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Kyoto University
FAUNAL CHANGE OF LATE MIOCENE AFRICA AND EURASIA: MAMMALIAN FAUNA FROM THE NAMURUNGULE FORMATION, SAMBURU HILLS, NORTHERN KENYA

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ABSTRACT The Namurungule Formation yields a large amount of mammals of a formerly unknown and diversified vertebrate assemblage of the late Miocene. The Namurungule Formation has been dated as approximately 7 to 10 Ma. This age agrees with the mammalian assemblage of the Namurungule Formation. Sedimentological evidence of this formation supports that the Namurungule Formation was deposited in lacustrine and/or fluvial environments. Numerous equid and bovid remains were found from the Namurungule Formation. These taxa indicate the open woodland to savanna environments. Assemblage of the Namurungule Fauna indicates a close similarity to those of North Africa, Southwest and Central Europe, and some similarity to Sub-Paratethys, Siwaliks and East Asia faunas. The Namurungule Fauna was the richest among late Miocene (Turolian) Sub-Saharan faunas. From an analysis of Neogene East African faunas, it became clear that mammalian faunal assemblage drastically has changed from woodland fauna to openland fauna during Astaracian to Turolian. The Namurungule Fauna is the forerunner of the modern Sub-Saharan (Ethiopian) faunas in savanna and woodland environments.

Key Words: Mammal; Neogene; Miocene; Sub-Saharan Africa; Kenya; Paleobiogeography; Paleoecology; Faunal turnover.

INTRODUCTION

I. Scope of Study

1. Late Miocene Gap of Sub-Saharan Mammalian Evolution

   In evolutionary paleontology, the late Miocene is an important age for mammalian evolution. The modern mammalian fauna appeared from this age in Eurasia. In Sub-Saharan Africa, the assemblage of the late Miocene mammalian faunas was very poor, and these faunas were represented by only the Ngorora upper E, Ngeringerowa and Nakali faunas before the commencement of the Japan and Kenya joint expedition to the Samburu Hills, northern Kenya. Because of this incompleteness of the late Miocene East African faunas, it is very difficult to compare with Eurasian and Sub-Saharan faunas of this age.

2. Hominoid Fossil

   In the human evolution, it is very important to study the origin of hominid and paleoenvironments of hominoids evolution in the Sub-Saharan Africa, because there is a large possibility that the fossil evidence for branching of the Hominidae from the
Homoidea will be discovered there. Furthermore, the paleoenvironmental change such as savannitisation seems to affect on the human evolution. The Namurungule Fauna is very important, from the viewpoint of the environmental change onto the hominoid evolution during the late Miocene. A hominoid fossil (Samburu large Hominoid) was discovered from the Namurungule Formation and it seems to be a possible common ancestor of the Hominidae and the African Apes (*Pan* and *Gorilla*) or the direct ancestor of the African Apes (Ishida et al, 1984).


Since the beginning of this century, many excavation teams visited and studied in Sub-Saharan Cenozoic sites, because Charles Darwin (1871) suggested that "it is somewhat more probable that our early progenitors lived on the African continent than elsewhere." in "The Descent of Man and Selection in Relation to Sex" (Chapter VI). Japan and Kenya excavation team (supported by the Japanese Ministry of Education, Science and Culture with its Grant-in-Aid for Overseas Scientific Survey) started to study Miocene sites in northern Kenya since 1980. The author joined this team as a vertebrate paleontologist since 1981. The excavation in the Samburu Hills was started from 1982 and we found new rich vertebrates sites including hominoid fossils from the Namurungule Formation. The author was a junior representative of the branch in Nairobi, Kenya of the Japan Society for Promotion of Science and a research student of the National Museums of Kenya from April, 1983 to March, 1984. And he investigated the middle to late Miocene Sites yielding vertebrate fossils of Kenya in 1983. And he has been also a member of the joint excavation team of Japan and Kenya as a vertebrate paleontologist from 1984 to 1986. This team excavated the Samburu Hills area in 1982 (Ishida, 1984), 1984, 1986, 1988 and Japanese team excavated the late Miocene Lake Albert area of Zaire in 1989 (Ishida & Yasui eds., 1992).

II. Historical View of Mammalian Interchange between Africa and Eurasia

The Mesozoic mammalian remains of Africa were found from the late Triassic or early Jurassic of Lesotho (Clemens et al., 1979), the late Jurassic of Tanzania (Clemens et al., 1979), the middle Jurassic to late Cretaceous of Morocco (Sigogneau-Russell et al. 1988) and the early Cretaceous of Cameroon (Jacobs et al., 1988). Eutherian mammals appeared in Africa from the late Paleocene. In the Paleocene and Oligocene, mammalian remains were found only from north and west Africa excluding Sub-Saharan area. After the Oligocene, a great number of mammalian fossil sites in Sub-Saharan Africa have been described and phylogeny of these taxa has been studied (reviewed in Maglio & Cooke eds., 1978). Many mammalian taxa immigrated into Sub-Saharan Africa. A great deal of studies have been published about the Neogene mammalian interchange between Africa and Eurasia (Thenius, 1972; Coryndon & Savage, 1973; Maglio, 1978; Thomas, 1979, 1981, 1984; Howell, 1980; Thomas et al., 1982; Adams et al., 1983; Savage & Russell, 1983; Bernor, 1983, 1986; Bernor & Hussain, 1985; Tassy, 1986).
III. Materials

The materials from the Samburu Hills are housed at the National Museums of Kenya (KNM) (Nairobi). The materials offered in this study were compared to African and Eurasian fossil mammals housed at the National Museums of Kenya (KNM) (Nairobi), British Museum (Natural History) (London), Laboratoire de Paléontologie, Muséum National d'Histoire naturelle (Paris), Laboratoire de Paléontologie des Vertébrés et de Paléontologie Humaine, Université de Paris VI (Paris), Department des Sciences de la Terre, Université Claude-Bernard, Lyon I (Villeurbanne) and Bayerischen Staatssammlung für Paläontologie und historische Geologie (München).

GEOLOGICAL BACKGROUND

I. Geology and Geochronology of the Namurungule Formation

The Samburu Hills form a belt about 30 km wide and about 80 km long trending in a north-southerly direction and beside the western wall of Suguta valley (Fig. 1).

![Fig. 1. Locality map of the Samburu Hills.](image)

The Neogene sediments and volcanics in the Samburu Hills consist of the Nachola, Aka Aiteputh, Namurungule, Nanyangaten, Kongia, Nagbarat and Tirr Tirr Formations (Fig. 2).
The Namurungule Formation yields a large amount of diversified vertebrates which appear to be of late Miocene in age thus belong to an assemblage heretofore unknown (Nakaya et al., 1984). Itaya & Sawada (in press) determined by K-Ar dating method the age of the Kongia and Nanyangaten Formations (5.7-7.3 Ma) clinounconformably overlying the Namurungule Formation and the Aka Aiteputh Formation (10-15 Ma) which underlies the Namurungule Formation. Consequently, the Namurungule Formation has been dated approximately as 8 to 10 Ma. This age agrees with the discovered mammalian assemblage of the Namurungule Formation (Nakaya et al., in press). Five paleomagnetic-zones were identified in the Samburu Hills. The Aka Aiteputh Formation is correlated to paleomagnetic-zone V in the period between 9.78 Ma and 10.3 Ma (Nakajima & Torii, in press).

![Geology and geochronology of the Samburu Hills.](image)

**Fig. 2.** Geology and geochronology of the Samburu Hills.

II. Excavation of the Namurungule Formation

1. 1982 Excavation

Osaka University expedition team collected fossil remains on the surface of the Namurungule Formation of the Samburu Hills at random in 1982 field season. We excavated at the SH-22 of the locality of "Samburu Large Hominoid" in detail. Fossil numbers at each locality in the Namurungule Formation and number of taxa from the Namurungule Formation are shown in the following figures (Fig. 3, 4).
Late Miocene Namurungule Fauna

Fig. 3. Number of vertebrate fossils from each localities in the Samburu Hills.

Fig. 4. Number of vertebrate taxa from the Namurungule Formation at 1982.
2. 1984 Excavation

In 1984 field season, Osaka University expedition team also collected fossil remains which were already surveyed in 1982 and newly discovered in 1984 randomly from the site surface of Samburu Hills and excavated locality SH-22 and some mammalian localities in detail.

3. 1986 Excavation

Osaka University expedition team also collected fossil remains which were already surveyed in 1984 randomly from the site surface of Samburu Hills in 1986 field season, and excavated locality SH-22 in detail. Fossil vertebrate localities show Figure 5.

4. 1988 Excavation

Osaka University expedition team also collected fossil remains which were already surveyed in 1986 randomly from the site surface of Samburu Hills in 1988 field season, and excavated locality SH-22 in detail by electric drilling machine.

5. Localities of Vertebrate Fossils and Stratigraphy of the Namurungule Formation

The Namurungule Formation consists of the Lower Member, Mud Flow, Upper Member in ascending order. The Lower Member consists of conglomerate, sand-stone, thin mud flow deposits, pyroclastics, alternating beds of sandstone and mudstone predominantly in sandstone. The Mud Flow consists of reddish mud flow deposits 10-20 meter thick. The Upper Member consists of alternating beds of sandstone and mudstone predominantly in mudstone.

The Lower Member of Namurungule Formation yields the following vertebrate localities.

Locality SH-1, 7-9, 20-24, 26, 27, 30, 34, 40, 43, 44, 49-58, 61-64.

In the Upper Member of Namurungule Formation, we found the following vertebrate localities.

Locality SH-4, 5, 10-16, 18, 19, 25, 28, 29, 32, 33, 35-39, 41, 42, 60 (Fig. 5).

6. Taphonomy of Vertebrate Fossils in Situ

Almost all fossils were collected from the surface of the Namurungule Formation in the Samburu Hills. Some mammalian remains were excavated in situ of the Namurungule Formation in 1984. Almost all fossils were destroyed and weathered on the end position of skeleton because of the rolling before embedded in the deposits. For example, the skull of *Hipparion* from locality SH-53 was missing the incisive and occipital part. The mandible of *Deinotherium* from locality SH-54 was also missing the incisive, ventral border and ramus part. These remains were discovered in the overturned position in the sediments. The surface of some astragali of Giraffidae seems to be dissolved in acid solution. The surface shape of these astragali are different from that of rolled remains in the river. The edge of articular surface of these astragali is sharper than the original shape of articular part. The edge of articular surface of rolled remains in the river is rounded. These astragali remains may be stomach stones of crocodiles (Pickford, pers. comm.).
Fig. 5. Localities of vertebrate fossils in the Samburu Hills.
Topographic maps are based on sheets "Lobar" (65/1), "Kangaurak" (65/3), "Sukuta Valley" (64/2) and "Lomaro" (64/4) of series Y 731 (D.O.S. 423) 1:50,000 Topographic map published by D.O.S. for the Kenya Government (Survey of Kenya), 1982. Each grid is 1 km square.
7. Paleoenvironments of the Namurungule Formation

Sedimentological characteristics of the Namurungule Formation indicate lacustrine and fluvial environments (Makinouchi et al., 1984; Sawada et al., in press). Taphonomical evidence also assists such environments of the Namurungule Formation. The most abundant remains are fresh water fish. Crocodilian and chelonian fossils are also rich in the Namurungule Formation (Nakaya et al., 1984, in press; Pickford et al., 1984).

THE NAMURUNGULE FAUNA

I. Significance of the Namurungule Fauna

Three formations, the Aka Aiteputh, Namurungule, Kongia Formation, yield Neogene vertebrate fossils in the Samburu Hills. In this chapter, fossil assemblage and sedimentological facies of these formations are described.

1. The Aka Aiteputh Fauna

This fauna is characterized by yielding abundant fossil primate remains (Pickford & Kuga, in press). The sedimentological facies indicates lacustrine environments, because the clastic sediments of the Aka Aiteputh Formation is mainly composed of fine sandstone and silt, and these fine sediments are partially silicified (Sawada et al., in press).

Mollusca
Gastropoda
   Ampullariidae
     *Lanistes carinatus*
   Pomatiasidae
     *Tropidophora (Ligatella) miocenica*

Bivalvia
   Mutelidae
     *Etheria elliptica*

Pisces

Reptilia
Crocodylia
   Crocodylidae
gen. et sp. indet.

Testudines
   Trionychidae
gen. et sp. indet.
Pelomedusidae
gen. et sp. indet.

Squamata
   Serpentes
gen. et sp. indet.

Aves
Late Miocene Namurungule Fauna

Mammalia
Primates
Cercopithecoidae
  *Nyanzapithecus* sp.
  *Victoriaiapithecus* sp.
Hominoidea
  *Proconsul* sp.
  *Kenyapithecus cf. africanus*
Rodentia
  *Paraphiomys cf. pigotti*
Proboscidea
  *Gomphotherium* sp.
  *Prodeinotherium* sp.
Perissodactyla
  Rhinocerotidae gen. et sp. indet.
Artiodactyla
  Anthracotheriidae
    *Hyoboops* sp.
    *Hemimeryx* sp.
Sanitheriidae
  *Diamantohyus africanus*
Suinae
  *Libycochoerus* sp. nov.
Climacoceridae
  *Climacoceras gentryi*
Tragulidae
  *Dorcatherium cf. pigotti*
  *Dorcatherium chappusi*
? Giraffidae ?
  *Walangania africanus*
Bovidae gen. et sp. indet

2. The Namurungule Fauna

The number of fossils of each taxon from the Namurungule Formation in 1982 excavation (Nakaya et al., 1984) is shown in Figure 4. for analyzing paleoenvironments of the fauna. Aqueous taxa (Pisces: Osteichthyes, Testudinata and Crocodylia) have numerous remains. This result supports the sedimentological and taphonomical evidence that the Namurungule Formation is lacustrine and/or fluvial in origin because of the predominant of the alternating bed and trough-type cross lamination of the coarse sediments (Sawada et al., in press). The appearance of numerous equids and bovids from the Namurungule Formation indicates the open country and/or woodland environments of the background (Nakaya et al., in press; Nakaya, 1987, 1989, 1993). Very large number of equid, giraffid and bovid remains shows that these taxa were social behavior animal. Very small number of chalicothere remains shows that this taxa was solitary animal on the view of paleoecological point.
Mollusca
Gastropoda
   *Limicolaria* aff. *martensiana*
   *Trochonania* (*Bloyetia*) aff. *nyroensis*

Pisces
Reptilia
Crocodylia
   Crocodylidae
      gen. et sp. indet.
Testudines
   Trionychidae
      gen. et sp. indet.
   Pelomedusidae
      gen. et sp. indet.
Squamata
   Sauria
      Varanidae
         gen. et sp. indet.
   Serpentes
      gen. et sp. indet.
Aves
   gen. et sp. indet.
Mammalia
Primates
   Hominoidea
      Genus and species nov.
Rodentia
   Thryonomyidae
      *Paraphiomyx* sp.
      *Paraulacodus* sp.
   Hystricidae
Carnivora
   Hyaenidae spp.
   Felidae
      Machairodontinae
         gen. et sp. indet.
Proboscidea
   Gomphotheriidae
      *Tetralophodon* sp. nov.
   Deinotheriidae
      *Deinotherium* cf. *bozasi*
Perissodactyla
   Equidae
      *Hipparion africanum*
   Chalicotheriidae
      gen. et sp. indet.
   Rhinocerotidae
Late Miocene Namurungule Fauna

Paradiceros mukirii
Chilotheridium pattersoni
Kenyatherium bishopi
Iranotheriinae sp. nov.

Artiodactyla
Suidae
Nyanzachoerus tulotos (small form)
Nyanzachoerus kanamensis (large form)

Hippopotamidae
Kenyapotamus coryndoni

Giraffidae
Palaeotragus sp. nov.
Samootherium ? sp.

Bovidae
Pachytragus laticeps
Miotragocerus sp.
Ouzocerus ? sp.
Gazella spp.

3. The Kongia Fauna

Of this fauna, mammalian remains have not yet been investigated in detail. Studies are confined to geochronological aspects. This Formation indicates lacustrine and/or fluvial in origin because of the predominance of fine sandstone and silt, and the alternation of sandstone and silt (Sawada et al., in press). The following taxa indicate riverine habitats.

Mollusca
Gastropoda
Burtoa nilotica
Chlamydarion aff. haans
Limicolaria aff. martensiana
Trochonania (Bloyetia) aff. nyroensis
Tropidophora (Ligatella) aff. anceps
Cleopatra aff. africana
Mellanoides tuberculata

Bivalvia
Mutela sp.

Insecta
Pisces
Reptilia
Squamata
Sauria
Varanidae
gen. et sp. indet.

Artiodactyla
Hippopotamidae
Hippopotamus sp.
II. Phylogeny and Paleobiogeography of the Namurungule Fauna

In this chapter, habitat of each taxa from the Namurungule Fauna, first appearance of the world and Sub-Saharan Africa, and distribution in the late Miocene are described (Nakaya et al., 1984, in press; Nakaya, 1987, 1989, 1993).

1. Primates

   Hominoidea gen. et sp. nov.

   This taxon, so called "Samburu Large Hominoid", is represented by the left Maxilla with cheek teeth from the Lower Member of Namurungule Formation. Samburu Hominoid is very unique and it is probable that this taxon is a common ancestor of australopithecine of the Hominidae and African ape (Pan and Gorilla) of the Hominoidea (Ishida et al., 1984, Groves, 1989). First appearance of Hominoidea was Aegyptopithecus from late Oligocene, Fayum, Egypt (Szalay & Delson, 1979). First appearance of this superfamily from Sub-Saharan Africa was Proconsul, Limnopithecus from early Miocene Karungu (Simonset al., 1978). Distribution of this taxon in the late Miocene was only "Samburu Hominoid" from this fauna in Sub-Saharan Africa. It has been made clear that ramapithecine from late Miocene Eurasia and Pongo (Orang-Utan) shared same clade (Martin, 1986). Because of this point of view, it has to be stressed that new hominoid fossil from the Namurungule Formation fills in the missing link of human evolution.

2. Rodentia

   Thryonomyidae

   Paraphiomys sp.

   One left mandible fragment with cheek teeth of Paraphiomys sp. from the Lower Member of Namurungule Formation occurs (Kawamura & Nakaya, 1984). First appearance of genus Paraphiomys was P. simonsi from Oligocene (25 Ma) of Fayum (Wood, 1968). First appearance of this taxon from Sub-Saharan Africa was Paraphiomys pigotti and P. stromeri from early Miocene (Lavocat, 1973). Only P. occidentalis is known from the late Miocene deposit of Morocco (Lavocat, 1961). Only one genus Paraphiomysis known.

