus > Merycopotamus											--N	EN	--N	--N	S-N				
HIPPOPOTAMIDAE																			
Morotochoerus								E	E	E	E								
Kenyapotamus									E	E	EN	E							
Chororatherium												E							
Hexaprotodon												E	E	E	E	E	...	*...*	>
Archaepotamus												EN	EN	EN	E	E	E		
Hippopotamus												E	E	SEN	SEN	EN	SEN	*SEN*	>
RUMINANTIA																			
TRAGULIDAE																			
Dorcatherium								E	E	SE	E	...							
Siamotragulus								E											
Afrotragulus								E	SE	S--									
Hyemosuchus													E	...	...	...	...	*...*	>
GELOCIDAE																			
Walangania > Palaeomeryx								E	SEN	E									
Prolibytherium									--N										
Propalaeoryx								E	SE	E									
Sperrgebietomeryx									S--										
Orangemeryx									S--										
Namibiomeryx									S--										
Nyanzameryx										E									

12	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
GIRAFFIDAE																			
Palaeotragus > Samotherium								E	E	EN	EN	EN	EN						
Canthumeryx								E	EN	EN	E								
Climacoceras								E	E	SEN	E								
Injanotherium										--N									
Giraffokeryx											E								
Afrikanokeryx											E								
Bohlinia													--N						
Giraffa													E	EN	SEN	EN	SEN	*SEN*	>
Sivatherium													SEN	SEN	SEN	SEN	SEN	*S--*	
BOVIDAE																			
Hypsodontus > Oiocerus									--N	EN	EN								
Namacerus									S--										
Kipsigicerus									--N	E	E								
?Sivoreas											E								
Samokeros											--N								
Miotragocerus											--N	...	EN	S--					
Mesembriportax														S--	S--				
Tragelaphus													E	SE	SEN	SE	SEN	*SEN*	>
Taurotragus																E	SEN	*SEN*	>
Ugandax													E	E	E				
Simatherium													E	SEN	S--	E			
"Leptobos"													--N	...	...	--N			
Jamous														--N					
Syncerus														S--	SEN	E	SEN	*SEN*	>
Pelorovis															E	SEN	SE	*--N*	
Brabovis														E					
Bos																--N	--N	*...*	>
Cephalophus										--N	E	E	EN	...	S-N	E	S--	*E*	>
Sylvicapra																	S--	*...*	>
Homoiodorcas > Protragocerus									S-N	EN	E								
Gazella										E	E	E	E	SEN	SEN	SEN	SEN	*EN*	>
Dytikodorcas											--N	...	--N						
Aepyceros												E	E	E	E	EN	E	*E*	>
Antilope														E	E	...	...	*...*	>
Antidorcas															SE	SE	SE	*...*	>
Parantidorcas														--N	--N				
Pelea																S--	S--	*...*	>
Litocranius																	E	*...*	>
Hispanodorcas													--N						
Madoqua													E	E	E	...	...	*E*	>
Raphicerus													EN	E	SE	...	S--	*SE*	>
Oreotragus														S--	S--	S--	S--	*SE*	>
Ourebia																E	SE	*SE*	>
Neotragus																E	...	*...*	>
"Pachytragus"										--N	EN	...							
Kobus													EN	SEN	E	EN	SE	*SEN*	>
Zephyreduncinus													E						
Menelikia													E	E	E	E	E		
Redunca														S--	SEN	SEN	SEN	*SEN*	>
Thaleroceros															E	E			
Gentrytragus										EN	E	...							
Hippotragus													--N	SEN	SE	E	SE	*SE*	>
Tchadotragus													--N	--N					
Saheloryx													--N						
Wellsiana														S--	...	...	S--		
Oryx														--N	EN	--N	S-N	*SE*	>
Damalacra														SEN					

