THE PALEOECOLOGY OF PROCONSUL

A Thesis
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The Faculty of Graduate Studies
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by
Jeffrey M. Wyman
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1. INTRODUCTION

Since 1909, when the first fossiliferous beds of East Africa were discovered, the African Dryopithecines have occupied a position of significance in the evolution of the Hominoidea. Even though they have been the subject of a considerable amount of research over the last 75 or so years they are still worthy of study for at least four major reasons. First, they are relatively well known with a large data base not only of morphological and metric observations, but also data of ecological significance. Second, they constitute almost all of the known African fossil Pongid species. Third, they have been linked morphologically, and in an evolutionary sense, to later and extant forms (Pilbeam 1969, Conroy and Fleagle 1972, Andrews 1978). Finally, to find ancestors for the Eurasian genera _Dryopithecus_ _Sivapithecus_, and _Ramapithecus_, it is necessary to return to the African Proconsulines as the only currently known potential precursors.

Considering the potential significance of the _Proconsul_ forms, it is perhaps surprising that the various species have been defined, and phyletic connections developed, almost exclusively on the basis of morphological data (for example, Simons and Pilbeam 1965, a 71 page monograph comprising a complete revision of the Dryopithecinae, contains only morphological information). The reliance on this mode of analysis, known as the typological species concept (Mayr 1963:16), while used out of necessity when dealing with a fossil form, has had an unfortunate impact upon the study of the African _Proconsul_ forms. There has been a tendency in the past to treat significant fossils, not as segments of the paleoecological community, but rather as discrete units separated from the matrix of geological, floral and faunal elements from which they were derived (as in Simons and Pilbeam 1965, Andrews 1974, 1976, Fleagle 1975, Andrews and Tekkaya 1980, LeGros Clark and Leakey 1951).

In other cases, some ecological information has been provided, if only in a cursory manner (Pilbeam and Simons 1971, Andrews 1978, Pilbeam 1969).

Fortunately, a number of researchers have published paleoecological data along with paleoprimatological information (Bishop 1964, Walker 1969). More recently, an ecologically based approach has been used in respect to the whole spctrum of African Proconsulines (Nesbit-Evans et al 1981, Pickford 1981).

Despite these efforts, however, a further broadening of the paleoecological approach in this area is appropriate. The objectives of this paper will be threefold. First, to assemble as much of the data concerning the genus _Proconsul_ as is available in published form. Information has been collected in the following areas: 1) paleogeology, 2) paleogeography, 3) dating, 4) abundance of Dryopithecines, 5) associated fauna, 6) associated flora. Second, to assemble all of this data into a picture of the paleoecology of each site, and of each species. And finally, to discuss various ecological theories as they apply to the African Proconsul forms. Briefly, those touched upon will be habitat diversity, interspecific relations and competition, and adaptive radiation. Finally, the genus Proconsul will be placed, as far as is possible, within the larger pattern of Miocene Hominoid evolution.

In an evolutionary sense the genus Proconsul was quite successful. As a significant Hominoid family it is important to understand, if possible, what type of environment(s) these early Hominoids were associated with. An examination of the available paleoecological information, and the application of a number of ecological theories, could lead to a greater understanding of the place of the Proconsul forms in the evolution of the Hominoidea.

2. HISTORY OF THE FINDS

1. 1909 - G.R. Chesnaye discovers fossils of Miocene age at Koru, Kenya
2. 1909 - G.R. Chesnaye discovers fossils of Miocene age at Karungu, Kenya.
3. 1911 - F. Oswald collects fossils at Karungu.
4. 1911 - Preliminary report on 1909 fossils prepared by C.W. Andrews.
5. 1914 - Oswald publishes a monograph on Karungu.
6. 1926-1927 - H.L. Gordon collects more fossils at Koru.
7. 1931 - A.T. Hopwood visits East Africa (Koru).
8. 1931-1932 - L.S.B. Leakey and D. Macinnes visit Rusinga Island and find Hominoid fossils.
9. 1932 - Leakey and Macinnes discover Miocene age beds at Songhor and Mfwangano Island.
10. 1932 - Sir Arthur Keith assigns some of the finds from Rusinga, Mfwangano and Songhor to the genus *Dryopithecus*.
11. 1933 - Hopwood describes all of the finds up to 1931; names *Proconsul* and *Limnopithecus*.
12. 1933 - Archdeacon W.E. Owen finds fossils at Ombo, Maboko Island, Mariwa, Majiwa and Chianda Uyoma.
13. 1933 - Arambourg discovers Miocene age deposits at Losidok.
14. 1934 - Macinnes and Owen excavate at Maboko.
15. 1934-1935 - Leakey finds more fossils at Rusinga
16. 1934 and 1938 - Macinnes excavates at Songhor.
17. 1940 and 1942 - Leakey excavates at Songhor.
18. 1944 - P.E. Kent describes most of the known sites.
19. 1947 - British Kenya Miocene Expedition begins work at Rusinga, Mfwangano, Karungu, Koru and Chianda Uyoma.

20. 1951 - Report on the finds of the B.K.M.E. by W.E. LeGros Clark and Leakey.

21. 1958 - W.W. Bishop describes Miocene age fossils from Napak and Moroto in Uganda.

22. 1958 - Leakey discovers fossils of mid-Miocene age at Fort Ternan.

23. 1965 - E.L. Simons and D. Pilbeam publish a revision of the Dryopithecinae.

24. 1969 - A Walker describes the site of Bukwa, Kenya.

25. 1970-present - Continuing excavations in East Africa, particularly at Songhor and Koru.

3. PROCONSUL: GENUS, SUBGENERA AND SPECIES

There are currently 5 recognized species of the genus Proconsul from the East African Miocene period. Three of these forms P. africanus, P. nyanzae and P. major have been placed into the subgenus Proconsul, while the other two species, P. gordoni and P. vancouveringi, have been placed in the subgenus Rangwapithecus (Andrews 1974). The former group of species are well established and accepted by the academic community at large (Simons and Pilbeam 1965, Pilbeam 1969, LeGros Clark and Leakey 1951, Napier and Davis 1959). While their phyletic position may be, and has been, changed (Andrews 1976), the species themselves seem secure. The Rangwapithecus species have not been seriously questioned since being named by Andrews (1970, 1974). The subgeneric definitions, based on morphological characters, is as follows:

1. Genus: Proconsul

   a) subgenus: Proconsul

      i) Contained species - 3, P. africanus, P. nyanzae, P. major.

      ii) Size range - siamang (P. africanus) to female gorilla (P. major).

      iii) Temporal range - Early to mid-Miocene.

      iv) Distribution - General over the East African Miocene Hominoid sites, most common at Rusinga, Mfwangano and Songhor.

      v) Discussion - see below.

   b) subgenus: Rangwapithecus

      i) Contained species - 2, P.(R.) gordoni, P.(R.) vancouveringi.

      ii) Size range - gibbon (P. vancouveringi) to siamang (P. gordoni).

      iii) Temporal range - Early Miocene.

      iv) Distribution - most common at Songhor, rare elsewhere.

      v) Discussion - see below.

Rangwapithecus and Proconsul are placed together in a single genus by Andrews on the basis of a number of shared morphologic characteristics. These are listed by him in a number of publications.

1. Presence of a superior transverse torus (1978:143).
2. Similar lower dentitions (1976:43).
3. Enamel thicknesses on molars and premolars are comparable (1976:54).
4. Relatively gracile mandibular and maxillary bodies (1976:54).
5. Reduced projection of snout (shared with all Dryopithecines (1976:53).
6. Narrow and shallow palate (1976:53).
7. Relatively gracile zygomatic regions, sloping posteriorly (1976:53).
8. Gracile alveolar processes (1876:53).
9. Relatively small incisors (1976:53).
10. Relatively small and slender canines (1976:53).
11. Upper premolars and molars relatively broad (1976:54).
12. Small M $\underline{1}$ and larger M $\underline{3}$, elongated M $\underline{3}$ (1976:54).
13. Presence of molar cingula (1976:54).

The distinctions between the two subgenera have also been described by Andrews (1978:192-202). They are:

1. *Rangwapithecus* is characterized by low and more widely flaring zygomatic processes than *Proconsul*.
2. *Rangwapithecus* has conspicuously extensive maxillary sinuses while *Proconsul* species have more restricted maxillary sinuses.
3. *Rangwapithecus* has a greater degree of molarization of the upper premolars than is common in *Proconsul*.
4. *Rangwapithecus* is characterized by greatly enlarged M3's, which are by far the biggest of the upper molars. In the *Proconsul* species the M3 is usually larger than the M1 but smaller than the M2.