   Paraulacodus sp.

   Only one isolated right upper incisor of Paraulacodus sp. is known from the Lower Member of Namurungule Formation (Kawamura & Nakaya, in press). First appearance of genus Paraulacodus is shown by P. indicus from the Chinji Formation of Pakistan (Flyn et al., 1983). First appearance of this taxon from Sub-Saharan Africa was represented by Paraulacodus johanesi from the late Miocene Chorora Formation of Ethiopia (Jacobs et al., 1980). Distribution of this genus in the late Miocene is represented by the Chorora and Namurungule Fauna only.

3. Carnivora

   Hyaenidae spp.
Hyaenidae from the Upper and Lower Member of Namurungule Formation consists of three taxa, based on tooth size. These hyaenids are represented by the isolated lower cheek teeth or fragments of mandible, therefore, genus and species cannot be determined precisely (Nakaya et al., 1984, in press). First appearance of Hyaenidae is known from Orleanian (MN 4) in Europe (Savage & Russell, 1983). First appearance of this taxon from Sub-Saharan Africa is shown by the early Miocene of Fort Ternan (Savage, 1978). Distribution of this family in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Hendey, 1974; Savage, 1978; Savage & Russell, 1983; Schmidt-Kittler, 1976, 1987).

Felidae

Machairodontinae gen. et sp. indet.

Only one isolated lower canine of Machairodontinae is found from the Lower Member of Namurungule Formation (Nakaya et al., in press). First appearance of this taxon is known from Vallesian (MN 9) in Europe (Savage & Russell, 1983). First appearance of this subfamily from Sub-Saharan Africa is represented by this Namurungule occurrence. Distribution of this subfamily in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Savage & Russell, 1983).

4. Proboscidea

Gomphotheriidae

_Tetralophodon_ sp. nov.

One Proboscidean skull was excavated from the Lower Member of Namurungule Formation on 1984, and it is now under preparation in the National Museums of Kenya. This skull has typical cheek teeth of the genus _Tetralophodon_, because the intermediate molar with four lophs is characterized by tetralophodont cusp pattern. In comparing with the angle of the basicranium of _Tetralophodon_ of Eurasia and of the Namurungule Fauna (Nakaya et al., in press), it is known that typical European _Tetralophodon_ (Tobien, 1973a, 1973b, 1978) has a low angle of the basicranium, however, the Namurungules specimen has a high angle (Fig. 6). _Paratetralophodon_ from the Siwaliks has also high angle of basicranium (Tassy, 1983). First appearance of genus _Tetralophodon_ is known as _T. longirostris_ from the Vallesian in Europe (Tobien, 1978). First appearance of this taxon from Sub-Saharan Africa is known as a Tetralophodont form gen. et sp. indet. from middle Miocene Ngorora Formation (member D) (Tassy, 1986). Distribution of this genus in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Tobien, 1978; Savage & Russell, 1983).

Deinotheriidae

_Deinotherium_ cf. _bozasi_

A mandible and cheek teeth of _Deinotherium_ are found from the Upper and Lower Member of the Namurungule Formation (Nakaya et al., 1984, in press). First appearance
of genus *Deinotherium* is known from the early Miocene of Eurasia. First appearance of Deinotheriidae from Sub-Saharan Africa is known as *Prodeinotherium hobleyi* from the early Miocene of Bukwa and Karungu and *Deinotherium cf. bozasi* from the late Miocene of Nakali and Namurungule Fauna. *D. bozasi* is distinguished from *P. hobleyi* in size and the morphology of skull and upper cheek teeth (Harris, 1973, 1975, 1976, 1978). *D. bozasi* is known from the late Miocene of East Africa and the Pliocene to Pleistocene of Sub-Saharan Africa (from Ethiopia to Mozambique) (Harris, 1977; Nakaya et al., in press). Distribution of this genus in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Osborn, 1936; Savage & Russell, 1983).

![Fig. 6. Angle of tetralophodont basicranium (Modified after Tassy, 1983).](image)

The skull of hipparionine (Equidae) from the Upper and Lower Member of Namurungule Formation will be described and discussed by the author and Watabe, on its phylogenetic relationships with other African and Eurasian forms (Nakaya & Watabe, 1990). On the basis of the cranial morphology, especially preorbital fossa (POF) and dentition, this skull is similar to *Hipparion africanum* (Arambourg, 1959) from Bou Hanifia of North Africa of Vallesian age, and the proportions of slender limb bones from the Namurungule Formation is also comparable with those of the same *Hipparion*. Furthermore, this skull shows similarities to *Cormohipparion perimense* (Bernor & Hussain, 1985) from the Siwaliks on the basis of the morphology of antero-dorsally located POF. The age of *H. africanum* is older than the Namurungule Formation, and the age of the Dhok Pathan Formation of the Siwalik Hills yielding *C. perimense* is later than...

![Fig. 7. Late Miocene fossil localities of large hipparionine from Africa and Eurasia.](image)

Chalicotheriidae genus and species indeterminate

One basal phalange of the manus of Chalicotheriidae was collected from the Upper Member of Namurungule Formation (Nakaya et al., 1984). First appearance of this family is known from Sparncisan (Eocene) of Southwest Europe (Savage & Russell, 1983). First appearance of this taxon from Sub-Saharan Africa is *Chalicotherium rusingense* from early Miocene of East Africa. *Ancylotherium hennigi* was distributed from the late Miocene to early Pleistocene of East and South Africa (Butler, 1978). Distribution of this family in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Savage & Russell, 1983).

Rhinocerotidae

*Paradiceros mukirii*

Cheek teeth of brachyodont Rhinocerotidae *Paradiceros mukirii* were found from the
Lower Member of Namurungule Formation (Nakaya et al., in press). First appearance of *P. mukirii* is known from the middle Miocene of Fort Ternan (Hooijer, 1968). This genus includes only one species; only *P. mukirii* occurs at Fort Ternan in Kenya. Distribution of this taxon in the late Miocene is known from this fauna only (Hooijer, 1966, 1968, 1971, 1972, 1973).

*Chilotheridium pattersoni*

Cheek teeth of hypsodont Rhinocerotidae being indicated to *Chilotheridium pattersoni* were found from the Lower Member of Namurungule Formation (Nakaya et al., in press). First appearance of *C. pattersoni* is known from the early Miocene (Hooijer, 1971). This taxon ranges from the early to late Miocene of East Africa. Distribution of this taxon in the late Miocene is known from East Africa only (Hooijer, 1966, 1968, 1971, 1972, 1973, 1978).

*Kenyatherium bishopi*

Some cheek teeth of *Kenyatherium bishopi* were found from the Lower Member of Namurungule Formation (Nakaya et al., in press). *K. bishopi* is from late Miocene of Nakali of particular interest among Rhinocerotidae characterized by a constricted protocone (Aguirre & Guérin, 1974). This taxon belongs to the subfamily Iranotheriinae. First appearance of this subfamily is known from the middle Miocene and it is represented by *Hispanotherium* from Iberian Peninsula (Crusafont-Pairo & de Villalta-Comella, 1947) and Turkey (Heissig, 1974), *Beliajevina* from Turkey (Heissig, 1974) and *Caementodon* from the Siwaliks (Heissig, 1972). Distribution of this subfamily in the late Miocene is represented by *Kenyatherium* from East Africa, *Iranotherium* from Iran (Mecquenem, 1908-1911) and *Sinotherium* from Northern China (Ringström, 1922, 1924, 1927) (Fig. 8).

![Fig. 8. Middle and late Miocene fossil localities of iranotheriinine from Africa and Eurasia.](image-url)
Iranotheriinae sp. nov.

Some specimens of the rhinocerotid from the Lower Member of the Namurungule Formation are not identified with any Sub-Saharan rhinocerotids (Hamilton, 1973b; Hooijer, 1966, 1968, 1971, 1972, 1973). *Kenyatherium bishopi* is similar to these materials on the basis of the morphology of cheek teeth. However, the cheek teeth of this taxon are larger than those of *K. bishopi* (Nakaya et al., in press), therefore, it appears from the above that these materials represent a new taxon.

6. Artiodactyla

Suidae

*Nyanzachoerus tulotos* (small form)

*Nyanzachoerus kanamensis* (large form)

Two different species of *Nyanzachoerus* on the basis of the cheek teeth size, were found from the Upper and Lower Members of Namurungule Formation (Nakaya et al., in press). *Nyanzachoerus* suggests an open country habitat. First appearance of this genus is known from the late Miocene of Bou Hanifia (Algeria) (Arambourg, 1968). First appearance of this taxon from Sub-Saharan Africa is known from the Namurungule Formation. *Nyanzachoerus* was distributed in North and East Africa during the late Miocene (Arambourg, 1968; Bernor, 1986; Cooke & Ewer, 1972; Harris & White, 1979, White & Harris, 1977, Wilkinson, 1976).

Hippopotamidae

*Kenyapotamus coryndoni*

Complete mandible and the cheek teeth of *Kenyapotamus* are found newly from the Upper and Lower Members of Namurungule Formation. *Kenyapotamus* includes only two species, *K. coryndoni* and *K. ternani*. Habitat of *Kenyapotamus* suggests on riverine habitat. First appearance of genus *Kenyapotamus* is known as *K. ternani* from the middle Miocene of Fort Ternan and Maboko of Kenya. *K. coryndoni* is known from late Miocene Ngeringerowa (Pickford, 1983) and the Namurungule Fauna only.

Tragulidae

gen. et sp. indet.

A left talus of Tragulidae was found from the Upper Member of Namurungule Formation. Tragulidae suggests a forest habitat. First appearance of Tragulidae from Sub-Saharan Africa is known as *Dorcatherium chappuisi* from the early Miocene of Moruorot, Kenya (Whintonworth, 1958). Distribution of this family in the late Miocene is known from Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Savage & Russell, 1983).

Giraffidae

*Palaeotragus* sp. nov.

The giraffid's cheek teeth from the Upper and Lower Members of Namurungule Formation is similar to those of *Palaeotragus primaevus*, but the shape of hypocone of
upper molar of them is different from other species of Giraffidae in Africa (Nakaya et al., 1984, in press). *Palaeotragus* suggests a wooded open country habitat. First appearance of this genus is known as *P. primaevus* from the early Miocene of Moruorot, Kenya (Singer & Boné, 1960; Gentry, 1978a; Hamilton, 1973a, 1978). Distribution of this genus in the late Miocene is known as *P. germaini* from Lothagam, Kenya (Churcher, 1979) in East Africa.

*Samotherium?* sp.

Some limb bones of giraffid were obtained from the Upper and Lower Members of Namurungule Formation. They are larger than specimens of *Palaeotragus* (Nakaya et al., in press). These materials are identified as *Samotherium?* sp. *Samotherium* suggests a wooded open country habitat. First appearance of *Samotherium* is known from the middle Miocene of Pasalar, Turkey (Bernor & Pavlakis, 1987). First appearance of this taxon in Sub-Saharan Africa is known as *Samotherium africanum* from the middle Miocene of Fort Ternan (Churcher, 1978). Distribution of this genus in the late Miocene is known to extend to East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Savage & Russell, 1983).

**Bovidae**

*Pachytragus laticeps*

Horn cores, compressed oval in section and curved uniformly, but gently backwards toward the tip, are discovered from the Lower Member of Namurungule Formation. They are identified as *Pachytragus laticeps* (Nakaya et al., 1984, in press and this work). This species was taxonomically revised to *Protoryx laticeps* by Solounias (1981). First appearance of *Pachytragus* and/or *Protoryx* is known from the late Miocene North Africa and Sub-Paratethys (Solounias, 1981; Savage & Russell, 1983). *Pachytragus* suggests an open country habitat. First appearance of this taxon from Sub-Saharan Africa confines to the Namurungule Formation. Distribution of this taxon in the late Miocene is *P. solignaci* from Beglia (Robinson, 1972) and the Namurungule Fauna in Africa. This genus group is widely known from Afro-Eurasia (East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia) during the late Miocene (Savage & Russell, 1983).

*Miotragocerus* sp.

A horn core, curved and spiral with an anterior keel, from the Lower Member of Namurungule Formation is identified as *Miotragocerus* (Nakaya et al., 1984). First appearance of this genus was Astaracian (Savage & Russell, 1983). *Miotragocerus* suggests an open country habitat. First appearance of this taxon from Sub-Saharan Africa is known from the Namurungule Fauna. This genus is known from Afro-Eurasia widely (East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia) during the late Miocene (Savage & Russell, 1983).
### Table 1. Faunal resemblance of the Namurungule Fauna and Eurasian faunas.

<table>
<thead>
<tr>
<th>Mammalia</th>
<th>Primates</th>
<th>Rodentia</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Thryonomyidae</td>
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<tr>
<td></td>
<td></td>
<td>Paraphiomy sp.</td>
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<td></td>
<td></td>
<td>Paraulacodus sp.</td>
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<td></td>
<td></td>
<td>Carnivora</td>
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<td></td>
<td></td>
<td>Felidae</td>
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<tr>
<td></td>
<td></td>
<td>Machairodontinae gen. et sp. indet.</td>
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<tr>
<td></td>
<td></td>
<td>Proboscidea</td>
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<td></td>
<td></td>
<td>Gomphotheriidae</td>
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<td></td>
<td></td>
<td>Tetralophodon sp. nov.</td>
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<td></td>
<td></td>
<td>Deinotheriidae</td>
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<tr>
<td></td>
<td></td>
<td>Deinotherium cf. bozasi</td>
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<td></td>
<td></td>
<td>Perissodactyla</td>
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<td></td>
<td></td>
<td>Equidae</td>
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<tr>
<td></td>
<td></td>
<td>Hipparion africanum</td>
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<tr>
<td></td>
<td></td>
<td>Chalicotheriidae gen. et sp. indet.</td>
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<tr>
<td></td>
<td></td>
<td>Rhinocerotidae</td>
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<tr>
<td></td>
<td></td>
<td>Paradiceros mukiri</td>
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<td></td>
<td></td>
<td>Chilotheridium pattersoni</td>
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<tr>
<td></td>
<td></td>
<td>Kenyatherium bishopi</td>
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<td></td>
<td></td>
<td>Iranotheriinae sp. nov.</td>
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<td></td>
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<td>Artiodactyla</td>
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<td></td>
<td></td>
<td>Suidae</td>
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<tr>
<td></td>
<td></td>
<td>Nyanzachoerus tulotos (small form)</td>
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<td></td>
<td></td>
<td>Nyanzachoerus kanamensis (large form)</td>
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<tr>
<td></td>
<td></td>
<td>Hippopotamidae</td>
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<td></td>
<td></td>
<td>Kenyapotamus coryndoni</td>
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<td></td>
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<td>Giraffidae</td>
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<tr>
<td></td>
<td></td>
<td>Palaeotragus sp. nov.</td>
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<tr>
<td></td>
<td></td>
<td>Samotherium ? sp.</td>
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<td>Bovidae</td>
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<td></td>
<td></td>
<td>Pachytragus laticeps</td>
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<td></td>
<td></td>
<td>Miotragocerus sp.</td>
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<tr>
<td></td>
<td></td>
<td>Ou曹操erus ? sp.</td>
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<tr>
<td></td>
<td></td>
<td>Gazella spp.</td>
</tr>
</tbody>
</table>

Notes: A: unique Sub-Saharan taxa; N: common with North Africa taxa; P: common with Sub-Paratethys taxa; S: common with Siwalik taxa; E: common with Eurasia taxa.
**Ouzocerus?** sp.

Skull and horn cores that are nearly circular in section with a sharp posterior keel, from the Upper and Lower Members of Namurungule Formation are identified as *Palaeoeras* sp. (Nakaya et al., 1984). However, *Ouzocerus* described newly is more similar to this specimen (this work). This genus includes only one species, *O. gracilis*, and is known from Vallesian of northern Greece for the first time (Bouvrain & Bonis, 1986) and the late Miocene Beglia Formation of Tunisia (Thomas, pers. comm.). First appearance of this taxon from Sub-Saharan Africa is known from the Namurungule Formation. Distribution of this taxon is known from East and North Africa and Sub-Paratethys during the late Miocene.

**Gazella** sp.

Some horn cores of *Gazella* were discovered from the Upper and Lower Member of Namurungule Formation (Nakaya et al., 1984, in press). This genus includes many species. *Gazella* suggests an open country habitat. First appearance of this genus is known from the early Miocene of Gebel Zelten, North Africa (Hamilton, 1973a). First appearance of this taxon from Sub-Saharan Africa is known as *Gazella* sp. from the middle Miocene of Fort Ternan (Gentry, 1978b). This genus is known from Afro-Eurasia widely (East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia) during the late Miocene (Gentry, 1966, 1967, 1970, 1971, 1978a, b,1980; Gentry & Gentry, 1978; Savage & Russell, 1983).

Resemblance of the Namurungule Fauna and other Eurasian faunas is shown in the Table 1.

III. Correlation and Resemblance of Neogene Mammalian Faunas of Sub-Saharan Africa and Eurasia

1. Late Miocene faunas of North Africa and Eurasia

   In this chapter, the author describes typical late Miocene (Astaracian, Vallesian, and Tuolian) faunas of North Africa and Eurasia for the sake of making comparison with mammalian faunas of Sub-Saharan Africa.

   (1) Eurasia (Western)

   West Eurasian Neogene mammals have been studied since the eighteenth century. Ages of the Eurasian Neogene mammalian fossil assemblage zones in Southwestern Europe, Greece and Iran were revised by Savage & Russell (1983). The following five mammalian ages and 13 mammalian zones during the Miocene and two ages and four zones during the Pliocene were established respectively by them.

   **Miocene**

   Agenian (20-25 Ma)
   
   MN 1
   MN 2a
   MN 2b
Late Miocene Namurungule Fauna

Orleanian (15-20 Ma)
  MN 3a
  MN 3b
  MN 4a
  MN 4b
  MN 5
Astaracian (12-15 Ma)
  MN 6
  MN 7
  MN 8
Vallesian (10-12 Ma)
  MN 9
  MN 10
Turolian (5-10 Ma)
  MN 11
  MN 12
  MN 13
Pliocene
  Ruscinian (-5 Ma)
    MN 14
    MN 15
Villafranchian (2- Ma)
    MN 16a
    MN 16b
    MN 17

(2) Siwaliks

Falconer & Cautley (1846-1849) started the study of geology and paleontology of the Siwalik Hills. Pilgrim (1913) divided mammalian faunas and strata of the Siwaliks into seven stages and correlated them to the standard Neogene stages in Europe. Colbert (1935) revised Pilgrim's correlation and compared it to equivalents in Europe and America. In 1960's, Ramapithecus from the Siwaliks was reevaluated as a human ancestor (Simons, 1961). During 1950-1970s, many teams (Dehm et al., 1958; Pilbeam et al., 1977) excavated again at the Siwalik Hills. Research on faunal assemblage (Pilbeam et al., 1977; Moonen et al., 1978) and phylogenetic studies of each taxa have been published (Dehm et al., 1958, 1963; Hussain, 1971; Heissig, 1972; Jacobs, 1978; Tassy, 1983; Pickford, 1988), and geochronological data of strata of this area were obtained. The results of stratigraphic study of Siwaliks are shown in the following table (Pilbeam et al., 1977; Opdyke et al., 1979).