13	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
Parmularius														SE	SEN	E	SEN		
Damaliscus / Beatragus														E	SEN	SEN	SEN	*SEN*	>
Damalborea														E	SE				
Praedamalis														E					
Parestigorgon															E				
Connochaetes														SE	SEN	SEN	SEN	*SEN*	>
Megalotragus															E	SEN	SE	*S--*	
Oreonagor															--N				
Awashia															E				
Numidocapra > Rabaticerus															E	SE	SEN	*S--*	
Alcelaphus																E	SEN	*...*	>
Sigmoceras																SE	E	*EN*	>
Rusingoryx																		*E*	
Benicerus										--N									
Protoryx											EN	E							
Damalavus											EN	...	...	...	E	SE			
Skouraia												--N							
Budorcas														SE	E				
Makapania														S--	SE	SE			
Ovibovini n. gen.															E				
Ammotragus																--N	--N	*...*	>
Capra																	--N	*--N*	>
Bouria																	E		
Nitidarcus																	E		
FERAE																			
HYAENODONTA -- HYAENODONTIDAE																			
Tinerhodon	--N																		
Lahimia	--N																		
Boualitomus		--N																	
Koholia		--N																	
Furodon		--N	--N																
Parvavorudon		--N	--N	...	--N														
Glibzegdouia			--N																
Pterodon			S--	...	--N	--N	...	E	SE										
Apterodon			--N	...	--N	--N	E												
Akhnatenavus					--N	--N													
Quasiapterodon					--N														
Metapterodon					--N	--N	...	E	SE										
Masrasector						--N	E												
Anasinopa						--N	...	...	EN	E									
Metasinopa						--N	...	E	--N										
Brychotherium						--N													
Falcatodon						--N													
Sectisodon						--N	...	E											
Pakakali							E												
Mlanyama							E	E											
Hyainailourous							E	E	SEN	E									
Simbakubwa								E											
Teratodon								E	--N										
Buhakia									--N										
Isohyaenodon								E	SE										
Exiguodon								E	E										
Megistotherium									EN	E	E								
Leakitherium									E	E	E								
Dissopsalis										E	E								
PRIONOGALIDAE																			
Prionogale								E	E										
Namasector									S--										

14	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	***NV2***	R
PHOLIDOTA -- PHOLIDOTIDAE																			
Pholidotid indet.			S--	…	…	--N													
Manis														S--	...	...	...	*...*	>
Phataginus														S--	E	...	S--	*S--*	>
Smutsia															E	...	...	*...*	>
CARNIVORA																			
AMPHICYONIDAE																			
Amphicyon									S--	EN									
Ysengrinia									S--										
Afrocyon									--N										
Cynelos > Hecubides									EN	E									
Agnotherium										E	SE								
Myacyon												E	E						
Bonisicyon.												--N	E						
URSIDAE																			
Hemicyon									E										
Agriotherium											--N	...	E	SEN					
Indarctos												--N							
Ursus															--N	--N	...	*--N*	
CANIDAE																			
Vulpes												EN	--N	SE	SEN	S--	S-N	*SEN*	>
Eucyon													E	E					
Nyctereutes														EN	SEN	E			
Canis															SEN	EN	SEN	*SEN*	>
Otocyon															EN	...	S--	*S--*	>
Prototocyon															E	...	...	*S--*	>
Lupullela															--N	--N	...	*...*	>
Lycaon																S--	SEN	*SEN*	>
Xenocyon																E			
MUSTELIDAE																			
Luogale									E										
Mionictis									--N										
Namibictis									S--										
Kenyalutra									E	...	...	...	E						
Djourabus												--N							
Torolutra													E	EN					
Hydrictis														E	E	...	...	*...*	>
Lutra														EN	EN	S--	SE	*SE*	>
Martes									--N	--N									
Mellalictis										--N									
Howellictis												--N							
Sivaonyx												--N	SEN	SEN	E	E			
Aonyx															E	E	SE	*S--*	>
Enhydriodon															E	...	...	*...*	>
Mustela																		*--N*	
Ictonyx															S--	...	S--	*S--*	>
Prepoecilogale														E	EN	S--			
Poecilictis															--N	...	...	*...*	>
Poecilogale															E	...	...	*...*	>
Vishnuonyx											E	...							
Eomellivora											E								
Ekorus												E							
Ekoromellivora												--N	E						
Plesiogulo												--N	EN						
Mellivora													E	E	SEN	...	S-N	*S--*	>