5. The three trigon cusps of M1-M2 are nearly egual in size in the Proconsul species but the protocone is commonly larger than the others in the Rangwapithecus species.

6. The Proconsul species have a developed protoconule: the protoconule is absent in the Rangwapithecus species.

7. The upper molars of Rangwapithecus are longer than broad while Proconsul (and other Dryopithecines) have upper molars broader than long.

8. Rangwapithecus exhibits a very steep wear gradient on the lower molars (i.e./ dentine exposed on M1 [mand.] while M3 [mand.] is almost unworn). The wear is more generalized in the Proconsul species.

9. Rangwapithecus incisors are relatively more narrow and high crowned than those of Proconsul (Andrews 1974:189).

10. The occlusal surface of the Rangwapithecus molars exhibit more wrinkling than is found on those of Proconsul (Andrews 1974:189).

3.1 PROCONSUL SPECIES

3.1.1 Proconsul africanus

1. Size - Subequal to a pygmy chimp, or siamang.

   a) Maxillary P3-M3 = 35-40mm.

   b) Mandibular P3-M3 = 40-45mm.

2. Temporal range - Early to mid-Miocene (Andrews and Walker 1976).

3. Distribution - Rusinga (common), Mfwangano, Songhor, Koru (Andrews 1978), and Ft. Ternan (?).

4. Hypodigm - 118 specimens comprising a complete dentition, mandible, maxilla, frontal, temporal and partial postcranial anatomy, including leg and foot bones.

P. africanus is best known from Rusinga where there have been at least 39 individuals found. Although quite widely distributed elsewhere, it is never very common outside of this site. P. africanus is the most studied of all the Proconsulines, primarily because there is additional material to augment the Since 1909, when the first fossiliferous beds of East Africa usual dental information common in fossil forms. A fairly complete forelimb, ascribed to P. africanus on the basis of size and provenance has been found (Napier and Davis 1959), and this has been compared to those from the extant genus Pan (Pilbeam 1969, Andrews 1978). P. africanus shares a suite of characteristics with the other Proconsul species (see above) to whom it appears to be similar morphologically, differing, however, in size (Andrews 1976:45).

3.1.2 Proconsul nyanzae

1. Size - approximately equal to a chimpanzee-somewhat larger than P. africanus.

   a) maxillary P3-M3 = 40-50mm.

   b) mandibular P3-M3 = 45-55mm.

2. Temporal range - Early to mid-Miocene (Andrews and Walker 1976).

3. Distribution - The Rangwa sites, Rusinga, Mfwangano and Karungu as well as Losidok(?) and Ft. Ternan(?).

4. Hypodigm - 103 specimens comprising a complete dentition, mandible, maxilla and a few postcranial remains including leg and foot bones.

P. nyanzae is best known from Rusinga where approximately 45 individuals have been found (Andrews and VanCouvering 1975). It is never common elsewhere, and is extremely rare outside of the Kisingiri sites. P. nyanzae shares many characteristics with P. africanus and P. major, differing from them primarily on the basis of size although it exhibits limited sectoriality in the P3 [mand.], a trait seen in neither of the other two Proconsul (Proconsul) forms (Andrews 1978).

3.1.3 Proconsul major

1. Size - Roughly equal to a female gorilla.

   a) mandibular P3-M3 = 65+mm.

2. Temporal distribution - Early Miocene.

3. Distribution - Common at the Tinderet sites of Songhor and Koru. Also widely distributed at the Northern (Uganda) sites such as Napak and Moroto.

4. Hypodigm - 75 specimens comprising the dentition (excluding lower incisors), most of the mandible, maxilla and nasal regions of the cranium, as well as a few postcranials (Andrews 1978).

P. major is the most widely distributed Proconsuline, occurring at some 7 sites. *P. major* is the largest of all the African Dryopithecines, and, while it shares most of the characters listed above with the other Proconsul forms, it also shows some size related differences (Andrews 1978). It has a very robust mandibular symphysis, greater mandibular breadth and great bilateral compression of the P3 [mand.] (relative to the other *Proconsul* species (Andrews 1978:200). A further unique feature associated with *P. major* is the presence of a true frontal sinus (Andrews 1978:213). As far as is known this feature is found elsewhere only in *Pan* and the Hominids.

3.2 RANGWAPITHECUS SPECIES

3.2.1 *Rangwapithecus gordoni*

1. Size - approximately equal to a pygmy chimpanzee. Slightly larger or equal to *P. africanus*.

   a) maxillary P3-M3 = 40 mm.. (one case) (Andrews 1974:189).

2. Temporal distribution - Early Miocene.

3. Distribution - Songhor (common). Known elsewhere only from Rusinga(?) and Mfwangano (one individual).

4. Hypodigm - 79 specimens comprising the complete dentition, most of the mandible, maxilla and palate, and a few postcranials (Andrews 1978).

A relatively new species, *P.(R.) gordoni* shares many characteristics with *P.(R.) vancouveringi* (see above), although the dentition of the latter form is not completely known. Morphologically similar to, but larger than, *P. vancouveringi* (Andrews 1970, 1974).

3.2.2 *Rangwapithecus vancouveringi*

1. Size - Approximately Siamang size. The smallest *Proconsul* form.

   a) Maxillary P3-M3 = 31mm. (one case)(Andrews 1974).

2. Temporal distribution - Early-Early Mid(?) Miocene.

3. Distribution - Rare, found at Rusinga, Songhor, Mfwangano and Maboko, but always infrequently. Distribution is unusual for a *Proconsul* species in that there is no single site where *P. vancouveringi* is common. This may be due to the fact that finds of this form are rare (Andrews 1978).

4. Hypodigm - Only 7 specimens had been attributed to this species as of 1974 but Andrews (1978) states that new specimens have been found since then. The exact number of fossils assigned to this species, however, is apparently still uncertain (Andrews 1978). The known material comprises the upper postcanine dentition and parts of the mandible.

Andrews (1974) states that *P. vancouveringi* is morphologically very similar to *P. gordoni* although there are differences in size and in the morphology of the M1 [max.]. In general, this form is poorly known.