Miocene
  Kamlial (before 13 Ma; Pilbeam et al., 1977)
  Chinji (11-13 Ma; Pilbeam et al. 1977)
  Nagri (9-10 Ma; Pilbeam et al., 1977)
  Dhok Pathan (6.5-9 Ma; Pilbeam et al., 1977)
Pliocene
  Tatrot (before 2.47 Ma; Opdyke et al. 1979)
Pinjor (after 2.47 Ma; Opdyke et al. 1979)

(3) China

Many researchers studied Chinese Neogene terrestrial mammals and furthermore, Quaternary mammals with *Sinanthropus pekinensis* (*Homo erectus*) until 1940's (Andersson, 1923; Bohlin, 1937; Koken 1885; Ringström, 1922, 1924, 1927; Schlosser, 1924; Teilhard de Chardin, 1926; Teilhard de Chardin & Young; 1930, 1931; Zdansky, 1930). Researchers of the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing) began again to study fossil vertebrates from China since 1948. Cenozoic terrestrial stratigraphy in China was revised by Yen et al. eds., (1984). Established Neogene terrestrial zones of mammals in China are as follows.

**Early Miocene**
- Xiejean (19-24 Ma)

**Middle Miocene**
- Shanwangian (15-19 Ma)
- Tungurian (12-15 Ma)

**Late Miocene**
- Bahean (9-12 Ma)
- Baodean (5-9 Ma)

**Pliocene**
- Gaozhuangian
- Youhean
- Nihewanian

The following typical faunas from Astaracian to Turolian Sub-Saharan Africa and Eurasia treated in the next chapter have been correlated as shown in Table 2.

<table>
<thead>
<tr>
<th>MIOCENE</th>
<th>East Africa</th>
<th>North Africa</th>
<th>West &amp; Central Europe</th>
<th>Sub-Paratethys</th>
<th>Siwaliks</th>
<th>North China</th>
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<tr>
<td><strong>Late</strong></td>
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<tr>
<td>Tuolian</td>
<td>Lukeino</td>
<td>Sahabi</td>
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<td>Yushe I</td>
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<td></td>
<td>Mpesida</td>
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<td>Namurungule</td>
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<td>Ngeringørøwa</td>
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<td></td>
<td>Nakali</td>
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<td>Ngorora E</td>
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<td>Ngorora</td>
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<td></td>
<td>Bou Hanifa</td>
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<td></td>
<td>Aka Aiteputh</td>
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<td><strong>Middle</strong></td>
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<tr>
<td>Astaracian</td>
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<td></td>
<td></td>
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<td></td>
<td>Chinji</td>
</tr>
</tbody>
</table>
2. North Africa

Many localities of mammalian fauna are known from the late Miocene of North Africa. The following mammalian faunas are represented as Vallesian faunas (Beglia and Bou Hanifia) and Turolian fauna (Sahabi).

(1) Beglia (Tunisia)

This fauna is correlated to Vallesian fauna (MN 9) of North Africa. Some bovid taxa of this fauna are similar with those of the Namurungule Fauna. Faunal list of the Beglia Formation is as follows (Robinson, 1972; Robinson & Black, 1969; Thomas, pers. comm.).

Mammalia
Rodentia
   *Africanomys* sp.
   *Testouromys* sp.
   *Mellalomys atiasi*
Creodonta
   Hyaenodontidae gen. et sp. indet.
Carnivora
   Mustelidae gen. et sp. indet.
   Hyaenidae
   *Ictitherium* sp.
   Felidae
   *Machairodus* sp.
   Canidae
   *Afrocyon* sp.
Sirenia
gen. et sp. indet
Artiodactyla
Bovidae
   *Pachytragus solignaci*
   *Ouzocerus* sp.

(2) Bou Hanifia, Oued-el-Hammam (Algeria)

This fauna is a typical Vallesian fauna (MN 9) in North Africa. Faunal list of the Bou Hanifia Fauna is as follows (Arambourg, 1959).

Aves
   *Struthio* sp.
Mammalia
Primates
   Cercopithecidae
   *Macaca flandrini*
Rodentia
   Hystricidae
   *Hystrix* sp.
Carnivora
   Hyaenidae
Hyena algeriensis
Tubulidentata
   Orycteropus mauritanicus
Proboscidea
gen. et sp. indet.
Perissodactyla
   Equidae
      Hipparion africanum
Rhinocerotidae
      Dicerorhinus primaevus
Artiodactyla
   Giraffidae
      Palaeotragus germaini
      Samaotherium sp.
   Bovidae
      Damalavus borocoi
      Gazella praegaudryi
      Tragocerus sp.
      Cephalophus sp.

(3) Sahabi (Libya)
This fauna is a typical Turonian fauna in North Africa. Richness of equid and bovid taxa indicates open-country fauna. Faunal list of the Sahabi Fauna is as follows (Boaz et al. eds., 1987).

Insectivora
   Soricidae
      Crocidurinae gen. et sp. indet.
Primates
   Hominoidea gen. et sp. indet.
   Cercopithecidae
cf. Libypithecus sp.
      Macaca sp.
Rodentia
   Sciuridae
cf. Atlantoxerus getulus
   Ctenodactylidae
      Sayimys sp.
   Cricetidae
      aff. Myocrictodon cherifensis
      Protatera yardangi
Muridae
      Progonomys sp.
Cetacea
   Delphinidae
cf. Lagenorhynchus sp.
Pliatanistidae gen. et sp. indet.
Carnivora
Ursidae
   *Indarctos atticus*
   *Agriotherium cf. africanum*
Viverridae
   *Viverra* sp.
Hyaenidae
   *Percrocuta eximia*
   *Percrocuta senyueki*
   *Hyenictitherium* sp.
   *Euryboas* sp.
Felidae
   *Machairodus* sp.
      sp. A
      sp. B
      sp. C
Phocidae
Proboscidea
   *Gomphotheriidae*
      *Amebelodon cyrenaicus*
   *Elephantidae*
      *Stegotetrabelodon lyicus*
Sirenia
   *Dugongidae*
      *Metaxytherium serresii*
Perissodactyla
   *Equidae*
      "*Hipparion*" cf. *africanum*
      "*Hipparion*" cf. *sitifense*
   *Rhinocerotidae*
      *Diceros neumayri*
Artiodactyla
   *Suidae*
      *Nyanzachoerus* cf. *devauxi*
      *Nyanzachoerus syrticus*
      *Nyanzachoerus kanamensis*
   *Anthracotheriidae*
      *Merycopotamus petrocchii*
Hippopotamidae
   *Hexaprotodon sahabiensis*
Giraffidae
   *Samotherium* sp.
Bovidae
   *Leptobos syrticus*
   *Miotragocerus cyrenaicus*
   *Redunca* aff. *darti*
?Hippotragus sp.
cf. Damalacra sp.
Raphicerus sp.
Gazella sp.
Prostrepsiceros (Prostrepsiceros) libycus

3. Southwestern and Central Europe

Many localities of mammalian fauna are known from the late Miocene in Southwestern and Central Europe. The following mammalian faunas are represented as Vallesian fauna (Eppelsheim) and Turolian faunas (Dorn-Dürkheim and Mt. Leberon).

(1) Eppelsheim (West Germany)

This fauna is correlated with Vallesian (MN 9). Faunal list of the Eppelsheim Fauna is as follows (Gabuniya, 1959; Klipsten & Kaup, 1836; Wenz, 1921, 1931).

Mammalia
Primates
Pliohiphopotes eppelsheimensis
Rodentia
Gliridae
Steneofiber jügeri
Carnivora
Ursidae
Simocyon diaphorus
Hyaenidae
Ictitherium robustum
Felidae
Pontosmilus ogygius
Machairodus cultridens
Proboscidea
Mastodon (=Gomphotherium) angustidens
Mastodon (=Gomphotherium) angustidens var. subtapiroidea
Mastodon gigantorosstris
Mastodon longirostris var. dubius
Mastodon longirostris var. grandis
Deinotheriidae
Deinotherium giganteus
Perissodactyla
Equidae
Anchitheirum sp.
Hipparion primigenium
Chalicotheriidae
Chalicotherium goldfussii
Rhinocerotidae
Aceratheriinae Tribe Aceratherini
Aceratherium incisivum
Brachypotherium goldfussii
Late Miocene Namurungule Fauna

Rhinocerotinae Tribe Rhinocerotini
  *Dicerorhinus schleiermacheri*
  *Dicerorhinus belvederensis*

Artiodactyla
  Suidae
    *Sus antiquus*
    *Listriodon* sp.
  Cervidae
    *Dorcattherium nau* 

Flora by Wenz (1921)
*Quercus farginervus*
*Quercus undulans*
*Fagus deukalionis*
*Fagus castaniaefolia*
*Laurophyllum crassifolium*
*Aralites lanceus*
*Bunelia oreadum*

Flora by Koenigswald (1929) [palynological]
*Cinnamomum* sp.
*Taxodium* sp.
*Sequoia* sp.

(2) Dom-Dürkheim (West Germany)
  This fauna indicates Tuolian fauna (MN 11). Faunal list of the Dorn-Dürkheim Fauna is as follows (Tobien, 1980).

Mammalia
Rodentia
  Sciuridae
    *Spermophilinus* sp.
    *Pliopetaurista bressana*
    *Pliopetes* sp.
    *Blackia* sp.
    *Miopetaurista* sp.
  Castoridae
    *Dipoides problematicus*
    *Palaeomys castoroides*
    *Palaeomys plassi* n. sp.
    *Trogontherium minutum rhenanum* n. sp.
    *Castor neglectus*
  Cricetidae
    *Epimeriones austriacus*
    *Kowalskia* sp. cf. *lavocati*
    *Collimys* sp. cf. *primus*
    *Cricetulodon* sp.
  Anomalomyidae
    *Prospalax petteri*
Pterospalax sp.
Muridae
Parapodemus lugdunensis
Zapodidae
Sminthozapus sp
Gliiridae
Muscardinus vireti
Glis sp. cf. minor
Microdyromys sp.

Carnivora
Hyaenidae
Percrocuta eximia
Mustelidae
Martes sp. cf. sansaniensis
Martes sp.
Promeles sp. D
Felidae
Pseudaelurus tournaeusis
Machairodus taracliensis
Felidarum inc. subfam.

Proboscidea
Gomphotheriidae
Tetralophodon longirostris
Deinotheriidae
Deinotherium giganteus

(3) Mt. Leberon (France)
This fauna is Turolian fauna (MN 13). Faunal list of the Mt. Leberon Fauna is as follows (Bemor & Pavlakis, 1987).

Mammalia
Carnivora
Viverridae
Herpestes guerini
Hyaenidae
Percrocuta eximia
Thallasictis wongii
Plioviverrops pentelici
Felidae
Machairodus aphanistus

Perissodactyla
Equidae
Hipparion prostylem
Rhinocerotidae
Aceratherium sp.
Dicerosrhinus schleiermacheri

Artiodactyla

Late Miocene Namurungule Fauna

Suidae

Microstonyx erymanthius

Cervidae

Dremotherium sp.

4. Sub-Paratethys

Many localities of mammalian fauna are known from the late Miocene in Sub-Paratethys. The following mammalian faunas are represented as Turolian faunas (Pikermi, Samos and Maragheh).

(1) Pikermi (Greece)

This fauna is famous Turolian fauna (MN 12) of Greece (Wagner 1857; Solounias, 1981). Faunal list of the Pikermi Fauna is as follows (Solounias, 1981).

Mammalia
Insectivora

Talpidae

Uropsilinae

Desmanella dubia

Erinaceidae

Gymnurinae

Galerix atticus

Galerix moedlingensis

Primates

Cercopithecidae

Colobinae

Mesopithecus pentelici

Lagomorpha

Ocotonidae

Proloagus cf. crusafonti

Leporidae

Alilepus sp.

Rodentia

Cricetidae

Cricetinae

Kowalskia cf. lavocati

Cricetodontinae Tribe Cricetodontini

Byzantinia pikermiensis

Muridae

Murinae

Parapodemus gaudryi

Occitanomys ? neutrum

Occitanomys ? provocator

Gliridae

Glirinae

Muscardinus sp.
Myomimus cf. dehmi

Hystricidae
Hystricinae
Hystrix primigenia

Carnivora
Family indet.
Simocyon primigenium

Ursidae
Indarctos atticus

Mustelidae
Mustelinae
Sinictis pentelici
Martes woodwardi
Plesiogulo sp.

Melinae
Promelis palaeattica

Mephitinae
Promephitis lartetii

Lutrinae
Enhydriodon laticeps

Hyaenidae
Ictitheriinae
Plioviverrops orbignyi
Ictitherium viverrinum
Thalassictis hyaenoides

Thalassictis (Lycyaena) chaeretis
Thalassictis (Lycyaena) sp. nov. (by Solounias 1981)

Subfamily indet.
Hyaenictis graeca
Hyaenictis eximia

Felidae
Felinae
Felis sp.
Felis attica

Subfamily indet.
Metalurus parvulus
Metalurus major

Machairodontinae
Machairodus giganteus
Paramachairodus orientalis

Proboscidea
Palaeomastodontidae
Mammut borsoni?

Gomphotheriidae
Gomphotheriinae
Stegotetrabelodon grandincisivus
Choerolophodon pentelici
Late Miocene Namurungule Fauna

Deinotheriidae

*Deinotherium* cf. *giganteum*

Hyracoidea

Procaviidae

*Pliozyra* *graecus*

Perissodactyla

Equidae

*Hipparion* sp. (large, one preorbital fossa)

*Hipparion minus*? (small, one preorbital fossa)

*Hipparion proboscideum* (large, two preorbital fossae)

*Hipparion matthewi* (small, no preorbital fossa)

Chalicotheriidae

*Chalicotherium* *goldfussi*

Rhinocerotidae

Aceratheriinae Tribe Aceratherini

*Aceratherium* cf. *incisivum*

Rhinocerotinae Tribe Rhinocerotini

*Dicerorhinus* *schleiernacheri*

*Dicerorhinus* *pachygnathus*

Artiodactyla

Suidae

*Sus* sp.

*Microstonyx* *erymanthius*

Cervidae

Cervinae

Cervinae gen. et sp. indet.

*Pliocerus* *pentelici*

Giraffidae

Palaeotraginae

*Palaeotragus* *rouenii*

Sivatheriinae

*Helladotherium* *duvernoyi*

Giraffinae

*Honanotherium* *speciosum*

*Honanotherium* *atticum*

Bovidae

*Miotragocerus-Tragoportax* complex

*Miotragocerus* *monacensis* var. A

*Miotragocerus* *monacensis* var. B

*Miotragocerus* *valenciennesi*

*Tragoportax* *amalthea*

*Tragoportax* *rugosifrons*?

Tribe Antilopini

*Prostrepsiceros* *rotundicornis* var. A

*Protragelaphus* *skouzesi*

*Gazella* *capricornis*

*Oioceros* *rothi*
Tribe Ovibovini

*Palaeoeras lindermayeri*

*Protoryx* complex

*Palaeoryx pallasi* var. A
*Palaeoryx pallasi* var. C
*Palaeoryx pallasi* var. D
*Sporadotragus parvidens*
*Protoryx carolinae*

Tribe Tragelaphini

*Selenoportax* sp.

(2) Samos (Greece)

This fauna is a typical Sub-Paratethys Turolian (MN 12, 13) fauna. Richness of hyaenid, equid and bovid taxa shows an open-country fauna. The bone bearing horizons on Samos Island is comparable to age of between 8.5 and 9.0 Ma by K-Ar dating method (Solounias, 1981). Faunal list of the Samos Fauna is as follows (Solounias, 1981).

Mammalia

Insectivora

Erinaceidae

Gymnurinae

*Galerix atticus*

Chiroptera

Vespertilionidae

Vespertilioninae

*Samonycteris majori*

Primates

Cercopithecidae

Colobinae

*Mesopithecus pentelici*

Rodentia

Sciuridae

*Spermophilinus* cf. *bredai*

Cricetidae

Cricetodontinae Tribe Cricetodontini

*Byzantinia hellenicus*

Gerbillinae

*Pseudomeriones pythagorasi*

Muridae

Murinae

*Occitanomys? provocator*

Spalacinae

*Pliospalax* cf. *sotirisi*

Hystricidae

Hystricinae

*Hystrix primigenia*
Late Miocene Namurungule Fauna

Carnivora
  Ursidae
    Ursavus cf. depereti
    Indarctos atticus
  Mustelidae
    Melinae
      Promeles palaeattica
      Promeles maraghana
  Mephitinae
    Promephitis lartetii
  Hyaenidae
    Ictitheriinae
      Plioviverrops orbignyi
      Ictitherium viverrinum
      Thalassictis wongii
      Thalassictis hyaenoides
      Thalassictis (Lycyaena) chaeretis
      Thalassictis (Lycyaena) sp. nov. (by Solounias 1981)
    Subfamily indet.
      Hyaenictis eximia
  Felidae
    Felinae
      Felis attica
    Subfamily indet.
      Metalurus parvulus
      Metalurus major
    Machairodontinae
      Machairodus giganteus
  Tubulidentata
    Orycteropodidae
      Orycteropus gaudryi
  Proboscidea
    Palaeomastodontidae
      Mammut borsoni?
    Gomphotheriidae
      Gomphotheriniinae
        Stegotetrabelodon grandincisivlls
        Choerolophodon pentelici
    Deinotheriidae
      Deinotherium cf. giganteum
  Hyracoidea
    Procaviidae
      Pliohyrax graecus
      Pliohyrax kruppii
    Perissodactyla
      Equidae
        Hipparion sp. (large, one preorbital fossa)
Hipparion minus (small, one preorbital fossa)
Hipparion proboscideum (large, two preorbital fossae)
Hipparion dietrichi (medium, no preorbital fossa)
Hipparion matthewi (small, no preorbital fossa)

Chalicotheriidae
Ancylotherium pentelicum

Rhinocerotidae
Aceratheriinae Tribe Aceratherini
Chilotherium samium
Chilotherium schlosseri
Chilotherium kowalewski

Rhinocerotinae Tribe Rhinocerotini
Dicerorhinus schleiernacheri
Dicerorhinus pachygnathus

Artiodactyla
Suidae
Microstonyx erymanthus
Potamochoerus hytheriordes

Tragulidae
Dorcatherium naui

Cervidae
Muntiacinae
Muntiacus sp.