15	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	*NV2*	R
VIVERRIDAE																			
Legetetia								E											
Kichechia								E	EN										
Herpestides									EN										
Ketketictis									--N										
Orangictis									S--										
Genetta										EN	...	E	E	S--	EN	E	S--	...	>
Vishnuictis										E									
Kanuites										E									
Tugenictis											E								
Viverra												E	E	SE	SEN	...	S--	...	>
Civettictis													E	E	SEN	...	S--	...	>
Sahelictis													--N						
Megaviverra													E	SE	E				
Pseudocivetta															E				
HERPESTIDAE																			
Leptoplesictis									SEN										
Ugandictis									E										
Herpestes										E	...	EN	E	E	SEN	S--	SE	*SE*	>
Gallerella												E	--N	--N	...	...	S--	...	>
Ichneumia													E	...	E	...	...	*...*	>
Helogale													E	E	SE	E	...	*SE*	>
Mungos														E	E	S--	...	...	>
Cynictis														S--	S--	...	S--	...	>
Atilax															SE	...	S--	*SE*	>
Crossarchus															SEN	...	...	...	>
Suricata															S--	S--	S--	...	>
Nandinia													E	...	...	...	...	...	>
STENOPLESICTIDAE																			
Mioprionodon							E	E	EN										
Africanictis									SE										
Moghradictis									--N										
PERCROCUTIDAE																			
Percrocuta										EN	EN	E							
Dinocrocuta										--N	...	--N							
BARBOUROFELIDAE																			
Ginsburgsmilus								E											
Afrosmilus								E	SE										
Syrtosmilus									--N	--N									
Vampyrictis											--N								
HYAENIDAE																			
Protictitherium										--N	E								
Lycyaena											--N								
Werdelinus												--N							
Hyaenotherium												E	...	E					
Ictitherium													E	E					
Ikelohyaena												E	...	E	S--				
Chasmaporthetes												EN	...	E	SEN	SE			
Hyaenictis												E	E	EN	S--				
Hyaenictitherium												EN	SE	SEN	--N				
Adcrocuta													--N						
Hyaena													--N	SE	SEN	E	SE	*SEN*	>
Parahyena														E	S--	E			
Crocuta														SE	SEN	SEN	SEN	*SE*	>
Pachycrocuta														SE	S--	...	...	...	>
Lycyaenops														S--	S--				
Pliocrocuta															--N				
Proteles															S--	S--	S--	...	>

16	TGT	ABD	LAZ	KEB	PHI	QAT	TKW	LEG	KIS	TIN	TUG	SUG	BAR	KER	SHU	NAT	NV1	***NV2***	R
FELIDAE																			
Diamantofelis									S--										
Namafelis									S--										
Katifelis									E										
Asilifelis									E										
Machairodus										--N	--N	EN	EN						
Lokotunjailurus												EN	E	S--					
Metailurus												E	E						
Dinofelis > Therailurus												EN	EN	SEN	SEN	SE			
Amphimachairodus												--N	EN	S--					
Felis / Lynx												--N	E	SE	SEN	E	SEN	*SEN*	>
Tchadailurus												--N							
Megantereon														SE	SE	S--	S--		
Homotherium														SE	SEN	E	S-N	*S--*	
Panthera														SE	SEN	SE	SE	*SEN*	>
Leptailurus														E	...	...	...	...	>
Acinonyx														S--	SEN	...	...	...	>
Caracal															SEN	...	...	...	>
PERISSODACTYLA																			
EQUIDAE																			
Hippotherium											EN	E	...	S--					
Cormohipparion												E	EN	--N					
Eurygnathohippus												E	EN	SEN	SEN	EN	SEN		
Cremohipparion													--N						
Equus															SEN	SEN	SEN	*SEN*	>
CHALICOTHERIIDAE																			
Butleria								E	E	E									
Chemositia													E						
Ancylotherium												E	E	SE	SE	E			
RHINOCEROTIDAE																			
Ougandatherium								E											
Brachypotherium								E	SEN	E	EN	E	E	EN					
Chilotheridium								E	SE	E	...	...	--N						
Rusingaceros									E										
Turkanatherium									E										
Paradiceros									E	E									
Victoriaceros									E	E									
Plesiaceratherium										E									
Ceratotherium											E	EN	EN	SE	SEN	EN	SEN	*SEN*	>
Kenyatherium												E							
Diceros														SEN	SE	E	SEN	*SEN*	>
Stephanorhinus													--N	EN					

REMARKS. Occurrences are noted in southern (‘**S**’), equatorial (‘**E**’) and northern (‘**N**’) realms; inferred occurrences (‘ **...** ’) are not attributed to realm. Extant genera are noted in column ‘R’ with symbol ‘>’. The genera are listed in the systematic order of Werdelin and Sanders (2010), with following exceptions: Anthracotheriidae are placed under Whippomorpha (Lihoreau et al., 2015b), Creodonta are placed under Ferae (Solé et al., 2009); Primates are classified per E.D.; Chiroptera are classified per Simmons et al. (2016). For convenience, Chiroptera are listed as a single group, with the families informally noted. Genera in Muridae and Bovidae are grouped in subfamily order. Synonymized genera are shown as *Senior > Junior* , and some closely related genera or families are treated in combination. Systematic rank is indicated by font style: ***CLASS***; **INFRACLASS**; ***COHORT/SUPERORDER***; **ORDER**; *SUBORDER / INFRAORDER*; FAMILY; *Genus.*