4. EAST AFRICAN MIOCENE FOSSIL SITES

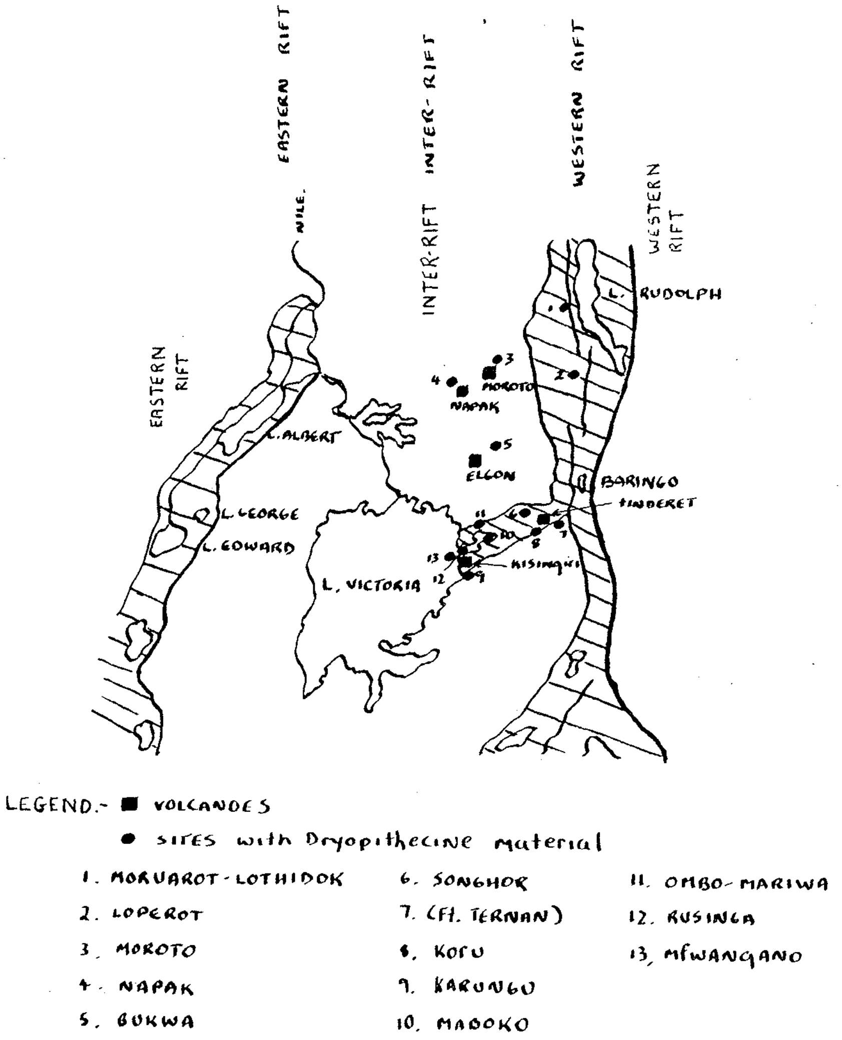


Figure 4.1: EAST AFRICAN MIOCENE FOSSIL SITES

4.1 THE PRESENT GEOLOGY/GEOGRAPHY OF EAST AFRICA

The fossil bearing locations of East Africa are all centered upon the rift valley system. This system, consisting of two great, and a number of smaller faults in the earth's crust, is usually divided into three components: 1) the Eastern Rift, 2) the Inter-rift and 3) the Western Rift. The faults cut across the extensive highlands of East Africa which lie at a general elevation of 2500-3000m (Andrews and VanCouvering 1975). Between the Eastern and Western Rift Valleys lies the Inter-rift, a shallow, somewhat depressed area partially occupied by Lake Victoria. A smaller fault, the Kavirondo, important because of its fossiliferous sites, lies in the Inter-rift. This fault runs from the Eastern edge of Lake Victoria to the Eastern Rift Valley.

The entire area is broken up by numerous mountains and highlands rising above the general elevation. The oldest of these mountains, now generally considerably eroded, appeared during the Miocene era. These volcanoes, Kisingiri, Tinderet, Elgon, Napak and Moroto and their surrounding areas, are the sites of the majority of the Miocene fossils from East Africa. Fig. 4.1 is a map showing the locations of these volcanoes, and of the East African Miocene fossil sites.

Vulcanism and uplifting continued from the Early Miocene to recent times with extensive highlands being raised during the Plio-Pleistocene rift movements (Andrews and VanCouvering 1975). Currently, the area is dominated by more recent volcanoes, Kenya, Kilimanjaro and Ngorongoro, which rise along the periphery of the Eastern Rift.

Because of the diverse landscape, drainage, climate and vegetation are also diverse (Andrews and VanCouvering 1975). The most confusing situation, however, exists in the underlying geology of the region. Because of the successive volcanic eruptions, multiple sedimentary formations and essentially distorted strata caused by folding and faulting, finding stratigraphic continuities over a wide area is very difficult. Although attempts have been made to correlate the stratigraphies of the various sites they have generally only been successful for nearby, or closely related sites (for example VanCouvering and VanCouvering 1976:160, Andrews and VanCouvering 1975:66-69).

Because the discussions of the geologies of the individual sites can become fairly technical a glossary of geological terms will be included here (drawn largely from Strahler 1970).

1. Basalt - an extrusive igneous rock.

2. Conglomerate - a mixture of sand, pebbles and large rocks cemented together with silica or calcium carbonate. The origin of the particles is clastic (they are produced by the disintegration of previous rocks), and they can either be rounded by weathering (conglomerate) or angular (breccia).

3. Sandstone, Siltstone and Shale - formed in the same manner as conglomerate but exhibiting a decreasing particle size.

4. Marl - a soft limestone formed by chemical precipitation from bodies of water heavily charged with lime in solution.

5. Tuff - formed of compacted volcanic ash extruded during volcanic eruptions. Any fine grained pyroclastic (volcanic ejecta) material settling to the ground may form tuff, even under water.}

6. Arkose - a sandstone containing grains of feldspar and quartz.

7. Nephelinite - a crystaline granular volcanic rock consisting of nepheline and augite; rocks where nepheline takes the place of feldspar.

8. Phonolites - a compact greyish rock containing crystals of glassy feldspar.

4.2 THE MIOCENE GEOLOGY/GEOGRAPHY OF EAST AFRICA

There seems to be general agreement that East Africa in the Early Miocene (@20 m.y. ago) typically had elevations lower than those found today. Both Andrews and VanCouvering and VanCouvering and VanCouvering cite an elevation of about 1000 m. for basement domes, later to become volcanoes, in this region. The former authors cite the Late Oligocene (1975:66) as the time of this uplift compared to the Early Miocene for the latter writers (1976:163). Either way, it is obvious from the sedimentological evidence that there was widespread volcanic activity throughout the entire region, probably beginning around the Oligocene/Miocene boundary. The African Rift system itself was likely developing throughout the Early Miocene and probably was much like it is today by Mid-Miocene times (VanCouvering and VanCouvering 1976:163). As well as the major faults, the Eastern and Western Rifts, this time also showed the development of a smaller fault, the Kavirondo Rift, trending ENE with the volcanoes Tinderet at the Eastern end and Kisingiri at the SW.

Throughout the Early Miocene the basement domes at Yelele, Moroto, Napak, Kadam, Elgon, Tinderet and Kisingiri developed into volcanoes. Evidence of increasing volcanic activity comes from almost all of the Miocene fossiliferous sites, where features associated with vulcanism are common (Andrews and VanCouvering 1975:68). Such features include tuffaceous beds and a general lack of fossil soil horizons and root casts. Both of these features have been considered indicative of alkaline conditions generally unsuitable for plant development (Andrews and VanCouvering 1975:68). Earlier studies (LeGros Clark and Leakey 1951) cited such barren areas as being indicative of an arid environment but a more likely explanation lies in the localized heavy alkalinity associated with volcanic ejecta.

Andrews and VanCouvering (1975:69) postulate that the drainage pattern may have been considerably different than that of today. Current drainage is either interior, into the small alkaline basins of the Inter-rift, or to the North, along fault lines, to the Nile River (Andrews and VanCouvering 1975). In the Miocene both the Inter-rift and the Western Rift may have drained to the West. Evidence for this lies in the consistency of the fossil fish from the two areas.

To the East, a fossil whale found at Loperot (East of the Eastern Rift) suggests that there must have been relatively easy access to the Indian Ocean through rivers in the area (Andrews and VanCouvering 1975). In fact, due to the low lying nature of the Eastern coastal regions today it is very possible that the coastline was actually much closer to the Eastern Rift in the Miocene than it is now (Andrews and VanCouvering 1975). A major river may have flowed eastwards down the Kavirondo Rift draining part of the Inter-rift, but there is, as yet, no real evidence to support this notion. If a permanent river did flow here it might have been significant as a barrier to the North-South movement of fauna.

4.3 THE MIOCENE CLIMATE OF EAST AFRICA

Present day climates can be examined in detail in a local area with the advantage of knowing continent wide, and world wide, climatological trends. Local paleoclimatology, however, is confused by a general lack of knowledge concerning paleoclimates over a larger area. Since the main influences acting to create climates are atmospheric patterns and the location of continents, mountains, and ocean currents; any speculations concerning a broader scope of paleoclimate will be tenuous as none of these variables are the same, in any area, today as they were in the past. Nevertheless, there has been some effort made to predict major climatic trends during the Miocene.

Schwarzback (1961) made some general observations concerning paleoclimates in Europe and Africa after taking into consideration such factors as continental drift (5-8 degrees North for Africa) and changing patterns of ocean currents brought about by the shifting continents. He feels that the Tertiary was considerably warmer than today (Schwarzback 1961:268). Currently East Africa is tropical to sub-tropical in climate. If it was even warmer during the Miocene it would be likely that tropical or sub-tropical conditions prevailed then also. This view of the East African Miocene temperature range has been supported by Walker (1972:210).

Using evaporates, bauxites, glacial deposits and biotherms Schwarzback analysed patterns of humidity, and hence rainfall, in Europe. He states that the Early Miocene was a period of high humidity (1961:64). This observation is supported by Kingdon who has studied the Miocene flora and fauna, concluding that there were wetter conditions during the Miocene (Kingdon 1971:64). A final piece of evidence comes from the red-bed deposits common in East Africa, many of which are of Miocene age. Red-beds are warm-temperate to sub-tropical or warmer assemblages, and their formation suggests that tropical temperature and rainfall conditions were present in the Miocene.

East Africa today does not have truly tropical levels of rainfall generally, although some localized areas receive very heavy precipitation. There may have been, however, considerably greater levels of rainfall in this region during the Miocene. Since the major tectonic uplifting was likely just beginning at this time it is probable that elevations were generally lower than they are today. A decrease in elevation likely would have reduced the amount of orographic precipitation falling on the windward side of the highlands (Andrews and VanCouvering 1975:72).