Cervinae
Cervinae gen. et sp. indet.
Pliocervus pentelici

Giraffidae
Palaeotraginae
Palaeotragus rouenii
Palaeotragus coelophrys
Samotherium boissieri

Sivatheriinae
Helladotherium duvernoyi
Helladotherium sp. nov. (by Solounias, 1981)

Giraffinae
Honanotherium speciosum

Bovidae
Miotragocerus-Tragopontax complex
Miotragocerus monacensis var. A
Miotragocerus monacensis var. B
Miotragocerus valenciennesi
Tragopontax amalthea
Tragopontax curvicornis
Tragopontax rugosifrons
Samokeros minotaurus var. A
Samokeros minotaurus var. B

Tribe Antiilopini
Late Miocene Namurungule Fauna

Prostrepsiceros rotundicornis var. B
Prostrepsiceros houtumschindleri var. A
Protragelaphus skouzesi
Gazella capricornis
Gazella mytilinii
Gazella dorcadoides
Oioceros wegneri
Sinotragus crassicornis
Prosinotragus kuhlmanni
Prosinotragus sp. nov. (by Solounias, 1981)

Tribe Ovibovini
Palaeorea lindermayeri
Criotherium argalioides
Parurmiatherium rugosifrons

Prootoryx complex
Palaeoryx pallasi var. B
Palaeoryx pallasi var. C
Palaeoryx pallasi var. D
Tragoreas oryxoides
Sporadotragus parvidens
Prootoryx crassicornis var. A (long-brained)
Prootoryx crassicornis var. B (short-brained)
Prootoryx laticeps var. A (long-brained)
Prootoryx laticeps var. B (short-brained)
Pseudotragus capricornis

Tribe Rupicaprini
gen. et sp. indet.

(3) Maragheh (Iran)
This fauna is a typical Turolian fauna of Sub-Paratethys (Mecquenem, 1908-1911, 1924-25; Kamei et al., 1977; Bernor et al., 1980; Solounias, 1981; Bernor, 1986). The Maragheh Formation is comparable to age of between 7 and 11 Ma by K-Ar dating method (Bernor et al., 1980). Faunal list of the Samos Fauna is as follows (Solounias, 1981).

Mammalia
Primates
Cercopithecidae
Colobinae
Mesopithecus pentelici
Rodentia
Muridae
Murinae
?Gerboa sp.
Carnivora
Ursidae
Indarctos atticus
Mustelidae
  Mustelinae
    Martes sp.
  Melinae
    Promeles palaeattica
    Parataxidea maraghana
    Parataxidea polaki

Hyaenidae
  Ictitherinae
    Thalassictis wongii
  Subfamily indet.
    Hyaenictis eximia

Felidae
  Felinae
    Felis attica
  Subfamily indet.
    Metalurus parvulus
  Machairodontinae
    Machairodus giganteus
    Paramachairodus orientalis

Tubulidentata
  Orycteropodidae
    Orycteropus gaudryi

Proboscidea
  Gomphotheriidae
    Gomphotheriinae
      Choerolophodon pentelici

Perissodactyla
  Equidae
    Hipparion sp. (large, one preorbital fossa)
    Hipparion minus (small, one preorbital fossa)
    Hipparion dietrichi (medium, no preorbital fossa)

  Chalicotheriidae
    Ancylotherium pentelicum

Rhinocerotidae
  Aceratheriinae Tribe Aceratherini
    Chilotherium persiae
  Rhinocerotinae Tribe Rhinocerotini
    Diceros pachygnathus
  Rhinocerotinae Tribe Elasmotherini
    Iranotherium morgani

Artiodactyla
  Suidae
    Microstonyx erymanthius

Cervidae
  Cervinae
    Pliocervus pentelici
Giraffidae
  Palaeotraginae
    *Palaeotragus coelophrys*
    *Samotherium boissieri*
  Sivatheriinae
    *Helladotherium duvernoyi*
Giraffinae
  *Homotherium atticum*

Bovidae
  *Miotragocerus-Tragoportax* complex
    *Miotragocerus monacensis* var. B
    *Samokeros minotaurus* var. A
Tribe Antilopini
  *Prostrepsiceros rotundicornis* var. B
  *Prostrepsiceros houtunschindleri* var. B
  *Protragelaphus skouzesi*
  *Gazella deperdita*
  *Oioceros rothi*
  *Oioceros atropatenes*
  *Oioceros rodleri*
  *Sinotragus* sp. nov. (Solounias, 1981)
Tribe Ovibovini
  *Urmithatherium polaki*
  *Protoryx* complex
    *Protoryx crassicornis* var. A (long-brained)
    *Protoryx crassicornis* var. B (short-brained) ?
    *Protoryx laticeps* var. A (long-brained)
    *Protoryx laticeps* var. B (short-brained) ?

5. Siwaliks

Many localities of mammalian fauna are known from the late Miocene in Siwaliks. The following mammalian faunas are represented as Astaracian fauna (Chinji), late Vallesian to early Turolian fauna (Nagri) and late Turolian fauna (Dhok Pathan).

(1) Chinji (Pakistan)

This fauna have none of cervids and Hipparion. Overall faunal resemblances are to Astaracian faunas of Eurasia. An age of between 11 and 13 Ma. Faunal list of the Chinji Fauna is as follows (Pilbeam et al., 1977).

Mammalia
Primates
  Hominoidea
    *Sivapithecus sivalensis*
    *Sivapithecus indicus*
    *Ramapithecus punjabicus*
Creodonta
  *Hyaeodonta*
Hyainailouros bugtiensis
Dissopsalis carnifex

Rodentia
Rhizomyidae
cf. Rhizomyidae gen. et sp. indet
Cricetidae
Copemys sp.
Megacricetodon sp.
Muridae
Antemus chinjiensis

Carnivora
Amphicyonidae
Amphicyoninae (large sp.)
Amphicyon sp.
Vishnucyon chinjiensis
Mustelidae
Martes lydekkeri
?Martes sp.
Vishnuonyx chinjiensis
Mustelinae sp.
Viverridae
?Viverra chinjiensis

Hyaenidae
Hyaenidae gen. et sp. indet.
Percrocuta carnifex

Felidae
’Sivasmilus’ (=Paramachairodus copei )
Sivaelurus chinjiensis
Felidae gen. et sp. indet.
?Sansanosmilus sp.

Tubulidentata
Orycteropodidae
Orycteropus sp.

Perissodactyla
Chalicotheriidae
Chalicotherium salinum

Rhinocerotidae
Rhinocerotidae spp.

Artiodactyla
Suidae
Listriodon pentapotamiae
Conohyus chinjiensis
Lophochoerus sp.
Merycopotamus pusillus
Dorcabune nagrii

Tragulidae
Tragulidae spp.
Giraffidae
   *Giraffokeryx* sp.

Bovidae
   *Protragocerus gluten*
   *Miotragocerus gradiens*
   *Kubanotragus sokolovi*
   *?Pseudotragus potwaricus*
   *Sivoreas eremita*
   *Gazella* sp.

(2) Nagri (Pakistan)

The bovids, suids, rodents and the two species of Hipparion of this fauna suggest a correlation with late Vallesian or early Turolian faunas. Upper half of Nagri Formation is probably comparable to age of between 9 and 10 Ma with age of Samos and Turkish faunas. The lower half of Nagri Formation suggests earlier Vallesian. Faunal list of the Nagri Fauna is as follows (Pilbeam et al., 1977).

Mammalia
Insectivora
   Soricidae
      gen. et sp. indet.

Primates
   *?Lorisidae*
      gen. et sp. indet.
   Hominoidea
      *Sivapithecus sivalensis*
      *Sivapithecus indicus*
      *Ramapithecus punjabicus*
      cf. *Gigantopithecus* sp.

Rodentia
   Sciuridae
      gen. et sp. indet.
   Gliridae
      gen. et sp. indet.
   Rhizomyidae
      *Rhizomyoides* sp.
      *Kanisamys sivalensis*

Muridae
   *Progonomys* n. sp.
   *Parapodemus* sp.
   cf. "*Mastomys* colberti"

Creodonta
   Hyaenodontidae
      cf. *Isohyaenodon* sp.

Carnivora
   Amphicyonidae
      *Amphicyon* sp.
Mustelidae
  ?Martes sp.
  Mustelinae sp.
  Eomellivora sp.
  Sivaonyx bathygnathus
Viverridae
  Viverrinae 2 sp.
  ?Herpestinae sp.
  ?Progenetta sp.
Hyaenidae
  Palyhyaena sivalensis
  ?Miohyena n. sp.
  Percrocuta carnifex
  Percrocuta grandis
Felidae
  ? Sivaelurus sp.
  Machairodontinae
Proboscidea
  Gomphotheriidae
    gen. et sp. indet.
  Deinotheriidae
    Deinotherium sp.
Perissodactyla
  Equidae
    Hipparion small and large spp.
  Chalicotheriidae
    Chalicotherium cf. salinum
Artiodactyla
  Suidae
    Propotamochoerus hysudricus
    Propotamochoerus sp.
    Conotyus sp.
    Tetracodonodon sp.
    Hippopotamodon sivalense (=Dicryphochoerus titan)
Tayassuidae
  Schizochoerus sp.
  Anthracotheriidae
    Merycopotamus namus
    Merycopotamus dissimilis
Tragulidae
  Dorcabune nagrii
  Dorcatherium majus
  Dorcatherium minus
  cf. Dorcatherium sp.
Giraffidae
  cf. Sivatherium sp.
Bovidae
Gazella sp.
Miotragocerus punjabicus
Selenoportax vexillarius
?Pseudotragus sp.
Boselaphini very small gen. et sp. nov.

(3) Dhok Pathan (Pakistan)

The Dhok Pathan fauna resembles those from late Turolian in Eurasia and North Africa. The Dhok Pathan Formation is probably comparable in age of between 8 and 9 Ma (or perhaps less) with age of Samos and Turkish faunas. Faunal list of the Dhok Pathan Fauna is as follows (Colbert, 1935; Pilbeam et al., 1977).

Mammalia
Primates
  Cercopithecidae
    Cercopithecus hasnoti
    Macaca sivalensis
Hominoida
  Dryopithecus frickae

Rodentia
  Rhizomyidae
    Rhizomyoides sp.
    Kanisamys sivalensis
Hystricidae
  Hystrix sivalensis

Carnivora
  Amphicyonidae
    Amphicyon lydekkeri
Ursidae
  Agriotherium palaeindicum
  Indarctos salmontanus
  Indarctos punjabiensis
Mustelidae
  ?Martes sp.
  Mustelinae sp.
  Eomellivora sp.
  Sivaonyx bathygnathus

Viverridae
  Viverrinae 2 sp.
  ?Herpestinae sp.
  ?Progenetidae sp.
Hyaenidae
  Palyhyaena sivalensis
  ?Miobyena n. sp.
  Percrocuta carnifex
  Percrocuta grandis
Felidae
  ? Sivaelurus sp.
  Machairodontinae

Proboscidea
  Gomphotheriidae
  gen. et sp. indet.
  Deinootheriidae
    Deinootherium sp.

Perissodactyla
  Equidae
    Hipparion small and large spp.
  Chalicotheriidae
    Chalicotherium cf. salinum

Artiodactyla
  Suinae
    Propotamochoerus hysudricus
    Propotamochoerus sp.
    Conotyus sp.
    Tetraconodon sp.
    Hippopotamodon sivalense (=Dicryphochoerus titan)

Tayassuidae
  Schizocoerus sp.

Anthracotheriidae
  Merycopotamus namus
  Merycopotamus dissimilis

Tragulidae
  Dorcabune nagrii
  Dorcatherium majus
  Dorcatherium minus
  cf. Dorcatherium sp.

Giraffidae
  cf. Sivatherium sp.

Bovidae
  Gazella sp.
  Miotragocerus punjabicus
  Selenoportax vexillarius
  ?Pseudotragus sp.
  Boselaphini very small gen. et sp. nov.

6. China

Many localities of mammalian fauna are known from the late Miocene in China. The following mammalian faunas are represented as early Turolian fauna (Baode) and late Turolian fauna (Yushe I).

(1) Baode, Shanxi

This fauna is correlated with early Turolian mammalian age of West Eurasia and richness of hyaenid, equid and bovid taxa indicate open-country environments. Faunal
list of the Baode Fauna is as follows (Yen et al. eds., 1984; Qiu et al., 1987).

Mammalia
Rodentia
  Castoridae  
    Sinocastor zdanskyi
Carnivora
  Amphicyonidae  
    Amphicyon sp.
  Ursidae  
    Sinocyon cf. primigenium  
    Indarctos lagrellii  
    I. sinensis
  Mustelidae  
    Eomellivora wimani  
    Lutra aonychoides  
    Martes palaeosinensis  
    Melodon incertum  
    Melodon major  
    Parataxidea crassa  
    Parataxidea sinensis  
    Plesiogulo brachygnathus  
    Propotorius minimus  
    Sinictis dolichognathus
Hyaenidae
  Hyaena honanensis  
  Hyaena variabilis  
  Ictitherium gaudryi  
  Ictitherium hyaenoides  
  Ictitherium sinensis  
  Ictitherium wongi  
  Lycyaena dubia
Felidae
  Homotherium palanderi  
  Homotherium tingi  
  Pseudaelurus major  
  Pseudaelurus minor
Proboscidea
  Gomphotheriidae  
    Tetralophodon exoletus
Perissodactyla
  Equidae  
    Hipparioninae  
    Hipparion (Hipparion) dermatorhinum  
    Hipparion (Hipparion) fossatum  
    Hipparion (Hipparion) hippidiodus  
    Hipparion (Hipparion) placodus
Anchitheriinae
Silhippus ziteli
Rhinocerotidae
Aceratheriinae
Chilotherium anderssoni
Chilotherium gracile
Chilotherium habereri
Chilotherium planifrons
Chilotherium samium
Chilotherium schlosseri
Chilotherium wimani
Rhinocerotinae
Dicerorhinus orientalis
Iranotheriinae (Elasmotheriinae)
Sinotherium lagrellii
Artiodactyla
Suinae
Chleuastochoerus stehlini
Potamochoerus hytheriordes
Sus erymanthius
Cervidae
Cervavitus novorossiae
Procaperolus latifrons
Giraffidae
Palaeotragus cf. coelophrys
Palaeotragus microdon
Samotherium sinense
Bovidae
Paraprotryx minor
Miotragocerus-Tragoportax complex
Tragocerus gregarius
Tragocerus lagrellii
Tragocerus spectabilis
Gazella altidens
Gazella dorcadoides
Gazella gaudryi
Gazella paotehensis
Sinotragus wimani
Plesiadax depereti
Plesiadax minor
Urmiatherium intermedium
Protoryx shansiensis
(2) Yushe Zone I, Shanxi
This fauna is correlated with late Tuolian mammalian age of West Eurasia and indicates woodland environments. Faunal list of the Yushe Zone I Fauna is as follows (Yen et al. eds., 1984; Qiu et al., 1987).
Late Miocene Namurungule Fauna

Mammalia
Rodentia
  Castoridae
    Sinocastor zdanskyi
  Cricetidae
    Prosiphneus murinus
Carnivora
  Ursidae
    Sinocyon cf. primigenium
    Hyaenarctis sp.
  Mustelidae
    Lutra aonychooides
    Martes palaeosinensis
    Plesiogulo brachygnathus
  Hyaenidae
    Ictitherium gaudryi
  Felidae
    Homotherium palanderi
    Pseudaelurus major
    Pseudaelurus minor
    Felis sp.
Proboscidea
  Gomphotheriidae
    Gomphotherium wimani
    Tetralophodon exoletus
    Tetralophodon sp.
    Anancus cuneatus
    Anancus sinensis
    Selenolophodon spectabilis
Stegodontidae
  Stegodon yushensis
Perissodactyla
  Equidae
    Hipparioninae
      Hipparion (Hipparion) platyodus
  Tapiridae
    Tapirus teiihardi
Rhinocerotidae
  Rhinocerotinae
    Dicerorhinus orientalis
    "Dicerorhinus palaeosinensis"
Artiodactyla
  Suidae
    Chleuastochoerus stehlini
    Sus erymanthus
  Cervidae
Axis speciosus
Eostyloceros blainvillei
Eostyloceros triangularis
Procapreolus latifrons
Cervavitus demissus
Cervavitus novorossiae
Procapreolus latifrons
Giraffidae
Palaeotragus decipens
Palaeotragus sp.
Honanotherium schlosseri
Bovidae
Dorcadoryx triguetricornis
Paraprotoryx killgusi
Sinoryx bombifrons
Tragocerus laticornis
Gazella gaudryi
Oioceros sp.
Protoryx bohlini
Protoryx yushensis
Tragoreas palaeosinensis

In the discussion section, The author analyses faunal resemblance from the evidence of well over 500 taxa of 22 Eurasian faunas shown in Appendix 1 (p. 103–112).

IV. Neogene Faunal Aspects and Paleoecology of Sub-Saharan Africa

The geographical distribution and paleoecology of Sub-Saharan faunas in each age is remarked in the following chapter (Fig. 9).

The following zonation of Sub-Saharan Africa is based largely on the radiometric age and faunal resemblance (Benefit & Pickford, 1986; Nakaya, 1987, 1989, 1993; Nakaya et al., in press; Pickford, 1981, 1982, 1986a, 1986b; this work). East African mammalian faunas are described in the following chapter (p. 50–75) in detail.

1. Miocene
(1) Agenian
The following Agenian (18–22 Ma) mammalian faunas are sporadically distributed in South Africa, Zaire and East Africa. Correlation of the Faunal Sets of East Africa is followed after Pickford (1981).
Pre Set I (early Agenian); Meswa (Kenya).
Set I (late Agenian); Malembe (Zaire: Hooijer, 1963, 1970), Napak (Uganda), Koru (Kenya), Songhor (Kenya), Kiahera (Kenya), Chemtwara (Kenya).
Late Miocene Namurungule Fauna

Fig. 9. Neogene vertebrate localities from the Sub-Saharan Africa.
Aa: Aka Aiteputh; Af: Afar; Ar: Arrisdrift; Aw: Middle Awash; Ch: Chemeron; Ek: Ekora; Er: East Rudolf; Ft: Fort Ternan; Ka: Karugamania; Km: Kirimun; Kn: Kanapoi; Ko: Koru; Kr: Karungu; La: Langebaanweg; Lk: Lukeino; Lo: Lothagam; Na: Napak; Ne: Ngorora E; Ng: Ngorora; Nk: Nakali; Nm: Namurungule; Nw: Ngeringerowa; Ma: Maboko; Mf: Mfwangano; Ml: Malembe; Mo: Moroto; Mp: Mpesida; Ob: Ombo; Om: Omo; Ru: Rusinga; Ot: Otavi; So: Songhor; Wt: West Turkana.