It appears to be widely accepted that tropical or subtropical climactic conditions were prevalent in the Early Miocene throughout much of Africa and Europe. In East Africa, the crucial impact upon local climate was probably made by uplifting due to volcanic activity. Such an event would alter both rainfall patterns and temperature gradients. If it is accepted that this uplifting was only beginning in the Early Miocene (@ 20 m.y.), and had not as yet reached any great altitude, several differences in the Miocene climate from that of today may be postulated:

1. Greater rainfall.

2. Rainfall distributed more evenly year round.

3. Generally slightly warmer temperatures

4. Few, if any, areas with a great temperature range due to altitude.

4.4 THE MIOCENE VEGETATION OF EAST AFRICA

Although vegetation will be discussed in following sections as it is inferred from floral remains found at each individual site, there are several overall patterns which should be analysed.

Andrews and VanCouvering list a number of vegetation types thought to be of great antiquity in the East African area: 1) tropical rainforest, 2) moist woodland, and 3) bushland. Also thought to be ancient, but not as long established as the previous three are: 1) montane forest and 2) coastal lowland evergreen forest (Andrews and VanCouvering 1975). Even if these vegetation types are long established the general concensus of most researchers seems to be that the forest biome was prevalent in the East African Miocene period(for example Andrews and VanCouvering 1975).

VanCouvering and VanCouvering (1976) believe that the entire Inter-rift area was covered by lowland forest but by Mid-Miocene times two biomes prevailed: upland, or montane, forest in the higher elevations and gallery forest in the lowland areas (VanCouvering and VanCouvering 1976:161). In support of the gallery forest concept Kingdon (1971:57) cites the presence of <u>Celtis</u> (Ulmaceae) fruits which have occasionally been found in the fossil sites. <u>Celtis</u>, still extant, is a mid-canopy forest tree found in the relic East African coastal lowland forest (VanCouvering and Miller 1969:19). All the above authors believe that the predominant vegetation type here was forest, but the exact nature of the forest is less certain. There is a change in the character of extant East African forests with altitude. Above 1300 meters (Moreau 1963) or above 1500 meters (Andrews and VanCouvering 1975) the forest changes from submontane to montane, the two biomes being surprisingly different.

As has been discussed earlier, the Early Miocene was probably the time of the first significant uplifting in this area. It is difficult to assess, therefore, when elevations of 1300-1500 meters would have been reached. It must be assumed that it would take a considerable length of time for a montane forest, significantly different in character, to evolve from a lowland or sub-montane forest. Thus, it would appear likely that, for most of the Early Miocene, the true montane forest would not have existed. If the montane forest can be ruled out it is probable that the majority of the forest at this time was lowland in nature, as was suggested by Andrews and VanCouvering (1975).

There is no question that there is evidence strongly suggestive of forest conditions. The exact extent of the woods is, however, more conjectural. Andrews and VanCouvering envision a great lowland forest stretching from the Congo basin to the East coast (1975). Furthermore, of the five ancient vegetation types they list, four are forest. Similarly, both biomes described by VanCouvering and VanCouvering (1976) as being of great antiquity are forest also. This almost precludes any other type of environment from having been present, and leads to immediate suppositions concerning the local environment at each site. It should also be considered that other environments, such as savanna, may be of great antiquity as well. This has, in fact, been suggested by Kingdon (1971:64). Even if the forest biome was widespread, local environments could vary considerably, and forest conditions should not be assumed in all instances.

5. METHODS OF FAUNAL ANALYSIS

5.1 FAUNA AS HABITAT INDICATORS

When a fossil is diagnosed as belonging to a form which is either extant or closely related to an extant form, it may be used as a habitat indicator species as defined by Nesbit Evans et al (1981). If the living form has a preferred habitat type, or is in some way linked to a particular environment, it is assumed that the fossil form may have exhibited a similar behavioral pattern (Nesbit Evans et al 1981:101). It must be remembered that this approach has several drawbacks, which have been outlined by the above authors (1981:101).

1. Few mammals are habitat specific to the necessary degree.
2. Habitat specificities can change with time and space.
3. Reliance on a single species or a few animals can be misleading unless it is absolutely certain that no faunal mixing has taken place, and that the entire fauna is derived from the same habitat.

Nevertheless, a good habitat indicator species is a valuable aid in determining the probable environment at a fossil site. Species which must be considered especially good are those which are very habitat specific (i.e. Anomalurids). Bigalke (1972:145-168) has prepared a list of extant families, and some genera, of mammals who are generally restricted to those particular environmental areas relevant to this paper.

1. INSECTIVORA
   - a) Potamogalidae (otter shrews) - aquatic feeders restricted to lowland forest (1 sp.) and montane forest (2 sp.).
   - b) Chrysochloridae (golden mole) - essentially non-forest dwellers - arid through moist grassland habitats.
   - c) Erinaceidae (hedgehogs) - arid - savanna dwellers.
   - d) Macroscelididae - arid through savanna dwellers except for the genus <u>Rhynchocyon which is a forest form</u>.
2. PRIMATES

a) Most Primates are considered to be forest indicators especially Lorisidae and Pongidae.

3. TUBULIDENTATA

   a) Aardvarks are generally found in a savanna setting but occur occasionally in the forest also.

4. LAGOMORPHA

   a) Rabbits and hares are common in arid through savanna zones - also known from woodland areas (1 sp.).

5. RODENTIA

   a) Dendromurinae - arboreal dwellers.

   b) Gerbillinae - savanna dwellers.

   c) Muscardinidae (dormice) - forest forms.

   d) Bathyergidae (mole rats) - non-forest forms.

   e) Pedetidae (spring hare) - arid dweller.

   f) Ctenodactylidae (gundis) - arid dwellers.

   g) Anomaluridae (flying squirrels) - forest forms.

   h) Sciuridae (squirrels) - particular species restricted to many specific habitats.

6. CARNIVORA

   a) Canidae - arid through savanna forms.

   b) Mustellidae - savanna dwellers.

   c) Herpestinae (mongoose) - arid through savanna form.

   d) Hyaenidae - savanna dwellers.

7. HYRACOIDEA

   a) Almost all hyraxes are found in arid through savanna environments with the exception of three species of Dendrohyrax.

8. PERISSODACTYLA

   a) Equidae - commonly savanna forms.

9. ARTIODACTYLA

a) Tragulidae - found in forests near water.

VanCouvering and VanCouvering (1976:172) have also prepared a list of certain faunal groups which are today associated with restricted environments. This list agrees essentially with Bigalke's except in regard to the preferred habitat of the Chrysochloridae. While Bigalke states that the Chrysochloridae prefers non-forest conditions, VanCouvering and VanCouvering list all 7 African species of this family as forest dwellers. Kingdon, an expert on the mammals of Africa, demonstrates that most Chrysochlorids are found in the forest and thus is in agreement with VanCouvering and VanCouvering (Kingdon 1971). If used as a habitat indicator, then, any species of Chrysochloridae should be considered indicative of forest conditions.

Under separate headings, the fauna from each East African Miocene site will be analysed. Fossil forms considered as good habitat indicator species will be those forms falling into the families listed above.

5.2 RELATIVE ABUNDANCES

Another approach to divining habitat from the fauna which dwelled there, involves examining the proportions of various faunal groups in fossil situations, and comparing them to those from extant environments. The proportions of these faunal groups, selected at any ordinal level, can be significant indicators of local environments. For example, the most common fauna in the evergreen forests of West Africa are arboreal rodents and primates, while in secondary forest small ungulates are more common (Bourliere 1963:49-50). Other indicators, such as the relative abundances of rodents, can also be revealing. In extant forests the number of species of rodents present is great and there are usually several forms which are more abundant than the others. In open woodland and grassland, however, the entire rodent fauna may be, and often is, dominated by a single species. This one form may alone account for up to 90% of all the rodents present in a particular area (Andrews and VanCouvering 1975).

On a more specific level the distribution of species of a single family may be significant. Squirrels, for example, show a great size range in the forest but in savanna conditions both arboreal and terrestrial forms have a similar and constant size range (Bigalke 1972). In all these cases, however, it is prudent to remember that "relative numbers of animals in the fossil record may reflect many things other than species dominance in the living community (Nesbit Evans et al 1981:106).

Recently, four other methods have been used in the analysis of a fossil fauna as a community. These methods are (Nesbit Evans et al 1981): 1) habitat spectra, 2) taxonomic habitat indices, 3) ecological diversity spectra and 4) socioecology.

5.3 HABITAT SPECTRA

Habitat spectra involves weighting each fossil species on a scale from 0-6 depending upon how closely related the species is to an extant form. The living species are then analysed in terms of the range of habitats in which they are found. This method will not be used in this paper because both methods of weighting (0-6 scale of relationship and habitat preferences) for further analysis seem to be somewhat subjective.

5.4 TAXONOMIC HABITAT INDICES

Taxonomic habitat indices are also used to analyse the entire fossil fauna as a community. In this method all extant species, genera and families of East African mammals have been scored for how much time they actually spend in any particular habitat. For example, the African elephant was analysed as 0.33 forest, 0.33 woodland-bushland, 0.23 grassland and 0.11 semi-desert (Nesbit Evans et al 1981:102). A generic score is reached by averaging the individual specific figures,and, the family score is an average of the generic values.

The authors then selected East African locations which are representative of particular environmental types. At all of these locations the species, genera and families known to inhabit the area were listed and their assigned values were averaged. The result was table 5.1 (from Nesbit Evans et al 1981).

The advantage of this method over the habitat spectra is that it is specific to the level chosen; species, genus or family. Mathematical values representing habitat preferences are assigned to the entire fauna of a site, or level within a site, on the basis of the habitat preferences of modern analogues to the fossil forms. The totals for the fossil sites can then be compared to the totals of the extant faunas from table 5.1. With this method, the more complete the fossil fauna, the higher the chances of achieving

TABLE 5.1

TAXONOMIC HABITAT INDICES FOR 11 MODERN MAMMALIAN COMMUNITIES

ENVIRONMENT	LEVEL	FOREST	W-B	GRASS	S-D	SWAMP
DECID.FOR-WOODLAND	Species	0.34	0.40	0.12	0.04	0.10
Amani	Genus	0.43	0.46	0.06	0.03	0.02
	Family	0.36	0.48	0.12	0.03	0.01
SEMI-DECID. FOREST	Species	0.57	0.20	0.10	0.02	0.11
Budongo	Genus	0.50	0.33	0.08	0.01	0.08
	Family	0.38	0.40	0.09	0.05	0.08
EVERGREEN FOREST	Species	0.68	0.21	0.03	0.00	0.12
Irangi	Genus	0.66	0.23	0.05	0.05	0.01
	Family	0.46	0.37	0.10	0.03	0.04
MONTANE FOREST	Species	0.44	0.32	0.12	0.00	0.12
Semliki	Genus	0.38	0.39	0.13	0.06	0.04
	Family	0.31	0.45	0.16	0.05	0.03
WOODLAND	Species	0.04	0.59	0.22	0.12	0.03
Banagi	Genus	0.13	0.67	0.16	0.03	0.01
	Family	0.24	0.50	0.16	0.07	0.03
BUSHLAND	Species	0.04	0.53	0.21	0.15	0.07
Tsavo	Genus	0.13	0.60	0.15	0.08	0.04
	Family	0.27	0.47	0.16	0.04	0.06
	Species	0.02	0.43	0.22	0.30	0.03
Jebel Mara	Genus	0.09	0.49	0.23	0.15	0.04
	Family	0.22	0.49	0.13	0.14	0.02
BUSHLAND-GRASSLAND	Species	0.10	0.54	0.24	0.03	0.09
Rwenzori	Genus	0.14	0.59	0.14	0.02	0.11
	Family	0.24	0.48	0.14	0.04	0.10
GRASSLAND	Species	0.00	0.53	0.32	0.15	0.00
Serengeti	Genus	0.05	0.63	0.25	0.06	0.01
	Family	0.16	0.58	0.16	0.09	0.01
FLOODPLAIN-GRASS.	Species	0.09	0.52	0.32	0.03	0.04
Kafue	Genus	0.12	0.50	0.28	0.03	0.07
	Family	0.20	0.49	0.16	0.04	0.11
FLOODPLAIN/FOREST	Species	0.20	0.48	0.15	0.09	0.08

Tana	Genus	0.31	0.49	0.13	0.05	0.02
	Family	0.34	0.44	0.14	0.04	0.04

values which may be comparable to those found today in East Africa. Thus, this method will not be used here when the fossil fauna is obviously incomplete.

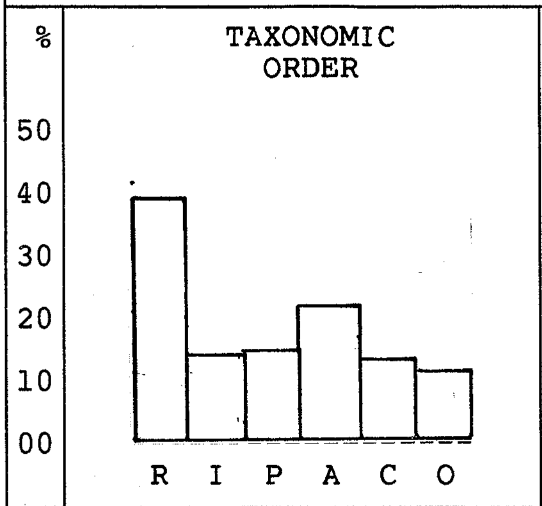
5.5 ECOLOGICAL DIVERSITY ANALYSIS

Ecological diversity analysis involves finding distinctive faunal patterns in extant mammalian communities, after analysis based on various criteria (mammal size, feeding type, locomotor type and taxonomic constitution at the ordinal level) (Nesbit Evans et al 1981). Andrews et al (1979) reviewed 23 African communities and found that their structure, based on the above characters, is similar in similar habitats, regardless of variations in taxonomic constitution. This method will be employed in this paper because most of the criteria used can be relatively easily estimated or assessed in a fossil situation. Also, this method can lead to some conclusions about a fossil site even when the fauna cannot be considered very complete. Ecological diversity analyses of modern mammalian communities may be seen in tables 5.2 - 5.6 (from Nesbit Evans et al 1981).

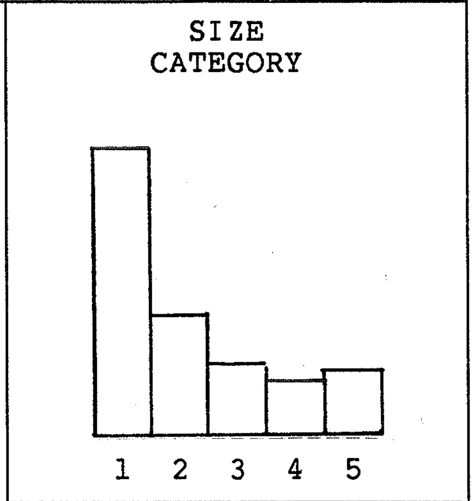
NM= mean number of species for M communities. LGM = purely terrestrial mammals. SGM = mainly terrestrial to lowest strata of vegetation.

TABLE 5.2

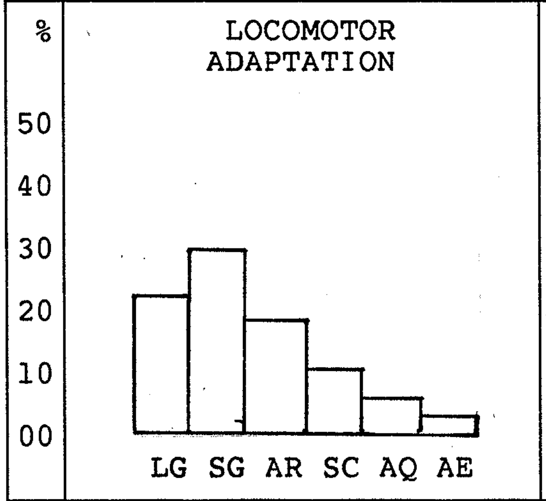
ECOLOGICAL DIVERSITY ANALYSIS-LOWLAND FOREST


TAXONOMIC ORDER

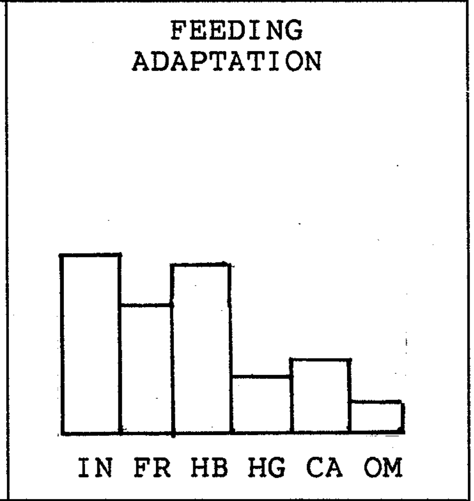
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER


SIZE CATEGORY

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.