(2) Orleanian

The following Orleanian (15-18 Ma) mammalian faunas are sporadically distributed in South Africa and East Africa. Correlation of the Faunal Sets of East Africa is followed after Pickford (1981). Some fauna are characterized by dominant Primates (Maboko Fauna).

Set II (early Orleanian); Hiwegen, Gumbo, Chianda (Rusinga Island, Kenya), Bukwa (Kenya), Moruorot (Kenya), Karungu (Kenya), Mfwangano (Kenya).
Set III (late Orleanian); Arrisdrift (Namibia; South West Africa early middle Miocene 14-18 Ma; Hendey, 1978), Ombo (Kenya), Maboko (Kenya), Buluk (Kenya), Loperot (Kenya), Kirimun (Kenya), Majiwa (Kenya).

(3) Astaracian

The following Astaracian (12.5-15 Ma) mammalian faunas are sporadically distributed in East Africa only. Correlation of the Faunal Sets of East Africa is followed after Pickford (1981). Some fauna are characterized by dominant Primates (Aka Aiteputh Fauna).

Set IV (Astaracian); Moroto (Uganda), Aka Aiteputh (Kenya), Fort Ternan (Kenya), Muryur (Kenya), Otavi BA-1, 47, 63, (Namibia: Conroy et al., 1992).

(4) Vallesian

The Vallesian (10.5-12.5 Ma) mammalian faunas are distributed in East Africa only. Hipparion appeared about 12.5 Ma in Sub-Saharan Africa. The Ngorora Fauna has rich assemblage.

Set V (Vallesian); Ngorora (Kenya), Otavi BA-31, 90 (Namibia: Conroy et al., 1992).

(5) Turolian

The following Turolian (5.5-10.5 Ma) mammalian faunas are sporadically distributed in East Africa only. This fauna is considered as a core of the Sub-Saharan mammalian faunas after Miocene. The mammalian assemblage of Sub-Saharan African faunas changed since late Astaracian. Some recent genera of mammals appeared in East Africa, in post-Vallesian age. Therefore, the Namurungule Fauna is very important, from the viewpoint of the process of the environmental change during the late Miocene and the effects of this paleoenvironmental change to the Hominoid evolution. Table 3 shows a list of taxa of the Ngorora Fauna of the Vallesian, the Nakali, Ngeringerowa, Ngorora E Formation (Benefit & Pickford, 1986) and Namurungule Fauna (Nakaya et al., in press; Kawamura & Nakaya, in press) of the Turolian East Africa. The Namurungule Fauna has rich assemblage among the Turolian faunas, however, other faunas have poor assemblage.

Set VI (early Turolian); Ngorora upper E (Kenya), Ngeringerowa (Kenya), Nakali (Kenya), Namurungule (Kenya).

Set VII (late Turolian); Mpesida (Kenya), Lukeino (Kenya) and Lothagam I (Kenya).

2. Pliocene

(1) Ruscinian

The following Ruscinian (3.5-5.5 Ma) mammalian faunas are distributed in East Africa and South Africa. The first family Hominidae (Australopithecus) appeared in these faunas.

Set VIII (Ruscinian); Afar (Ethiopia), Middle Awash (Ethiopia), Chemeron (Kenya), Ekora (Kenya), Kanapoi (Kenya), Lothagam (Kenya), Laetoli (Tanzania), Otavi BA-8, 54 (Namibia: Conroy et al., 1992), Langebaanweg (South Africa).
Table 3. A list of taxa of each fauna of the Vallesian to early Turolian mammalian faunas of East Africa.

<table>
<thead>
<tr>
<th>Taxa / Locality</th>
<th>NM</th>
<th>NG</th>
<th>NE</th>
<th>NK</th>
<th>NW</th>
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<tbody>
<tr>
<td>Hominoidea small form</td>
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<tr>
<td>Hominoidea large form</td>
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<td>Cercopithecoidea indet.</td>
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<td>Colobinae sp.</td>
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<td>Microcolobus tugenensis</td>
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<td>Agnotherium sp.</td>
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<tr>
<td>Eomellivora sp.</td>
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<tr>
<td>Sivaonyx sp.</td>
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<tr>
<td>Hyaenidae (Percrocuta sp.)</td>
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<td>Canidae small sp.</td>
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<td>Orycteropus chemeldoi</td>
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<td>Choerolophodon ngorora</td>
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<tr>
<td>Tetralophodon sp.</td>
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<tr>
<td>Deinotherium sp. cf. bozasi</td>
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<tr>
<td>Parapliocharax sp.</td>
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<tr>
<td>Hipparion large form</td>
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<td>Hipparion small form</td>
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<tr>
<td>Ancylotherium sp.</td>
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<tr>
<td>Aceratherium/Dicerorhinus sp.</td>
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<tr>
<td>Chilotheridium petersi</td>
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<td>Paradiceros sp.</td>
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<tr>
<td>Brachypotherium lewisi</td>
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<td>Kenyatherium bishopi</td>
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<tr>
<td>?Conohyus sp.</td>
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<td>Nyanzachoerus sp.</td>
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<td>Tayassuidae</td>
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<td>Kenyapotamus coryndoni</td>
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<tr>
<td>Kenyapotamus sp.</td>
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<tr>
<td>Dorcatherium pigotti</td>
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<td>Palaeotragus sp.</td>
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<td>Giraffidae large form(Samotherium sp.)</td>
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<td>Climacoceras gentryi</td>
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<tr>
<td>Protragocerus labidatus</td>
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<tr>
<td>Sivoreas/Palaeoeras sp.</td>
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<td>Hippotraginae/Reduncini</td>
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<td>Homolodrphas tugenium</td>
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<tr>
<td>?Antidorcas sp.</td>
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<tr>
<td>Pseudotragus? gentryi</td>
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<td>Pachytragus sp.</td>
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<tr>
<td>Gazella sp.</td>
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<td>Paraphiomys pigotti</td>
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<td>Paraulacodus sp.</td>
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</tbody>
</table>

Note: NG: Ngorora A-D; NE: Ngorora Upper E; NK: Nakali; NW: Ngeringerowa (Benefit & Pickford, 1986); NM: Namurungule (Nakaya et al., in press; Kawamura & Nakaya., in press).
V. Development of Neogene Mammals in East Africa

The age of some Neogene mammalian sites from East Africa has been determined by radiometric dating methods. The age of many sites were determined by stratigraphical correlation and faunal resemblance. The following description shows mammalian assemblages, age (radiometric and so on), and paleoenvironment at each location (country).

(1) Meswa (Kenya)
The age of this fauna was determined as Faunal Set Pre-Set I by faunal assemblages and this fauna must have inhabited in subaerial environments deduced from sedimentological evidence (Andrews et al., 1981; Pickford, 1986a). Faunal list of the Meswa Fauna is following Pickford (1986a).

Mammalia
Primates
Oreopithecidae gen. nov.

Artiodactyla
Walangania africanus

(2) Napak (Uganda)
The age of this fauna was determined as 19-25 Ma by K-Ar dating and as Faunal Set I by faunal assemblages and this fauna must have inhabited in subaerial environments deduced from sedimentological evidence (Bishop, 1962, 1967; Pickford, 1981). Faunal list of the Napak Fauna is as follows (Bishop, 1962, 1967).

Mammalia
Insectivora
Miohyncocyon clarki
Myohyrax oswaldi
Hiwagicyon juvenalis
Parageogale aletris
Protenrec tricuspis
Gymnuechinus leakeyi
Gymnuechinus camptolophus
Amphichinus rusingensis
Galerix africanus
Propotto leakeyi
Molossidae sp. nov.
Emballonuridae gen. et sp. indet.
Megalodermatidae gen. et sp. indet.
Komba minor
Komba robustus

Primates
Progaloago songhorensis
Mioeoticus sp.
Dendropithecus macinnesi
Limnopithecus legetet
Proconsul africanus
Proconsul nyanzae
Rangwapithecus gordonii
Nyanzapithecus vancouveringi

Rodentia
Kenyalagomys rusingae
Kenyalagomys minor
Paraphiomys pigotti
Paraphiomys stromeri
Epithiophius coryndoni
Elimerimys woodi
Diamantomys leuderitzi
Kenamys mariae
Simonimys genovefae
Myophiogus arambourgi
Plohelosphobius leakeyi
Paranomalurus simia
Paranomalurus walkeri
Megapedetes pentadactylus
Pedetidae gen. et sp. nov.
Protarsomys macinnesi
Vulcaniscius africanus
Teratodon enigmae
Pterodon nyanzae
Anasinopa leakeyi
Metapterodon kaiseri

Creodonta
Leakeytherium hiwagi
Hyenodon andrewsi
Hyenodon pilgrimi
Hecubides euryodon
Hecubides macrodon
Kichechia zamanae
Afrosmilus africanus

Tubulidentata
Myorycteropus africanus

Proboscidea
Prodeinotherium hobyi
Archaeobelodon sp.
Eozygodon morotoensis

Hyracoidea
Pachyhyrax championi
Prohyrax baetae

Perissodactyla
Chalicotherium rusingense
Dicerorhinus leakeyi
Aceratherium acutirostratum  
Brachypotherium heinzeli

Artiodactyla  
Hyoboops africanus  
Masritherium aequitorialis  
Diamantohyus africanus  
Libycochoerus jeanelli  
Kenyasus rusingensis  
Nguruwa kijivium  
Dorcatherium chappuisi  
Dorcatherium pigotti  
Dorcatherium parvum  
Canthumeryx sirtensis  
Propalaeoryx nyanzae  
Walangania africanus

(3) Koru (Kenya)

The age of this fauna was determined as Faunal Set I by faunal assemblages and this fauna must have inhabited in subaerial, apron of central volcano, and intermittent deposition with pedogenesis environments deduced from sedimentological evidence (Bishop, 1967; Pickford, 1981, 1986a). Faunal list of the Koru Fauna is as follows (Bishop, 1967).

Mammalia  
Insectivora  
Amphechinus rusingensis  
Erythrozootes chamerpes  
Prochrysochloris miocaenicus  
Rhynchocyon clarki  
Saccolaimus incognita

Primates  
Progalago sp.  
Limnopithecus legetet  
Proconsul africanus  
Proconsul nyanzae

Rodentia  
Teratodon spekei  
Hecubides euryodon

Proboscidea  
Deinotherium sp.

Perissodactyla  
Chalicotherium rusingense

Artiodactyla  
Dorcatherium songhorensis  
Palaeomeryx africanus

(4) Songhor (Kenya)

The age of this fauna was determined as Faunal Set I by faunal assemblages and this
fauna must have inhabited in subaerial, apron of central volcano, intermittent deposition with pedogenesis environments deduced from sedimentological evidence (Bishop, 1967; Pickford, 1981, 1986a). Faunal list of the Songhor Fauna is as follows (Bishop, 1967).

Mammalia
Insectivora
   *Rhynchocyon clarki*
   *Rhynchocyon rusingae*
   *Protenrec tricuspis*
   *Gymnuechinus songhorensis*
   *Amphechinus rusingensis*
   *Galerix africanus*
   *Prochrysochloris miocaenicus*

Primates
   *Progalago doriae*
   *Progalago robustus*
   *Progalago minor*
   *Limnopithecus legetet*
   *Limnopithecus macinnesi*
   *Proconsul africanus*
   *Proconsul nyanzae*
   *Proconsul major*

Rodentia
   *Paraphiomys pigotti*
   *Paraphiomys small form*
   *Diamantomys sp.*
   *Megapedetes pentadactylus*
   Pedetidae small form
   *Teratodon enigmae*
   *Teratodon spekei*
   *Bathyergoides sp.*
   *Cricetodon* sp.
   Anomaluridae large form
   Anomaluridae small form

Creodonta
   *Hyaenodon andrewsi*
   *Hyaenodon pilgrimi*
   *Hecubides matthewi*
   *Kichechia zamanae*

Carnivora
   *Metalurus africanus*
   *Hyotherium sp.*

Hyracoidea
   *Megalohyrax championi*
   *Myohyrax sp.*
   *Bunohyrax sp.*
Proboscidea
  *Gomphotherium* sp.
Perissodactyla
  *Chalicotherium rusingense*
Artiodactyla
  *Dorcatherium songhorensis*
  *Palaeomeryx africanus*

(5) Rusinga (Kenya)

The mean age of Rusinga Group was determined as 17.9 Ma (Hiwegi Formation: 16.9-34.5 Ma, Rusinga Agglomerate: 16.6-21.9 Ma, Kiahera Formation: 17.2-22.9 Ma) by K-Ar dating (Drake et al., 1988) and as Faunal Set II by faunal assemblages (Pickford, 1981). Faunal list of the Songhor Fauna is as follows (Drake et al., 1988).

Mammalia
Insectivora
  *Miohyncocyon clarki*
  *Myohyrax oswaldi*
  *Hiwagicyon juvenalis*
  *Parageogale aletris*
  *Protenrec tricuspis*
  *Gymnuechinus leakeyi*
  *Gymnuechinus camptolophus*
  *Amphechinus rusingensis*
  *Galerix africanus*
  *Propotto leakeyi*
  Molossidae sp. nov.
  Emballonuridae gen. et sp. indet.
  Megalodermatidae gen. et sp. indet.
  *Komba minor*
  *Komba robustus*

Primates
  *Progalago songhorensis*
  *Mioeuoticus* sp.
  *Dendropithecus macinnesi*
  *Limnopithecus legetet*
  *Proconsul africanus*
  *Proconsul nyanzae*
  *Rangwaphitecus gordoni*
  *Nyanzapithecus vancouveringi*

Rodentia
  *Kenyalagomys rusingae*
  *Kenyalagomys minor*
  *Paraphiomys pigotti*
  *Paraphiomys stromeri*
  *Epiphiomys coryndoni*
  *Elimerimys woodi*
Late Miocene Namurungule Fauna

Diamantomys leuderitzi
Kenyamys mariae
Simonimys genovefae
Myophiomys arambourgi
Plohelioptebius leakeyi
Paranomalurus soniae
Paranomalurus walkerii
Megapedetes pentadactylus
Pedetidae gen. et sp. nov.
Protarsomys macinnesi
Vulcanisciurus africanus
Teratodon enigmae
Pterodon nyanae
Anasinopa leakeyi
Metapterodon kaiseri
Leakeytherium hiwerg
Hyaenodon andrewsi
Hyaenodon pilgrimii
Hecubides euryodon
Hecubides macrodon
Kichechia zananae

Carnivora
Afrosmilus africanus

Tubulidentata
Myorycteropus africanus

Proboscidea
Prodeinotherium hobleyi
Archaebelodon sp.
Eozygodon morotoensis

Hyracoidea
Pachyhyrax championi
Prohyrax bateae

Perissodactyla
Chalicotherium rusingense
Dicerorhinus leakeyi
Aceratherium acutirostratum
Brachypotherium heinzelini

Artiodactyla
Hyoboops africanus
Masritherium aequitorialis
Diamantoxyus africanus
Libycochoerus jeaneUi
Kenyasus rusingensis
Nguruwa kijivium
Dorcatherium chappuisi
Dorcatherium pigotti
Dorcatherium parvum
Canthumeryx sirtensis
Propalaeoryx nyanzae
Walangania africana

(6) Karungu (Kenya)

The age of this fauna was determined as 17.5-17.7 Ma by K-Ar dating (Drake et al., 1988) and as Faunal Set II by faunal assemblages (Pickford, 1981). This fauna must have inhabited in lacustrine, lake margin and swamp, wet part of flood plain and large river system in volcanic arena deduced from sedimentological evidence (Pickford, 1981). Faunal list of the Karungu Fauna is as follows (Drake et al., 1988).

Mammalia
Primates
  Dendropithecus macinnesi
  Proconsul nyanzae
Rodentia
  ? Kenyalagomys rusingae
  Paraphiomys pigotti
  Paraphiomys stromeri
  Diamantomyx leuderitzi
  Anasinopa leakeyi
  Metapterodon kaiseri
  ? Kichechia zamanae
Carnivora
  Afrosmilus africanus
Tubulidentata
  Myorycteropus africanus
  Orycteropus minutus
Proboscidea
  Prodeinotherium hобleyi
  Archaeobelodon sp.
Hyracoidea
  Myohyrax oswaldi
  Pachyhyrax championi
  ? Prohyrax bateae
Perissodactyla
  Chalicotherium rusingense
  Dicerorhinus leakeyi
  Aceratherium acutirostratum
  Brachypotherium heinzeli
Artiodactyla
  Hyoboops africanus
  Masritherium aequitoralis
  Diamantoxyx africanus
  Libycochoerus jeanneli
  Kenyasus rusingensis
  Dorcatherium chappuisi
Late Miocene Namurungule Fauna

\[\textit{Dorcatheirium parvum}\]
\[? \textit{Canthumeryx sirtensis}\]
\[\textit{Propalaeoryx nyanzae}\]
\[\textit{Walangania africanus}\]

(7) Mfwangano (Kenya)

The age of this fauna was determined as 21.7 Ma (Kiahera Formation) by K-Ar dating (Drake et al., 1988). This fauna must have inhabited in subaerial, apron of central volcano, intermittent deposition with pedogenesis, and dry part of floodplain in volcanic arena deduced from sedimentological evidence (Pickford, 1981). Faunal list of the Kiahera Formation of the Mfwangano Fauna is as follows (Drake et al., 1988).