LOCOMOTOR ADAPTATION

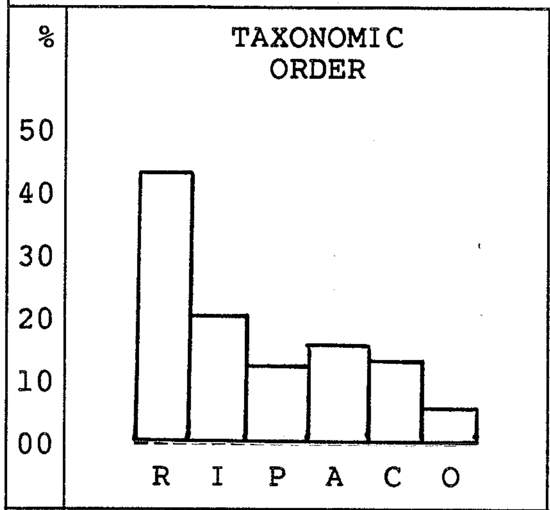
LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL


FEEDING ADAPTATION

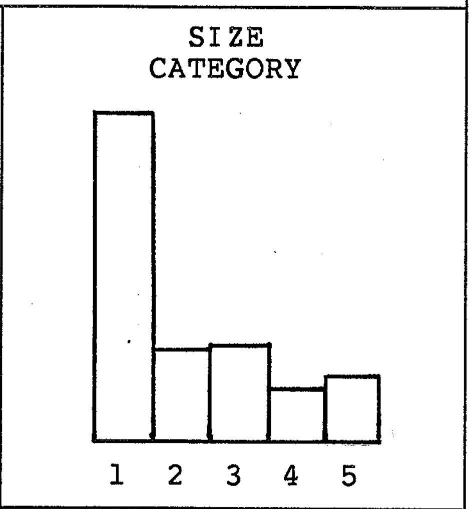
IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 5.3

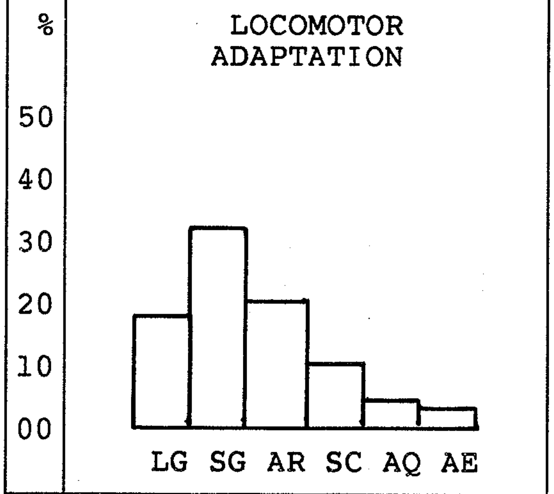
ECOLOGICAL DIVERSITY ANALYSIS-MONTANE FOREST


TAXONOMIC ORDER

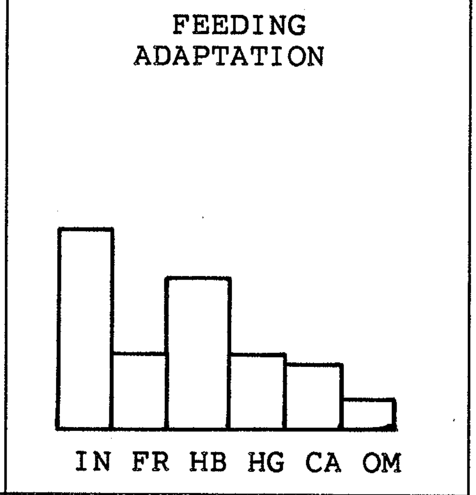
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER


SIZE CATEGORY

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.


LOCOMOTOR ADAPTATION

LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

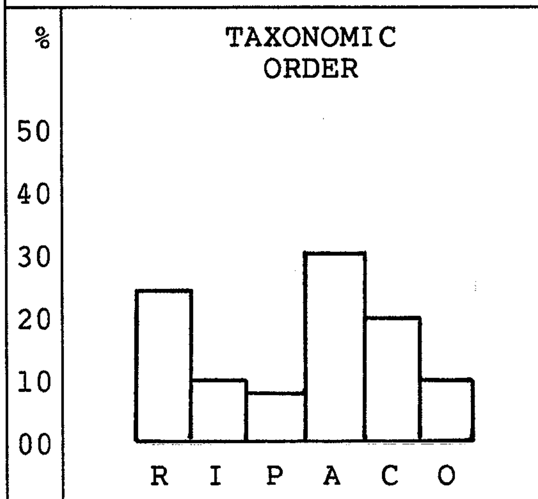

FEEDING ADAPTATION

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 5.4

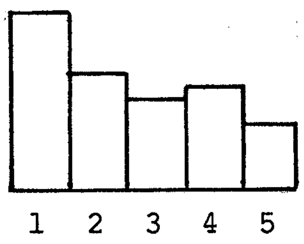
ECOLOGICAL DIVERSITY ANALYSIS-FLOODPLAIN

TAXONOMIC ORDER



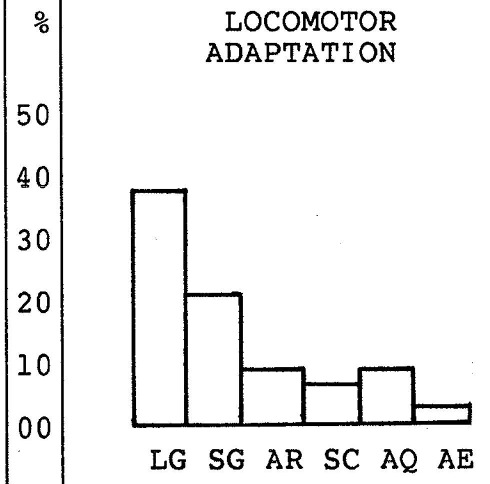
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

SIZE CATEGORY



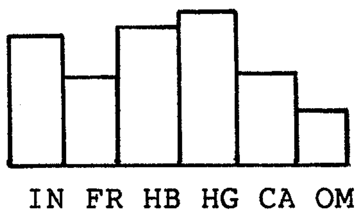
1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.