**Mammalia**

*Myohyrax oswaldi*
*Komba robustus*

**Primates**

*Dendropithecus macinnesi*
*
*Proconsul africanus*
*Proconsul nyanzae*

**Rodentia**

*Kenyalagomys rusingae*
*Paraphiomys pigotti*
*Paraphiomys stromeri*
*Diamantomys leuderitzi*
*Megapedetes pentadactylus*
*Hecubides euryodon*

**Proboscidea**

*Prodeinotherium hobleyi*

**Hyracoidea**

*? Pachyhyrax championi*

**Perissodactyla**

*Brachypotherium heinzelini*

**Artiodactyla**

*Masritherium aequitorialis*
*Kenyasus rusingensis*
*Nguruwa kijivium*
*Dorcatheirium pigotti*
*Propalaeoryx nyanzae*
*Walangania africanus*

(8) Buluk (Kenya)

The age of this fauna was determined as 17.3 Ma by K-Ar dating and as Faunal Set III by faunal assemblages. This fauna must have inhabited in a shallow or intermittent aquatic environments and interdistributary or behind-shore lagoon facies deduced from sedimentological evidence (Harris & Watkins, 1974; Pickford, 1981). Faunal list of the Buluk Fauna is as follows (Harris & Watkins, 1974).
Reptilia
Crocodylia
Crocodylidae
gen. et sp. indet.
Testudines
gen. et sp. indet.
Mammalia
Creodonta
gen. et sp. indet.
Proboscidea
*Platybelodon kisumuensis*
*Prodeinotherium hobleyi*
Hyracoidea
*Megalohyrax championi*
Perissodactyla
*Dicerorhinus* sp.
Artiodactyla
*Listriodon* sp.
(9) Kirimun (Kenya)

The age of this fauna was determined as 11.5-15 Ma by K-Ar and fission track dating and as Faunal Set III by faunal assemblages (Pickford, 1981). Sanithere and tragulid (Artiodactyla) indicates woodland environments (Kawamura & Nakaya, 1982; Pickford 1982; Matsuda et al., 1986). Faunal list of the Kirimun Fauna is as follows (Kawamura & Nakaya, 1982; Pickford, 1982).

Mollusca
Gastropoda
Ampullariidae
*Saulea lithoides*
Cyclophoridae
*Maizania lugubrioides*
Pomatiasidae
*Ligatella* sp.
Enidae
? *Edouardia* sp.
Achtinidae
*Burtoa cf. nilotica*
*Limicolaria* sp.
Pisces
fam., gen. et sp. indet.
Reptilia
Crocodylia
Crocodylidae
gen. et sp. indet.
Testudines
Testudinidae
Late Miocene Namurungule Fauna

-Mammalia
  -Rodentia
    -Thryonomyidae
      -Paraphiomys cf. pigotti
      -Paraphiomys sp.
    -Pedetidae
      -? Megapedetes sp.
    -Cricetodontidae
      -Afrocricetodon sp.
    -Carnivora
      -fam., gen. et sp. indet.
  -Proboscidea
    -Gomphotheriidae
      -gen. et sp. indet.
    -Deinotheriidae
      -? Prodeinotherium sp.
  -Hyracoidea
    -Procaviidae
      -gen. et sp. indet.
  -Perissodactyla
    -Rhinocerotidae
      -Brachypotherium heinzeli
  -Artiodactyla
    -Sanitheriidae
      -Sanitherium sp.
    -Tragulidae
      -Dorcatherium cf. pigotti
      -Dorcatherium sp.

(10) Ombo (Kenya)

The age of this fauna was determined as Faunal Set III by faunal assemblages and this fauna must have inhabited in lake margin, swamp, large river system in volcanic arena deduced from sedimentological evidence (Bishop, 1967; Pickford, 1981). Faunal list of the Ombo Fauna is as follows (Bishop, 1967).

-Mammalia
  -Primates
    -? Mesopithecus sp.
  -Creodonta
    -Hyaenodon sp.
    -Hyaenodon andrewsi
    -Pterodon nyanzae
    -Hyoboops (Merycops) africanus
  -Proboscidea
Gomphotherium sp.
Deinotherium sp.
Perissodactyla
  Rhinocerotidae
Artiodactyla
  Suidae
    Dorcatherium pigotti
  Tragulidae

(11) Maboko (Kenya)

The age of this fauna was determined as 12.5 Ma by K-Ar dating and as Faunal Set III by faunal assemblages (Pickford, 1981). This fauna must have inhabited in dry and wet part of floodplain in volcanic arena deduced from sedimentological evidence (Pickford, 1981). Faunal list of the Maboko Fauna is as follows (Bishop, 1967).

Mammalia
Primates
  Proconsul nyanzae
  Kenyapithecus africanus
  ? Mesopithecus sp.
  Anasinopa leakeyi
Hyracoidea
  Megalohyrax championi
Proboscidea
  Gomphotherium sp.
  Deinotherium sp.
Perissodactyla
  Rhinocerotidae
Artiodactyla
  Suidae
  Tragulidae
    Dorcatherium pigotti
    Dorcatherium chappuisi
    Dorcatherium parvum
    Brachyodus aequatorialis

(12) Aka Aiteputh (Kenya)

The age of this fauna was determined as 11.5-15 Ma by K-Ar dating and as Faunal Set III by faunal assemblages (Pickford & Kuga, in press). However, radiometric age indicate Faunal Set IV. Richness of Primates indicates woodland fauna. Faunal list of the Aka Aiteputh Fauna is shown in the previous chapter (p. 8-9).

(13) Fort Ternan (Kenya)

The age of this fauna was determined as 12.5-14 Ma by K-Ar dating and as Faunal Set IV by faunal assemblages (Pickford, 1981). Faunal list of the Fort Ternan Fauna is as follows (Bishop, 1967; Pickford, 1981).

Mammalia
Late Miocene Namurungule Fauna

Primates
   *Kenapithecus wickeri*
   ? *Proconsul nyanzae*
Cercopithecidae
Rodentia
   *Kenyamys leakeyi*
Carnivora
Proconsulidae
Artiodactyla
   Ruminants
   Suinae
   Giraffidae
   Hippopotamidae
      *Kenyapotamus ternani* (14) Ngorora (Kenya)
The age of this fauna was determined as 10.2-12.7 Ma by K-Ar dating and stratigraphic position (Chapman & Brook, 1978; Pickford, 1978a; Hill et al., 1985). This fauna represents Faunal Set V of the East Africa (Pickford, 1981). Faunal list of the Ngorora A-D Formation is as follows (Benefit & Pickford, 1986).

Mammalia
Primates
   Hominoidea large sp.
   Hominoidea small sp.
   Cercopithecoida indet.
Carnivora
   *Agotherium* sp.
   *Eomellivora* sp.
   *Sivaonyx* sp.
   *Percrocuta tobiieni*
   Canidae small sp.
Tubulidentata
   *Orycteropus chemeldoi*
Proboscidea
   *Choerolophodon ngorora*
   *Tetralophodon* sp.
   *Deinotherium* sp. cf. *bozasi*
Hyracoidea
   *Parapliohyrax* sp.
Perissodactyla
   *Chilotheridium pattersoni*
   *Aceratherium* or *Diceros rhinus*
   *Brachypotherium* cf. *lewisii*
Artiodactyla
   ? *Conohyus* sp.
Lopholistiodon kidogosana
Tayassuidae
Kenyapotamus coryndoni
Tragulidae
Dorcattherium cf. pigotti
Palaeotragus primaevus
? Samotherium sp.
Climacoceras gentryi
Protragocerus labidotus
Sivoreas eremita
Homidorcas tugenium
? Antidorcas sp.
Pseudotragus ? gentryi
Pachytragus aff. solignaci

(15) Ngorora upper E (Kenya)
The age of this fauna was determined as Faunal Set VI by faunal assemblages. Faunal list of the Ngorora upper E Formation is as follows (Benefit & Pickford, 1986).

Mammalia
Proboscidea
Choerolophodon ngorora
Hyracoidea
Parapliohydrax sp.
Perissodactyla
Hipparion primigenium
Artiodactyla
Kenyapotamus coryndoni
Palaeotragus primaevus
Pseudotragus ? gentryi

(16) Ngeringerowa (Kenya)
The age of this fauna was determined as Faunal Set VI by faunal assemblages (Benefit & Pickford, 1986). Faunal list of the Ngeringerowa Fauna is as follows (Benefit & Pickford, 1986).

Mammalia
Primates
Microcolobus tugenensis
Proboscidea
Deinotherium sp. cf. bozasi
Perissodactyla
Hipparion primigenium
Artiodactyla
Nyanzachoerus sp.
Kenyapotamus coryndoni
Palaeotragus primaevus
? Hippotraginae or ? Reduncini
Late Miocene Namurungule Fauna

(17) Nakali (Kenya)
The age of this fauna was determined as late Vallesian by correlation with Mediterranean mammalian fauna (Aguirre & Leakey, 1974; Aguirre & Guérin, 1974) and as Faunal Set VI by faunal assemblages (Benefit & Pickford, 1986). Nakali fauna is the nearest site of Namurungule fauna. Faunal list of the Nakali Formation is as follows (Benefit & Pickford, 1986).

Mammalia
Primates
Colobinae sp.
Proboscidea
? Choerolophodon ngorora
Deinotherium sp. cf. bozasi
Perissodactyla
Hipparion primigenium
Kenyatherium bishopi
Artiodactyla
Nyanzachoerus sp.
Kenyapotamus sp.
Tragulidae
Dorcatherium cf. pigotti
? Palaeotragus primaevus
? Hippotraginae or ? Reduncini

(18) Namurungule (Kenya)
The age of this fauna was determined as 7-10 Ma by K-Ar dating and stratigraphy and as the Turolian Fauna by faunal assemblages. Richness of equid and bovid taxa indicates openland fauna (Nakaya et al., 1984, in press). Faunal list of the Namurungule Formation is shown in the previous chapter (p. 9-11).

(19) Chorora (Middle Awash, Ethiopia)
The age of this fauna was determined as 9-10.5 Ma by radiometric dating. Faunal list of the Chorora Formation is as follows (Jacobs et al., 1980; Kalb et al., 1982a, 1982b, 1982c).

Mammalia
Rodentia
cf. Dendromurinae
Paraulacodus johanesi
Paraphiomys sp. 1
Paraphiomys sp. 2
Rodentia gen. et sp. indet.
Carnivora
Homotherium sp.
Proboscidea
Gomphotheriinae indet.
Perissodactyla

_Hipparchion cf. primigenium_
_Dicerorhinus (Stephanorhinus) aff. leakeyi_

Artiodactyla

Suiaae gen. et sp. indet.
?Palaeotraginae
Bovidae gen. et sp. indet.

(20) Mpesida (Kenya)
The age of this fauna was determined as about 7 Ma. and as Faunal Set VII by faunal assemblages (Benefit & Pickford, 1986). Faunal list of the Mpesida Formation is as follows (Gentry, 1978a).

Mammalia
Artiodactyla

Tragelaphini
Antilopini
?Alcelaphini
Bovidae indet.

(21) Lukeino (Kenya)
The age of the Member A of Lukeino Formation was determined as about 6.0-6.7 Ma and as Faunal Set VII by faunal assemblages (Benefit & Pickford, 1986). This fauna must have inhabited in lacustrine environments deduced from sedimentological evidence. Faunal list of the Member A and B of the Lukeino Formation is as follows (Pickford, 1978b; Gentry, 1978a).

Mammalia
Primates

Cercopithecidae
Hominidae
Lagomorpha

gen. et sp. indet.

Rodentia

_Hystrix_ sp.
gen. et sp. indet.

Carnivora

_Enhydrion_
cf _Ichneumia_ sp.
cf _Crocuta_
Felidae gen. et sp. indet.

Tubulidentata

_Orycteropus_ sp.

Proboscidea

_Anancus_ sp.
_Stegotetrabelodon_ sp.
_Primelephas_ sp.
_Deinotherium_ sp.
Late Miocene Namurungule Fauna

*Hipparion* cf. *sitifense*
*Chalicotheriidae*
cf. *Ceratotherium* sp.
*Nyanzachoerus tulotos*
*Hippopotamus* sp.
*Giraffa* sp.
*Tragelaphini*
*Reduncini*
*Hippotragini*
*Neotragini*
*Antilopini* cf. *Aepyceros*
*Gazella* sp.
*Cephalophini*
*Alcelaphini*

(22) Lothagam 1 (Kenya)
The age of this fauna was determined as before 3.7 Ma by K-Ar dating and stratigraphy and as Faunal Set VII by faunal assemblages (Benefit & Pickford, 1986). This fauna must have inhabited in fluvial environments deduced from sedimentological evidence (Behrensmeyer, 1976). Faunal list of the Lothagam 1 Formation is as follows (Smart, 1976).

**Mammalia**

**Primates**
cf. *Parapapio* sp.
cf. *Cercocebus* sp.
*Australopithecus* sp. cf. *africanus*

**Rodentia**
Anomaluridae (non gliding form)

**Carnivora**
*Civettictis* sp.
*Euryboa* sp.
Felinæ (large primitive form)
*Machairodontinae*

**Tubulidentata**
*Leptorycteropus guilielmi*

**Proboscidea**
Anancinae (primitive form)
*Primelephas gomphotheroides*
*Stegotetrabelodon orbis*
*Deinotherium* sp.

**Perissodactyla**
*Hipparion primigenium*
*Hipparion sitifense* (pygmy form)
*Hipparion turkanense*
*Brachypotherium lewisi*
*Ceratotherium praecox*
Artiodactyla

*Nyanzachoerus tulotos*
*Nyanzachoerus aff. jaegeri*
*Hippopotamus (Hexaprotodon) sp. A*
*Hippopotamus (Hexaprotodon) sp. B (pygmy form)*
*Giraffa sp.*
*Pachytragus aff. Hippotraginae*
*aff. Kobus sp.*
*aff. Redunca sp.*
*aff. Aepyceros sp.*
*aff. Damaliscus sp.*
*Hippotragini*
*Miotragocerus sp.*
*Tragelaphus sp. A*
*Tragelaphus sp. B*
*Gazella sp. A (large form)*
*Gazella sp. B (small form)*
*Antilope sp.*

Neotragini aff. *Rhynchotragus* sp.

(23) Adu-Asa (Middle Awash, Ethiopia)

The age of this fauna was determined as the latest Miocene to earliest Pliocene by radiometric age and stratigraphy (Kalb et al., 1982a). Faunal list of the Adu-Asa Formation is as follows (Kalb et al., 1982a, 1982b, 1982c).

Mammalia
Chiroptera indet.
Primates

*cf. Paracolobus chemeroni*
Colobinae indet. (Kuseralee type)
Rodentia gen. et sp. indet.
Carnivora
Felidae gen. et sp. indet.
Hyenaenidae gen. et sp. indet.
Carnivora gen. et sp. indet.
Proboscidea

*Anancus sp. A (cf. Lothagam type)*
*Anancus sp. B (cf. kenyensis )*
*Stegotetrabelodon cf. orbus*
*“Stegodibelodon” schneideri*
*Primelephas cf. gomphotheroides*
*aff. “Mammuthus subplanifrons”*
*Deinotherium sp. (small)*

Perissodactyla

*Hipparion cf. primigenium*
*Hipparion sp.*
*Diceros bicornis*
*Ceratherium* cf. *praecox*

Artiodactyla

*Nyanzachoerus* *kanamensis*
*Nyanzachoerus* cf. *tulotos*
*Kolpochoerus* sp. A
*Hexaprotodon* sp. (large)
*Sivatherium maarusium*
Giraffidae gen. et sp. indet.
*Miotragocerus* sp.
*Kobus* cf. *subdolus*
*Tragelaphus* sp. (cf. Lothagam type)
*Tragelaphus* af. *nakuae*
cf. *Gazella* sp.
cf. *Ugandax gautieri.*
cf. *Mesembriportax acrae*
Boselaphini indet.
Reduncini indet.
Hippotragini indet.
Alcelaphini indet.

Bovidae indet.

(24) Sagantole (Middle Awash, Ethiopia)

The age of this fauna was determined as the early Pliocene by radiometric age and stratigraphy (Kalb et al., 1982a). Faunal list of the Sagantole Formation is as follows (Kalb et al., 1982a, 1982b, 1982c)

Mammalia

Primates

*Cercopithecus* sp.
cf. Papionini indet.(small)
*Parapapio* sp.
*Theropithecus oswaldi* cf. *darti*

Rodentia gen. et sp. indet.

Carnivora indet.

Proboscidea

*Anancus* sp. B (cf. *kenyensis*)
*Anancus* sp. C (aff. *kenyensis*)
*Anancus* sp. D (sp. nov.)
*Mammuthus subplanifrons*
*Mammuthus* sp. nov. (Hadar type)
*Elephas* cf. *ekorensis*
*Loxodonta adaurora*
*Deinotherium bozasi*

Perissodactyla

*Hipparion* sp.

Rhinocerotidae gen. et sp. indet.

Artiodactyla
Nyanzachoerus kanamensis
Nyanzachoerus jaegeri
Kolpochoerus afarensis
Notochoerus cf. eulis
Hexaprotodon sp. (large)
Sivatherium maursium
Miotragocerus sp.
Kobus cf. subdolus
Tragelaphus aff. nakuae
Boselaphini indet.
Hippotragini indet.
Alcelaphini indet.
Bovidae indet.

(25) Ekora (Kenya)
The age of this fauna was determined as 2.5-4 Ma by K-Ar dating. Faunal list of the Ekora Formation is as follows (Behrensmeyer, 1976).

Mammalia
Proboscidea
Anancus sp.
Elephas ekorensis
Loxodonta adauros
Perissodactyla
Ceratotherium praecox
Artiodactyla
Nyanzachoerus cf. plicatus

(26) Kanapoi (Kenya)
The age of this fauna was determined as 2.5-4 Ma by K-Ar dating. This fauna must have inhabited in transitional (littoral, deltaic) environments deduced from sedimentological evidence. Faunal list of the Kanapoi Formation is as follows (Behrensmeyer, 1976).

Mammalia
Primates
Parapapio jonesi
cf. Australopithecus
Lagomorpha
Lepus sp.
Rodentia
Hystrix sp.
Tatera sp.
Carnivora
Enhydriodon sp. nov.
Hyaena sp.
Machairodontinae indet.
Proboscidea
Late Miocene Namurungule Fauna

Anancus sp.
Elephas ekorensis
Loxodonta adaurora
Deinotherium bozasi

Perissodactyla
Hipparion primigenium
Ceratotherium praecox

Artiodactyla

Nyanzachoerus pattersoni
Nyanzachoerus plicatus
Nyanzachoerus spp.
Notochoerus cf. capensis
Notochoerus cf. euilus
Hippopotamus sp. nov.
Giraffa sp. nov.
Giraffa sp.
Tragelaphus sp.
Reduncini sp.

(27) Lothagam 3 (Kenya)

The age of this fauna was determined as after 3.7 Ma by K-Ar dating and stratigraphy and as Faunal Set VIII by faunal assemblages (Benefit & Pickford, 1986). This fauna must have inhabited in fluvial environments deduced from sedimentological evidence. Faunal list of the Lothagam 3 Formation is as follows (Behrensmeyer, 1976).