LOCOMOTOR ADAPTATION



LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

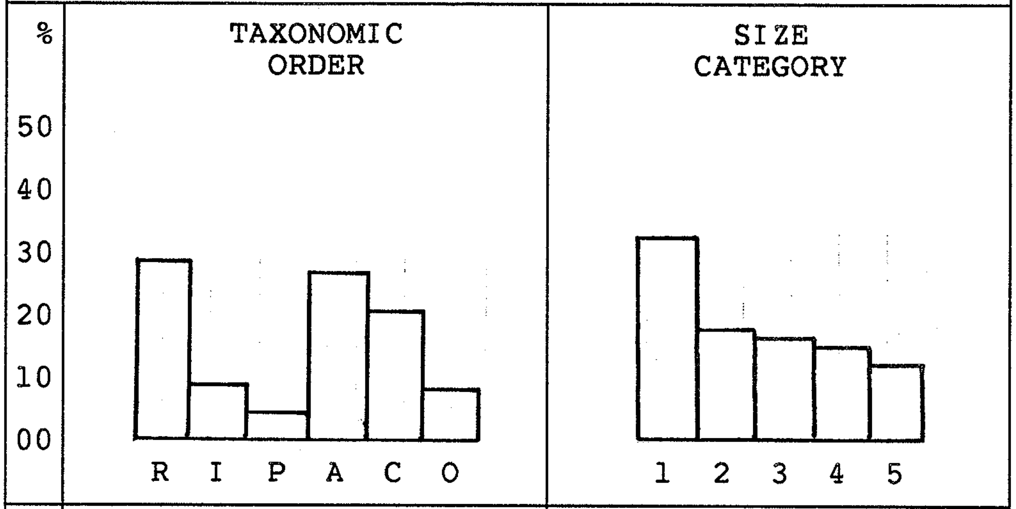
FEEDING ADAPTATION



IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

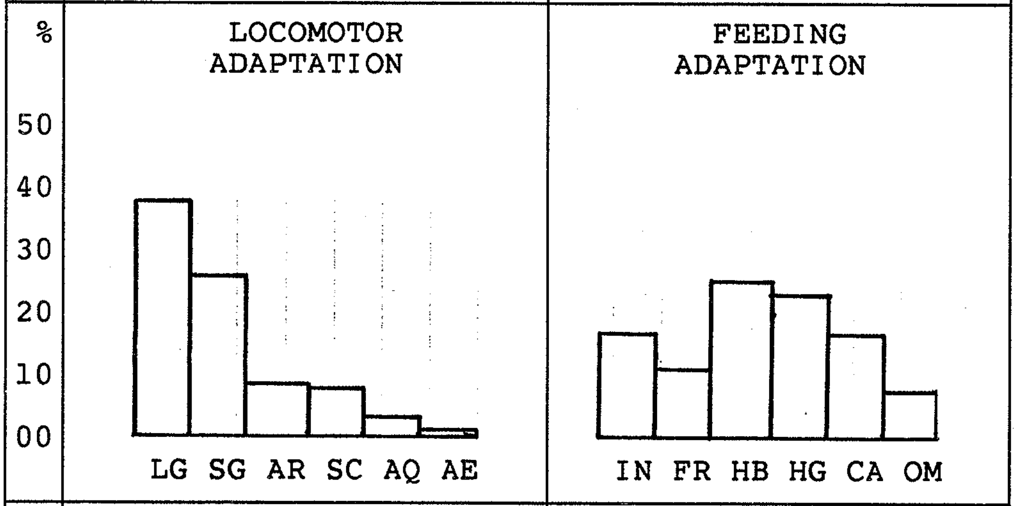
TABLE 5.5

ECOLOGICAL DIVERSITY ANALYSIS-WOODLAND/BUSHLAND



R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



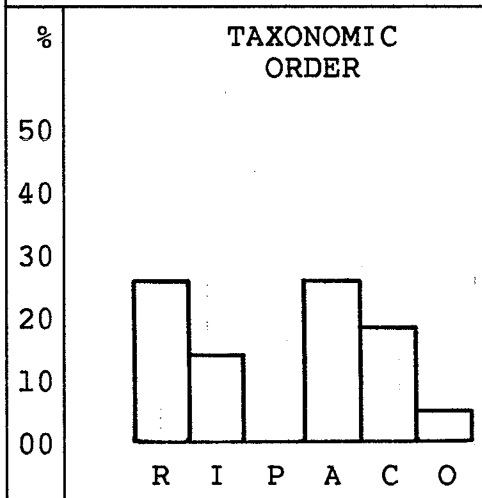
LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 5.6

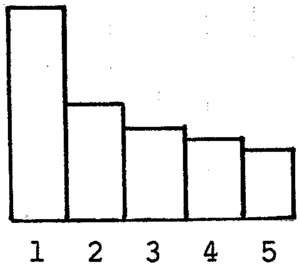
ECOLOGICAL DIVERSITY ANALYSIS-GRASSLAND

TAXONOMIC
ORDER



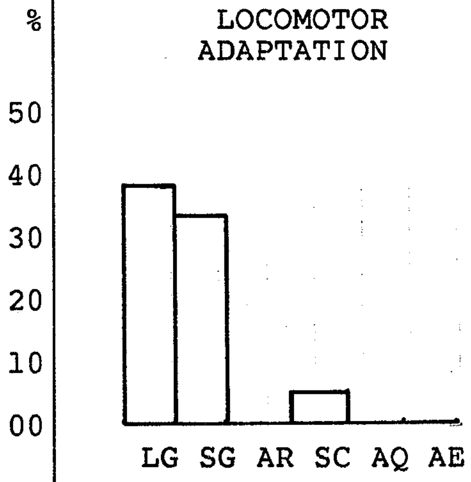
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

SIZE
CATEGORY



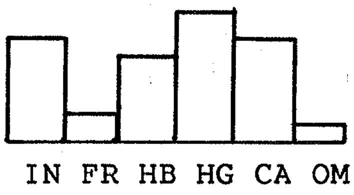
1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.

LOCOMOTOR
ADAPTATION



LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

FEEDING
ADAPTATION



IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

5.6 SOCIOECOLOGY

Socioecology involves predicting feeding behavior, social behavior and habitat preferences from the morphology of fossil species (Jarman 1974, Nesbit Evans et al 1981). At present socioecology has apparently only been used in regard to the living African bovids, and only has application, then, to fossil bovids (Nesbit Evans et al 1981) Because of its limited relevance this method will only be briefly referred to in this paper.

All of the above approaches involve the analysis of a fossil fauna by comparing and contrasting this fauna to one or more extant ones. Unfortunately, there is necessarily some innaccuracy involved in this, especially in assuming that the ecological preferences of species, genera and/or families will not have altered substantially over millions of years. The use of a number of methods of faunal analysis, however, should result in greater accuracy. Thus, habitat indicator species, relative abundances of selected faunal groups, taxomomic habitat indices and the ecological diversity analysis will all be used here in an attempt to divine the environment at the various East African fossil sites to the greatest degree of certainty possible.

6. DEPLETIONS IN THE EAST AFRICAN FOSSIL ASSEMBLAGE

Over the years a number of researchers have considered the problem of the completeness of a fauna as represented at a fossil site. Shotwell (1955) has listed some general trends in fossil populations, trends which can be applied to a broad spectrum of fossil situations. According to Shotwell, there are certain types of mammals which are likely to be missing from fossil assemblages (1955:329). Specifically, animals with arboreal habits will probably be under-represented, irrespective of their adundance in the area. Likewise, mammals with solitary habits, or those dwelling in more remote or inaccessable areas, as well as those who have a low population density, will probably also be under-represented (Shotwell 1955:329). To determine if any groups of mammals from the East African Miocene are likely seriously over or under-represented it is necessary to combine the fauna from all of the sites in order to analyse any overall trends. This combined faunal assemblage has been compared to extant mammalian faunas from various parts of the world, and from a variety of environments.

Table 6.1 shows the breakdown of extant mammalian faunas, at the generic level, from a number of locations. Table 6.2 shows the relative proportions of mammalian orders from these locations, and the percentages they constitute of the total mammalian fauna. The data for tables 6.1 and 6.2 has been drawn from Walker (1975).

Bats, generally falling into one or more of Shotwell's categories, would seem to bear out his observations as they apply to the East African fossil sites. Only 4 genera of bats are known from these sites, a figure which is considerably less than the number known from all of the modern environments sampled, with the exception of the deciduous forest of West Europe (6) and the grasslands of North America (7). Compared to the more forested environments, in which the number of genera of bats range from 14 to 58, the Chiroptera would seem to be considerably under-represented in the East African Miocene fossil record. In terms of percentages, bats constitute less than 4% of the total number of Miocene genera known. This compares to extant rainforests (30% avg.), evergreen forest (North Australia only)(24%), woodland-savanna environments (19% avg.), and the more open steppe-grassland environments (16% avg.). This illustrates that the number of genera of bats from the Miocene probably constitutes too low a percentage of the total fauna to be accurate. Thus, it may be concluded that bats are generally under-represented in the East African Miocene sites.

Although not as clear as the previous example, it is also possible that the Rodentia could be generally under-repre-

TABLE 6.1

NUMBERS OF MAMMALIAN GENERA

ORDER	E.Afr. Miocen sites total	Cent. Amer. rain-forest	N.Sou. Amer. rain-forest	South Asia rain-forest	Cent. Africa rain-forest	North Austr. everg. forest
MONOTREMATA	-	-	-	-	-	1
MARSUPIALIA	-	6	8	-	-	30
LIPOTYPHLA	9	4	1	22	13	-
MACROSCELIDEA	4?	-	-	-	-	-
DERMOPTERA	-	-	-	1	-	-
CHIROPTERA	4	58	61	49	32	14
PRIMATES	10	6	11	13	10	1
EDENTATA	-	7	8	-	-	-
PHOLIDOTA	-	-	-	1	1	-
LAGOMORPHA	2	2	1	3	2	-
RODENTIA	24	37	41	66	41	11
CETACEA	-	-	1	5	-	-
CREODONTA	12	-	-	-	-	-
CARNIVORA	6	19	18	37	27	-
PINNIPEDIA	-	1	4	1	-	-
TUBULIDENTATA	2	-	-	-	1	-
PROBOSCIDEA	6	-	-	1	1	-
HYRACOIDEA	5	-	-	1	3	-
SIRENIA	1	1	1	1	-	1
PERISSO.	6	1	1	4	3	-
ARTIO.	22	5	3	25	23	-

TOTAL	112	147	159	230	157	58

sented in the Miocene sample. There are 24 genera of rodents described from the Miocene of Africa (VanCouvering and VanCouvering 1976), compared to 46.2 (avg.) in extant tropical rainforests, 43.6 (avg.) in extant woodland-savanna biomes, 13.5 (avg.) in extant deciduous forests and 30 (avg.) in extant steppe-grassland environments. The percentages of rodent genera in the above examples are: Miocene sample 21%, rainforests 26.5% (avg.), woodland-savannas 30% (avg.), deciduous forests 32% (avg.) and grasslands 38% (avg).