Mammalia
Primates
Simopithecus sp.

Proboscidea
Loxodonta adaurora
Deinotherium bozasi

Perissodactyla
Hipparion (Stylohipparion) sp.

Artiodactyla

Nyanzachoerus plicatus
Notochoerus cf. euilus
Hippopotamidae indet.
Tragelaphus sp.
Bovidae indet.

(28) Laetoli (Tanzania)

The age of this fauna was determined as 3.49-4.32 Ma by K-Ar dating (Drake & Curtis, 1987). In the upper Laetoli Beds, grass pollen predominates (50-80%) over that of the composite. This palynological evidence indicates short or medium grassland (Bonnefille et al., 1987). Faunal list of the Laetoli Bed is as follows (Leakey & Harris eds., 1987).
Reptilia
Testudinidae
  *Geochelone (Aldabrachelys) laetoliensis*
  *Geochelone (Geochelone) brachygularis*
Serpentes
Boidae
  *Python sebae*
Colubridae
cf. *Rhamphiophis* sp.
Elapidae
  *Naja robusta*
Viperidae
  *Bitis arietans* or *oldtuvaiensis*
Aves
Falconiformes
  *Torgos* sp.
Galiformes
  *Francolinus* spp.
  *Numida* sp.
Columbiformes
  *Streptopelia* sp.
Strigiformes
  *Bubo* sp.
Mammalia
Macroscelidea
  Macroscelididae
    *Rhynchocyon plioicaenicus*
Insectivora
  Soricidae
    ? *Crocidura* sp.
Primates
  Lorisidae
    *Galago sadimanensis*
Cercopithecidae
  *Parapapio ado*
  cf. *Papio* sp.
  cf. *Paracolobus* sp.
  Colobinae gen. et sp. indet.
Hominidae
  *Australopithecus afarensis*
Rodentia
Sciuridae
  *Paraxerus* sp.
  *Xerus* sp.
  *Xerus* cf. *janenschii*
Cricetidae
  Gerbillinae gen. et sp. indet.
Late Miocene Namurungule Fauna

Tatera cf. inclusa
Dendromus sp.
Steatomys sp.
Saccostomus major

Muridae
Thallomys laetolilensis
Mastomys cinereus
Muridae gen. et sp. indet.

Bathyergidae
Heterocephalus quenstedti

Hystricidae
Hystrix leakeyi
Hystrix cf. makapanensis
 Xenohystrix crassidens

Lagomorpha
Pedetidae
Pedetes laetoliensis
Pedetes cf. surdaster

Leporidae
Serengetilagus praecapensis

Carnivora
Viverridae
Herpestes (Galerella) palaeoserengetensis
Herpestes (Herpestes) ichneumon
Helogale palaeogracilis
? Cynictis sp.
Mungos dietrichi
Viverra leakeyi

Mustelidae
Propoeicologale bolti
Mellivora capensis

Canidae
? Megacyon sp.
aff. Canis brevirostris
Vulpes sp.
cf. Otocyon sp.
Canidae gen. et sp. indet.

Hyaenidae
Crocuta sp. nov.
Hyaenidae spp.

Felidae
Homotherium sp.
Dinofelis sp.
Leo aff. gombazagensis or palaeosinensis
Leo cf. pardus
Felis spp.
Felidae gen. et sp. indet.
Proboscidea
  Elephantidae
    *Loxodonta exoptata*
  Deinotheriidae
    *Deinotherium bozasi*

Tubulidentata
  Orycteropodidae
    *Orycteropus* sp.

Perissodactyla
  Equidae
    *Hipparion* cf. *ethiopicum*
    *Hipparion* sp.
  Chalicotheriidae
    *Ancylotherium hennigi*
  Rhinocerotidae
    *Cetatherium praecox*
    *Diceros bocornis*

Artiodactyla
  Suidae
    *Notochoerus euilus*
    *Potamochoerus porcus*
    *Kolpochoerus limnetes*
  Giraffidae
    *Giraffa stillei*
    *Giraffa jumae*
    *Giraffa* cf. *jumae*
    *Sivatherium maurusium*
    *Sivatherium* cf. *maurusium*
  Camelidae
    *Camelus* sp.
  Bovidae
  Tragelaphini
    *Tragelaphus* sp.
  Bovini
    *Simatherium kohllarseni*
    *Brabovus nanincisus*
  Hippotragini
    *Praedamalis deturi*
    ? Hippotragini sp. nov.
  Alcelaphini
    *Parmularius pandatus*
    Alcelaphini sp. indet.
  Neotragini
    *Madoqua avifluminis*
    ? *Raphicerus* sp.
  Antilopini
    *Gazella janenschii*
Tribe et gen. indet. aff. *Pelea* sp.
Bovidae indet.

(29) Langebaanweg (South Africa)
The age of the Verswater Formation in ‘E’ Quarry, Langebaanweg was determined as 4-6 Ma by faunal assemblage and stratigraphy. Marine to Littoral (Bed 1), Estuarine and Terrestrial (Bed 2) and Estuarine (Bed 3) environments were shown by sedimentological evidence. Marine invertebrates and shark teeth were yielded in the phosphate of the Bed 1. This fauna must have inhabited in Marine (Bed 1) and Estuarine (Bed 2 and 3) Faunal Units (Hendey, 1974). Faunal list of the Verswater Formation is as follows (Boné & Singer, 1965; Hendey, 1974; Gentry, 1980).

Mollusca

*Trigonephrus* sp.

Selachii

*Isurus* cf. *glaucus*

*Lamna nasus*

*Carcharias* sp.

*Carcharias ferox*

*Rhinoptera* cf. *dubia*

*Glopias vulpes*

Reptilia

cf. *Testudo* sp.

Aves

cf. *Struthio* sp.

Mammalia

Insectivora

*Elephantulus* sp.

*Soricidae* spp.

*Chrysochloris* sp.

Primates

cf. Cercopithecidae

Rodentia

Muridae spp.

Bathyergidae spp.

Lagomorpha

gen. et sp. indet.

Pholidota

cf. *Manis* sp.

Tubulidentata

*Orycteropus* sp.

Carnivora

Phocidae

*Prionodelphis capensis*

Ursidae

*Agriotherium africanum*

Viverridae
**Herpestes spp.**  
**Viverra leakeyi**  
**Genetta sp.**

**Mustelidae**  
*Mellivora aff. punjabiensis*  
*Enhydriodon africanus*

**Canidae**  
Canidae gen. et sp. indet.

**Hyaenidae**  
*Percrocuta australis*  
*Hyaena abronia*  
*Hyaena sp. B*  
*Hyaenictis prelorfex*  
Hyaenidae gen. et sp. indet.

**Felidae**  
*Machairodus sp.*  
*cf. Homotherium sp.*  
*Dinofelis diastemata*  
*Felis aff. issiodorensis*  
*Felis obscura*

**Cetacea**  
fam. gen. et sp. indet.

**Hyracoidea**  
*cf. Procavia antiqua*

**Proboscidea**  
Gomphotheriidae  
Elephantidae  
*Mammuthus subplanifrons*

**Perissodactyla**  
Equidae  
*Hipparion albertense baardi*  
Rhinocerotidae  
*Cetatotherium praecox*

**Artiodactyla**  
Suidae  
*Nyanzachoerus sp.*  
*aff. Diamantohyus*  
*Libytherium oldvaiense*

**Giraffidae**  
*Giraffa gracilis*

**Bovidae**  
Tragelaphini  
*Tragelaphus spp.*  
Bovini  
*Simatherium demissum*

**Boselaphini**  
*Mesembriportax acrae*
Reduncini

*Kobus subdolus*

*Kobus* spp.

Alcelaphini

*Damalacra neanica*

*Damalacra acalla*

Neotragini

*Raphicerus partalius*

Antilopini

*Gazella* sp.

Ovibovini gen. et sp. indet.

**DISCUSSION**

### I. Statistical Analysis of Faunal Resemblance between Sub-Saharan Africa and Eurasia

The faunal resemblance of mammalian faunas of Sub-Saharan Africa and Eurasia is analyzed in this chapter.

Mammal provinces of Miocene Africa and Eurasia were divided into five areas (Africa, Iberian, Europe, West Asia and India) by Coryndon & Savage (1973) and Bernor (1983, 1984) proposed eight provinces (Southwest Europe, East and Central Europe, Roumania-West C.I.S., Sub-Paratethys, North Africa, Siwalik, East Africa and China). In this work, mammalian provinces are followed largely the scheme of Bernor (1983, 1984). East African province (Bernor, 1983, 1984) is the same as Sub-Saharan, and Roumania-West C.I.S. (Bernor, 1983, 1984) province is included in Sub-Paratethys in this work.

Previous researchers emphasized the Miocene faunal connection between Sub-Saharan Africa and Siwaliks (general: Coryndon & Savage, 1973; Bovidae: Thomas, 1979, 1981; Hipparionine: Bernor & Hussain, 1985). However, it has been pointed out that the discussion of connection between Sub-Saharan Africa and Siwaliks is based largely on fragmental remains from the middle to late Miocene Sub-Saharan sites. The following discussion of the biogeography between Sub-Saharan and Eurasia is based on new and rich mammalian fossils from the late Miocene Namurungule Formation, Samburu Hills, Northern Kenya.

Statistical approaches are very useful for analyzing the resemblance of faunas. Simpson’s formula is simple and useful for analyzing resemblance between two faunal...
assemblages. This index is dividing the common taxa numbers by the total taxa numbers of smaller fauna. Cluster analysis is also useful for multivariant analysis between faunas of Sub-Saharan Africa and Eurasia. In this thesis, the author analyzed species, genera and families of Sub-Saharan Africa and Eurasian faunas by Simpson's Index and genera and families of the same area by cluster analysis. Because subfamily and tribe are not mainly used in classification except Rhinocerotidae (Perissodactyla) and Bovidae (Artiodactyla) in both statistic methods and common taxa are very few in the specific level for using cluster analysis.

Over 500 taxa from the following mammalian fauna are analyzed by Simpson's Index (Simpson, 1960) and cluster analysis (Tanaka et al., 1984).

Namurungule (early Turonian, Samburu Hills, Kenya), Aka Aiteputh (Astaracian, Samburu Hills, Kenya), Kongia (late Turonian, Samburu Hills, Kenya), Ngorora (Vallesian, Baringo Basin, Kenya), Ngorora upper E (early Turonian, Baringo Basin, Kenya), Ngeringerowa (early Turonian, Baringo Basin, Kenya), Nakali (early Turonian, Baringo Basin, Kenya), Mpesida (late Turonian, north Baringo Basin, Kenya), Lukeino (late Turonian, north Baringo Basin, Kenya), Bou Hanifia (late Vallesian, Algeria), Sahabi (Turonian, Libya), Eppelsheim (late Vallesian, West Germany), Dorn-Dürkheim (late Turonian, West Germany), Mt. Lebérón (early Turonian, France), Pikermi (middle Turonian, Greece), Maragheh (Turonian, Iran), Samos (early to middle Turonian Greece), Chinji (Astaracian, Pakistan), Nagri (late Vallesian or early Turonian, Pakistan), Dhok Pathan (late Turonian, Pakistan), Baode (early Turonian, Shanxi, China), Yushe Zone I (late Turonian, Shanxi, China) (Table 2).

Faunal resemblance is analyzed by various statistic methods. Faunal resemblance of two faunas is calculated by the following formulas (Shuey et al., 1978).

1. Jaccard
   \[ \frac{C}{N_A+N_B-C} \]

2. Burt-Pilot
   \[ \frac{2C}{N_A+N_B} \]

3. Kulczynski
   \[ \frac{C(N_A+N_B)}{2N_A N_B} \]

4. Otsuka
   \[ \frac{C}{\sqrt{N_A N_B}} \]

5. Simpson
   \[ \frac{C}{N_1} \]

6. Braun-Blaunquet
   \[ \frac{C}{N_2} \]

C is common taxa number of two faunas, NA is total taxa number of A Fauna, NB is
total taxa number of B Fauna, \( N_1 \) is total taxa number of smaller fauna, \( N_2 \) is total taxa number of larger fauna.

Simpson's formula is the simplest and has little influence of sample size and emphasizes faunal resemblance (Simpson, 1960). Simpson's Index is shown on percentage:

\[
\frac{C \times 100}{N_1}
\]

The author examined faunal resemblance of each two faunas by Simpson's index. In the specific level, the Namurungule Fauna indicates the resemblance to the following East and North African faunas; Nakali (50%), Ngorora upper E (33.33%), Ngeringerowa (33.3%), Lukeino (33.3%), and Bou Hanifia (33.33%) (Table 4). In the generic level, the Namurungule Fauna indicates the resemblance to the following faunas of East and North Africa and Sub-Paratethys; Nakali (75%), Ngorora upper E (57.14%), Ngeringerowa (55.56%), Bou Hanifia (50%) and Samos (44.44%), Mpesida (40%) (Table 5). In the family level, the Namurungule Fauna indicates the resemblance to the following faunas of East and North Africa and Southwestern and Central Europe; Bou Hanifia (100%), Ngorora upper E (85.71%), Mt. Lebérion (83.33%), Eppelsheim (83.33%) and Mpesida (80%) (Table 6).

The reciprocal number of Simpson's index (\( N_1/C \)) is used for showing the dissimilarity on the group average method of cluster analysis (by CLUST program, Tanaka et al., 1984). In the case that Simpson's index is zero, the dissimilarity is uncountable. Therefore, analysis of all faunas in the case of species and the Aka Aiteputh and Dorn-Dürkheim faunas in the case of genera are omitted from the cluster analysis. In the generic level, the Namurungule and only East African faunas make large cluster (Nakali; firstly, Ngorora upper E; secondly, Ngorora and Ngeringerowa; thirdly) (Fig. 10). The Namurungule, East and North African and west European faunas make large cluster (Bou Hanifia; firstly, Nakali, Mt. Lebérion and Sahabi; secondly) in family level (Fig. 11). Using the raw data of Sub-Saharan and Eurasian faunas, faunal resemblance of each fauna was examined by group average method in cluster analysis on the basis of dissimilarity of Minkowsky distance (by CLUST program, Tanaka et al. eds., 1984). In the generic level, the Namurungule and East (Aka Aiteputh, Kongia, Ngorora E, Ngeringerowa, Nakali, and Lukeino) and North African (Bou Hanifia) and South-Western European (Mt. Lebérion) faunas make first large cluster and Dorn-Dürkheim faunas make next large cluster (Fig. 12). In the family level, the Namurungule and Eppelsheim faunas make first cluster, Lukeino faunas make next cluster, and Kongia, Mpesida, Bou Hanifia, Mt. Lebérion, Ngorora E, Ngeringerowa, Nakali and Dhok Pathan faunas make next large cluster (Fig. 13).

The Namurungule Fauna resembles faunas of Astaracian to late Turolian East Africa firstly, late Vallesian to Turolian North African faunas secondly, late Vallesian to Turolian Central and Southwest European faunas thirdly, early to middle Turolian Sub-Paratethys fauna and late Turolian Siwalik fauna lastly. On the basis of the above results, the Namurungule Fauna indicates similarity with the faunas of North Africa, South Western Europe and Sub-Paratethys.
Table 4. Faunal resemblance of the Namurungule Fauna, African and Eurasian faunas in specific level by the Simpson's index.

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Note: NM; Namurungule, AA; Aka Aiteputh, KG; Kongia; NG; Ngorora, NE; Ngorora upper E, NW; Ngeringerowa, NK; Nakali, LK; Lukeino, MP; Mpesida, SB; Sahabi, BH; Bou Hanifia, ML; Mt. Lebérón, EP; Eppelsheim, PK; Pikermi, SM; Samos, MG; Maragheh, CJ; Chinji, NR; Nagri, DP; Dhok Pathan, BD; Baode, YS; Yushe, DD; Dorn-Dürkheim. Total number of taxa is put in parentheses.
Table 5. Faunal resemblance of the Namurungule Fauna, African and Eurasian faunas in generic level by the Simpson's index.

|   | NM | AA | NG | NE | NW | NK | LK | MP | SB | BH | ML | EP | PK | SM | MG | CJ | NR | DP | BD | YS | DD |
|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
|   | NM NM(18) | 1 | 5 | 4 | 5 | 6 | 4 | 2 | 5 | 2 | 2 | 4 | 7 | 8 | 7 | 3 | 4 | 2 | 6 | 5 | 3 |
| AA | 8.333 AA(12) | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| NG | 33.33 | 25 NG(28) | 5 | 7 | 3 | 1 | 2 | 1 | 1 | 3 | 5 | 7 | 10 | 6 | 9 | 1 | 9 | 3 | 5 | 6 | 1 |
| NE | 57.14 | 0 NE(7) | 4 | 5 | 2 | 1 | 1 | 1 | 1 | 2 | 4 | 5 | 3 | 2 | 3 | 1 | 2 | 2 | 2 | 1 |
| NW | 55.56 | 11.11 NW(9) | 5 | 3 | 1 | 2 | 2 | 2 | 3 | 6 | 7 | 4 | 3 | 3 | 2 | 2 | 2 | 3 | 1 |
| NK | 75 | 0 NK(8) | 3 | 1 | 2 | 2 | 2 | 2 | 5 | 5 | 4 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 1 |
| LK | 26.67 | 0 LK(15) | 3 | 4 | 1 | 1 | 1 | 2 | 5 | 6 | 3 | 3 | 4 | 3 | 2 | 3 | 1 |
| MP | 40 | 0 MP(5) | 3 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 1 |
| SB | 27.78 | 0 SB(34) | 2 | 5 | 3 | 10 | 10 | 10 | 5 | 5 | 3 | 3 | 1 | 2 |
| BH | 50 | 0 BH(4) | 3 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 3 | 2 |
| ML | 20 | 0 ML(10) | 5 | 6 | 5 | 4 | 3 | 2 | 2 | 2 |
| EP | 22.22 | 8.333 EP(18) | 7 | 5 | 2 | 9 | 9 | 5 | 3 | 4 | 3 |
| PK | 38.89 | 0 PK(56) | 37 | 22 | 10 | 9 | 5 | 11 | 11 | 6 |
| SM | 44.44 | 8.333 SM(58) | 26 | 10 | 13 | 7 | 14 | 10 | 6 |
| MG | 38.89 | 0 MG(34) | 6 | 6 | 3 | 11 | 7 | 3 |
| CJ | 16.67 | 38.33 CJ(50) | 30 | 12 | 5 | 4 |
| NR | 22.22 | 8.333 NR(62) | 19 | 7 | 7 | 2 |
| DP | 11.11 | 8.333 DP(21) | 5 | 4 |
| BD | 33.33 | 0 BD(35) | 18 | 3 |
| YS | 27.78 | 0 YS(34) | 2 |
| DD | 16.67 | 0 DD(27) | 11.11 | 7.407 | 0.00 | 16.67 | 22.22 | 22.22 | 11.11 | 0 | 7.407 | 0 | 11.11 | 7.407 |

Note: NM; Namurungule, AA; Aka Aiteputh, KG; Kongia, NG; Ngorora, NE; Ngorora upper E, NW; Ngeringerowa, NK; Nakali, LK; Lukeino, MP; Mpesida, SB; Sahabi, BH; Bou Hanifia, ML; Mt. Leberon, EP; Eppelsheim, PK; Pikermi, SM; Samos, MG; Maragheh, CJ; Chinji, NR; Nagri, DP; Dhok Pathan, BD; Baode, YS; Yushe, DD; Dorn-Dürkheim. Total number of taxa is put in parentheses.
Table 6. Faunal resemblance of the Namurungule Fauna, African and Eurasian faunas in family level by the Simpson’s index.

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Note: NM; Namurungule, AA; Aka Aiteputh, KG; Kongia, NG; Ngorora, NE; Ngorora upper E, NW; Ngeringerowa, NK; Nakali, LK; Lukeino, MP; Mpesida, SB; Sahabi, BH; Bou Hanifia, ML; Mt. Lebéron, EP; Eppelsheim, PK; Pikermi, SM; Samos, MG; Maragheh, CJ; Chinji, NR; Nagri, DP; Dhok Pathan, BD; Baode, YS; Yushe, DD; Dorn-Dürkheim. Total number of taxa is put in parentheses.
Fig. 10. Dendrogram by the cluster analysis on the basis of the faunal dissimilarity of the Namurungule Fauna, African and Eurasian faunas (in generic level by the reciprocal number of Simpson's index).


Fig. 11. Dendrogram by the cluster analysis on the basis of the faunal dissimilarity of the Namurungule Fauna, African and Eurasian faunas (in family level by the reciprocal number of Simpson's index).
Fig. 12. Dendrogram by the cluster analysis on the basis of taxa of the typical Astaracian to Turolian African and Eurasian faunas (in generic level by Minkowsky’s distance).

Fig. 13. Dendrogram by the cluster analysis on the basis of taxa of the typical Astaracian to Turolian African and Eurasian faunas (in family level by Minkowsky’s distance).
### Table 7. Range chart of mammalian faunas from the Neogene Sub-Saharan Africa.

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II. Faunal Change of the Late Miocene Sub-Saharan Africa

In this chapter, the author analyzes faunal change of the Neogene mammalian faunas in Sub-Saharan Africa and establishes the position of the faunal turnover in Neogene Sub-Saharan Africa to the Namurungule Fauna.

In faunal change of late Miocene East Africa, Maglio (1978) reviewed patterns of faunal evolution of Africa. According to Maglio (1978), the rate of endemism is constant through the Cenozoic Era, the rate of turnover has two peaks (from Eocene to early Miocene and Pliocene) in the Cenozoic Era and the rate of extinction decreased constantly by genera through Neogene in the Africa. Savage & Russell (1983) also studied faunal turnover in Europe and North America during Cenozoic Era. They examined the number of total, standing, first appearing, disappearing and running mean on the genera and family.

In this work, the first and last appearances of mammalian taxa from the Neogene Sub-Saharan Africa are considered in detail. The "Half-life" of fauna is analyzed in each order of mammals and each faunal set (mammalian stage in Sub-Saharan Africa). Furthermore, the faunal turnover of Sub-Saharan mammal through late Miocene is discussed.

Table 7 shows range of the first appearance and last appearance of mammalian taxa (mainly species and genera of large mammals) from Neogene Sub-Saharan Africa.

Figure 14 is the numbers of the first, last appearance and total taxa in each faunal set. The number of the first appearance line has two peaks. The first peak (Set IV) indicates the appearance of the new Astaracian taxa. The second peak (Set VII) shows the appearance of the Pliocene taxa. The intermediate zone between two peaks (Set V and VI) also shows the appearance of the new late Miocene taxa. The number of the last appearance line has one broad peak. This peak (Set IV to VI) indicates constant extinction from the Astaracian to Turolian. The first and second peak of first appearance is comparable to the broad peak of the last appearance. The number of total taxa has one peak (Set IV). This peak shows rich faunal assemblage of the intermediate zone of old and new faunas in Miocene.

Figure 15 is the percentage of the first and last appearance of taxa by total taxa of each faunal set. The percentage of the first appearance has three peaks; the first peak (Pre Set I and Set I) indicates the first diversity of the Neogene fauna in the Sub-Saharan Africa, the second peak (Set IV) shows the diversity of middle Miocene fauna after the extinction of early Miocene taxa and the third peak (Set VII) indicates the diversity of late Miocene fauna after the extinction of middle Miocene taxa. The percentage of the last appearance shows one broad peak. The beginning of the peak (Set IV) indicates the extinction of many early Miocene taxa, the middle of the peak (Set V) shows the extinction of many early to middle Miocene taxa. The maximum of the peak indicates the extinction of almost all middle Miocene and some early late Miocene taxa. The second and third peak of first appearance is comparable to the broad peak of the last appearance. There is large gap of faunal turnover between Faunal Set III and IV. It is evident that this gap indicates some paleoenvironmental change.
Fig. 14. Number of the total, first appearance and last appearance mammalian taxa of each Faunal Set from the Neogene Sub-Saharan Africa.

Fig. 15. Percentage of the first appearance and last appearance mammalian taxa by total taxa of each Faunal Set from the Neogene Sub-Saharan Africa.
Table 8. Half-life of the total taxa of the mammalian faunas from the Neogene Sub-Saharan Africa.

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Result of "Half-life" analysis to total taxa.

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<th>Next</th>
<th>Average</th>
<th>Half-life</th>
<th>HL Av.</th>
<th>Mean Long.</th>
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Note: Left upper table shows number of first and last appearance of total taxa. Left lower table shows cumulate number of first and last appearance of total taxa. Right upper table shows the result of calculation of "Half-life" in previous and next stage and average of each stages. HL; half-life, FA; first appearance, LA; last appearance, Long.; longevity, Av.; average.
In the next faunal analysis, the author examines half-life of fauna in Neogene Sub-Saharan Africa. Late Professor Björn Kurten of University of Helsinki proposed "Half-life" concept (Kurten, 1959, 1972, 1988). Following Kurten, the half-life is based on the distribution by first and last appearances of taxa during unit stage, and is calculated by the cumulative distribution showing the total number of taxa, belonging to different temporal strata, present at a given time. The average percentage of previous-stages and next-stage taxa in a given fauna is obtained. The results happen to be identical in this case, but this is not always the case. A weighted mean percentage is obtained. The half-life, expressed with the local age as a unit is calculated. Weighted mean percentages for temporal strata in faunas two stages apart are obtained in analogous way. The half-life is calculated on this basis. In this case, three-stages survival could be used to check the estimates based on one and two-stage survival, and the author repeated the same calculation until stage that reveals no survival. The half-life of fauna is different on the basis of taxa, space and time. The author calculate the half-life and mean longevity of fauna based on taxa and faunal sets.

In the case of half-life of fauna based on taxa, half-life of total taxa is 1.43 (Faunal set) stage (2.70 Ma) (Table 8), Proboscidea is 1.99 stage (3.75 Ma), Perissodactyla is 1.79 stage (3.38 Ma), Carnivora (including Creodonta) is 1.52 stage (2.87 Ma), Artiodactyla is 1.48 stage (2.79 Ma), Primates is 1.30 stage (2.46 Ma), Hyracoidea is 1.52 stage (2.88 Ma), Rodentia is 2.53 stage (4.77 Ma).

Rodentia has the longest half-life of fauna, but this sample consists of only two taxa. These taxa were added in the Namurungule Fauna. Therefore the half-life of Rodentia is not discussed. Hyracoidea also consists of two taxa, therefore the half-life of this taxon is not discussed in this work. The half-life of Primates (2.46 Ma) is the shortest in the taxa of the Sub-Saharan Africa. Proboscidea (3.75 Ma) has the longest half-life in large mammal (Fig. 16). Kurten (1972) estimated specific half-life during the Cenozoic Era. In Miocene to early Pleistocene, Proboscidea (2.4 Ma) has the longest half-life and Carnivora (1.6 Ma) has the shortest half-life. The value of half-life of Sub-Saharan Africa is longer than Kurten's result. This result is based on the difference of area and taxonomic hierarchy. Because taxonomic hierarchy is used in not only species but also genera in the case of Sub-Saharan Africa. Furthermore, the faunal half-life of taxa from Sub-Saharan Africa seems to be more stable than that from Eurasia.

In the case of half-life of fauna based on each faunal set (stage), half-life of total taxa of Pre-Set I is 3.93 (Faunal Set) stage (7.4 Ma), Set I is 2.82 stage (5.3 Ma), Set II is 2.43 stage (4.6 Ma), Set III is 2.17 stage (4.1 Ma), Set IV is 1.70 stage (3.2 Ma), Set V is 1.62 stage (3.1 Ma), Set VI is 1.66 stage (3.1 Ma), Set VII is 1.56 stage (2.9 Ma) and Set VIII is 1.56 stage (2.9 Ma). The half-life of total taxa on each faunal set decreases to set III and is constant from set IV to VIII in Neogene of Sub-Saharan Africa (Fig. 17). This result indicates large gap of faunal turn over between Faunal Set III and IV and the increasing of the faunal stability after Faunal Set IV (Astaracian) in Sub-Saharan Africa.

The rise and fall of the total taxa of each Faunal Set from the Neogene Sub-Saharan Africa on the basis of half-life is examined. The following diagram shows the rising and falling curve by a logarithmic scale of each faunal set (Fig. 18). The inclination of rising
curve is changed to steeper between Faunal Set III and IV. It indicates that the rate of faunal turnover is increased after Faunal Set IV (Astaracian).

![Bar chart showing half-life of total and each taxa of mammalian faunas from the Neogene Sub-Saharan Africa.](image1)

**Fig. 16.** Half-life of the total and each taxa of the mammalian faunas from the Neogene Sub-Saharan Africa.

![Line graph showing half-life of the total taxa of the mammalian faunas from each Faunal Sets of the Neogene Sub-Saharan Africa.](image2)

**Fig. 17.** Half-life of the total taxa of the mammalian faunas from each Faunal Sets of the Neogene Sub-Saharan Africa.
Fig. 18. Diagrammatic representation of the rise and fall of the total taxa of Faunal Set I to VII from the Neogene Sub-Saharan Africa on the basis of half-life.

Fig. 19. Increase of the open land taxa. Solid line: percentage of the open land taxa number in the total taxa number. Gray line: percentage of the first appearance open land taxa in the first appearance taxa. Number on the gray line: number of the first appearance open land taxa in the first appearance taxa. Box symbol: average percentage of the open land taxa number by the total taxa number (left: the average percentage during Pre-Set I to Set III, right: the average percentage during Set IV to Set VIII).
As mentioned above, some geological event occurred at late Orleanian to Astaracian (approximately 15-16 Ma). This geological event might be caused by the increasing of the taxa of the indicators (Equidae, Bovidae and some Suidae) of the open-country and/or open woodland environments in the Sub-Saharan Africa. The percentage of the open land taxa number by the total taxa number increases after Faunal Set IV. The number and percentage of the first appearance of open land taxa by the first appearance taxa increases after Faunal Set IV also. The average percentage of the open land taxa number by the total taxa number during Faunal Set IV to VIII (37.8 %) is clearly larger than the average percentage of the open land taxa number by the total taxa number during Faunal Set Pre-Set I to III (9.1 %) (Fig. 19).

CONCLUSION

I. Late Miocene Mammalian Interchange of Eurasian and Sub-Saharan Africa

Phylogenetic research of mammalian taxa of the Namurungule Fauna indicates a similarity to the Turolian faunas from Sub-Paratethys and North Africa. The Miocene mammalian faunas of Sub-Saharan Africa shows resemblance with late Vallesian to Turolian of North Africa, Sub-Paratethys, Southwest and Central Europe faunas based on Simpson's index of faunal resemblance and cluster analysis based on the dissimilarity of mammalian faunas (Fig. 20). The close resemblance between the Miocene Sub-Saharan and Siwalik mammalian faunas should not to be stressed in earlier studies.

II. Late Miocene Faunal Change of Sub-Saharan Africa

Maglio (1978) briefly states the stability of the Miocene mammalian faunas on the basis of the patterns of faunal evolution of Africa. Assemblage of the mammalian faunas from early Miocene was comparatively stable and had long half-life in Sub-Saharan Africa on the basis of the results of this work. However, mammalian assemblage changed drastically at the middle Miocene (Astaracian) in Sub-Saharan Africa. A great number of early to middle Miocene mammalian taxa were extinct and the modern mammalian taxa appeared in this period. The half-life of middle and late Miocene mammalian faunas is shortened compared with the early Miocene faunas in the East Africa. This geological event of faunal turnover occurred by the immigration and divergence of open land taxa. It is evident that the rise of open land taxa is related to the environmental change for the plateau phonolite and basalt volcanism in the middle Miocene East Africa (Pickford, 1981; Williams & Chapman, 1986) and the worldwide warm and arid event (savannitisation) of continental temperate zone in the middle to late Miocene (Liu, 1988). In the middle Miocene (16 Ma) Pacific region, it has been proposed that the tropical event is recognized from shallow marine faunas of the Southwestern Japan (Tsuchi, 1986; Ogasawara, 1988). African and Eurasian land connection was also established before the middle Miocene (16 Ma±) (Bernor et al., 1980). The age of the middle Miocene mammalian turnover indicates similar age of the 21st. peak of periodical extinction of marine animals (Sepkoski, 1986; McGhee, 1989). However, Patterson & Smith (1989) denied periodicity in extinction on the basis of omitting noise component of non-monophyletic group. They considered that some peaks of extinction was recognized on the basis of peaks in diversity. This middle Miocene peak of extinction also suggests the diversity of marine animals followed by marine tropical event.

The Astaracian faunal turnover in Sub-Saharan Africa is considered to be caused by immigration and diversity of open country mammalian taxa and that was related to the worldwide middle Miocene warm event and the plateau volcanism in middle Miocene East Africa.

Furthermore, the Pleistocene and modern taxa and their direct ancestors of Sub-Saharan Africa appeared from the late Miocene faunas of East Africa. It has been made clear that the Namurungule Fauna is the forerunner of the modern Sub-Saharan mammalian fauna of savanna environments.
III. Application to the Human Evolution

As mentioned before, the Hominoid Fossil was found from the Namurungule Formation. The savannitisation in the Sub-Saharan Africa began in middle Miocene, which is related to the similar condition happened in Eurasian continent from middle to late Miocene. It should be emphasized that the more advanced development and spreading of open-country environments in the Sub-Saharan Africa compared with Eurasian arid event played an important role in the Hominoids evolution. Because, the bipedalism is the most important character of Hominidae which is distinguished from large ape. The origin of bipedalism seems to be closely related to the environmental change from forest to open land (Foley, 1984).

Human evolution in East Africa is accelerated by the savannitisation of Sub-Saharan Africa which commenced earlier than that of Eurasia and continued throughout the Neogene.

SUMMARY

The Namurungule Fauna indicates a close similarity with the Turolian faunas from Sub-Paratethys and North Africa. The Miocene mammalian faunas of Sub-Saharan Africa shows resemblance with late Vallesian to Turolian of North Africa, Sub-Paratethys, Southwest and Central Europe faunas.

Mammalian assemblage has changed drastically during the middle Miocene (Astaracian). This geological event of faunal turn over is marked by the increase of open land taxa. It indicates the spreading of the warm and arid environments (savannitisation) in the middle to late Miocene East Africa.

Furthermore, the Pleistocene and modern taxa appeared from the late Miocene East African faunas. The Namurungule Fauna is the pioneer of the modern Sub-Saharan mammalian fauna of savanna environments.

The advanced savannitisation in the Sub-Saharan Africa played an important role in the hominization that human ancestors got bipedalism which is caused by their invasion from forest to savanna environments.

ACKNOWLEDGMENTS The author is deeply grateful to Professor emeritus Satoru Uozumi of Hokkaido University, Professor Hidemi Ishida of Kyoto University, Professor emeritus Tadao Kamei of Kyoto University for continuous guidance during the course of this work, and is much indebted Mr. Richard Leakey of National Museums of Kenya, Mr. Mahito Watabe of Historical Museum of Hokkaido (present address: Hayashibara Museum of Natural Science), Drs., Alan Gentry of British Museum (Natural History), Vera Eisenmann, Martin Pickford and Herbert Thomas of Institut de Paléontologie, Pascal Tassy of Université Paris VI, Yoshinari Kawamura of Aichi University of Education, Haruo Saegusa of Shinshu University (Present address: Hyogo Museum of Nature and Human Activity), Keiji Iwata of Hokkaido University, Yoshinari Togo of Hokkaido University of Education, and Morio Akamatsu of Historical Museum of Hokkaido for
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Pickford, M. 1978a. Geology, palaeoenvironments and vertebrate faunas of the mid-Miocene


——— Accepted February 14, 1994

Author's Name and Address: Hideo NAKAYA, *Department of Earth Sciences, Faculty of Education*, *Kagawa University, 1-1, Saiwai-cho, Takamatsu, 760, Japan.*
### Appendix 1. Total taxa of Afro-Eurasian faunas

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| Stagodon yushensis | 1 |
| Elephantidae | 1 |
| Primelephas sp. | 1 |
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- Rhinocerotidae gen. et sp. indet. 1
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- Aceratherium intermedium intermedium 1
- Aceratherium intermedium comanatum 1
- Aceratherium kowalewski 1
- Aceratherium persiae 1
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  - Dicerorhinus pachygathus 1
  - Dicerorhinus broeni 1
  - Dicerorhinus cf. sivalensis 1
  - Dicerorhinus vidali 1
- Iranotheriinae (Elasmotheriinae)
  - Caementodon oettingenae 1
  - Iranotherium morgani 1
  - Kenyatherium bishopi 1
  - Sinotherium lagrelii 1

**Artiodactyla**

**Suidae**
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- Conohyus indicus 1
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- Conohyus sp. 1
- Dicoryphochoerus haydeni 1
- Dicoryphochoerus robustus 1
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- Dorcabune nagrii 1
- Hippophyus deitterai 1
- Hippopotamodon sivalense (Dicryphochoerus titan) 1
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Total Number of Taxa: 23