Considering that most rodents are of very small size, and that many have behavioral patterns like those described by Shotwell, it would not be surprizing if they were under-represented in the Miocene fauna from East Africa. If it is also considered that the percentage of rodents from the Miocene is higher than it normally would be due to the almost total absence of bats, it would become even more likely that the number of rodent genera represented is too low.

Comparisons between other orders of mammals yield a variety of results. The proportions of insectivores, lagomorphs, carnivores (including creodonts) and sirenians are compatible with the figures from extant environments. Even allowing for a reduction in percentage to compensate for anticipated greater numbers of bats and rodents would not seriously alter these results. The orders Primates and Tubulidentata are a little high compared to extant populations but not inordinately so. In fact, the percentage of primates (9) from the Miocene is very similar to those from extant woodland-savanna biomes (8% avg.). Adjusting the primate and tubulidentate values down slightly would actually make them even more comparable to the percentages obtained from extant populations.

The proportions of Miocene Proboscidea, Hyracoidea and Perissodactyla are high by the standards of any modern analogues. Even reducing these values somewhat would not put them into the range of any type of extant environment. It is possible that there were simply more of these types of mammals in the Miocene than is common today. Conversely, it is also possible that more of the larger forms such as proboscideans and some perissodactyls can be more clearly identified, thus making a greater number of specific and generic distinctions possible. This would not likely be the case with hyraxes and other perissodactyls, however, as many of these forms are small in size, and no more easily identified than other mammals. There is no reason to assume that, over

TABLE 6.2

NUMBERS OF MAMMALIAN GENERA CONTINUED

ORDER	E.Nor Amer. decid for.	West Europ decid for.	East Afric for/ sav.	South Afric wood/ sav.	E.Sou Amer. for/ sav.	North Amer. grass -land	Cent. South Amer. sav.
MONOTREMATA	-	-	-	-	-	-	-
MARSUPIALIA	1	-	-	-	7	1	7
LIPOTYPHLA	3	5	11	14	-	6	-
MACROSCELIDEA	-	-	-	-	-	-	-
DERMOPTERA	-	-	-	-	-	-	-
CHIROPTERA	10	6	26	26	16	7	26
PRIMATES	1	1	9	8	5	1	14
EDENTATA	-	-	-	-	5	1	10
PHOLIDOTA	-	-	1	1	-	-	-
LAGOMORPHA	2	2	2	2	1	3	1
RODENTIA	11	16	46	45	23	37	40
CETACEA	-	-	-	-	2	-	-
CREODONTA	-	-	-	-	-	-	-
CARNIVORA	4	10	25	28	10	14	11
PINNIPEDIA	4	1	-	3	5	3	4
TUBULIDENTATA	-	-	1	1	-	-	-
PROBOSCIDEA	-	-	1	1	-	-	-
HYRACOIDEA	-	-	3	3	-	-	-
SIRENIA	-	-	-	1	1	1	-
PERISSO.	-	-	2	3	1	-	1
ARTIO.	3	4	29	24	3	4	3

TOTAL	39	45	156	160	79	78	117

time, these groups have not become somewhat reduced (since the Miocene).

The situation with the Artiodactyla is similar. The percentage (20%) is greater than is found in most extant populations. The woodland-savanna environments of East and South Africa, however, contain 19% and 15% artiodactyls respectively, and they are generally common in most recent and fossil environments in Africa (Andrews and VanCouvering 1975). Thus, there is no reason to assume that artiodactyls did not constitute a slightly higher percentage of the total fauna than would be common in extant populations.

The analysis of the general East African Miocene fauna points out that at each site there are certain factors which must be considered in addition to the actual fauna present. For example, since bats and rodents seem to be generally deplete, it must be considered that at each site they may be under-represented. Similarly, at sites where artiodactyls are very abundant it should be remembered that this could reflect the true situation, rather than being an artifact of deposition and/or fossilization.

According to Shotwell (1955:328), a reasonably complete fossil fauna should show:

1. An Eltonian pyramidal relationship.

2. More herbivores than carnivores.

3. A generalized food energy cycle with a controlling balance in the fauna.

The concept of "Eltonian pyramid" is now usually included in the concepts of food chain, food web and trophic levels. The general theory, however, is still the same. Feeding starts with autotrophs capable of photosynthesizing solar radiation. The next level is comprised of herbivores feeding on these plants. Next in the food chain, feeding upon the herbivores, are the first level carnivores, followed by succeeding levels of carnivores (Hardesty 1977:50-51).

A general rule of thumb seems to be that each level contains about 10% of the total number of animals in the level beneath it. This is, of course, simplified, as some animals, such as man, feed directly from a number of trophic levels. It can be seen that the East African fossil fauna generally conforms to this schema as herbiverous forms far

TABLE 6.3

PERCENT OF TOTAL MAMMALIAN GENERA - BY ORDER

ORDER	E.Afr. Miocen sites total	Cent. Amer. rain-forest	N.Sou. Amer. rain-forest	South Asia rain-forest	Cent. Africa rain-forest	North Austr. everg. forest
MONOTREMATA	-	-	-	-	-	2
MARSUPIALIA	-	4	5	-	-	52
LIPOTYPHLA & MACROSCELIDEA	11	2.7	0.6	10	8	-
DERMOPTERA	-	-	-	0.4	-	-
CHIROPTERA	4	39.5	38	21	20	24
PRIMATES	9	4	7	6	6	2
EDENTATA	-	5	5	-	-	-
PHOLIDOTA	-	-	-	0.4	0.6	-
LAGOMORPHA	2	1.4	0.6	1.3	1.3	-
RODENTIA	21	25	26	29	26	19
CETACEA	-	-	0.6	2	-	-
CREODONTA & CARNIVORA	16	13	11	16	17	-
PINNIPEDIA	-	0.6	2.5	0.4	-	-
TUBULIDENTATA	2	-	-	-	0.6	-
PROBOSCIDEA	5	-	-	0.4	0.6	-
HYRACOIDEA	4	-	-	0.4	2	-
SIRENIA	1	0.6	0.6	0.4	-	2
PERISSO.	5	0.6	0.6	2	2	-
ARTIO.	20	3.4	2	11	15	-

TABLE 6.4

PERCENT OF TOTAL MAMMALIAN GENERA - BY ORDER CONTINUED

ORDER	E.Nor Amer. decid for.	West Europ decid for.	East Afric for/ sav.	South Afric wood/ sav.	E.Sou Amer. for/ sav.	North Amer. grass -land	Cent. South Amer. sav.
MONOTREMATA	-	-	-	-	-	-	-
MARSUPIALIA	2.5	-	-	-	6	9	1.2
LIPOTYPHLA & MACROSCELIDEA	7.5	11	9	9	-	-	8
DERMOPTERA	-	-	-	-	-	-	-
CHIROPTERA	26	13	17	16	22	20	9
PRIMATES	2.5	2.2	6	5	12	6	1.2
EDENTATA	-	-	-	-	8.5	6	1.2
PHOLIDOTA	-	-	0.6	0.6	-	-	-
LAGOMORPHA	5	4	1.2	1.2	0.8	1.3	4
RODENTIA	28	36	29	28	34	29	47
CETACEA	-	-	-	-	-	1.5	-
CREODONTA & CARNIVORA	10	22	16	18	9	13	18
PINNIPEDIA	10	2.2	-	2	3	6	4
TUBULIDENTATA	-	-	0.6	0.6	-	-	-
PROBOSCIDEA	-	-	0.6	0.6	-	-	-
HYRACOIDEA	-	-	2	2	-	-	-
SIRENIA	-	-	-	0.6	-	1.2	1.2
PERISSO.	-	-	1.2	2	0.8	1.2	-
ARTIO.	7.5	9	19	15	2.5	4	5

outweigh carniverous creatures. The proportion of carniverous genera (16%) is very similar to the proportions found in extant populations, and conforms to data presented by Savage (1977:268) suggesting that carnivores should comprise at least 10% of all mammalian genera.

It appears then, that the first two of Shotwell's postulates can be demonstrated in the general East African fossil fauna. Although an Eltonian pyramid cannot be fully demonstrated without a comprehensive analysis carried out using more factors than are completely available in a fossil situation, the data suggests that such a relationship indeed existed. The second postulate, that there should be more herbivores than carnivores, is demonstrated by the number of genera which fall into each group. Of the third, that there should be a generalized food energy cycle with a controlling balance in the fauna, it can only be stated that the percentages of the various orders of mammals from the Miocene do not, except in the instances mentioned above, diverge considerably from those found in extant populations. Thus, taken as a whole, using extant populations as analogues, the fossil fauna from the East African Miocene seems to constitute a reasonably complete unit.

This Miocene unit as a whole, however, has very little bearing on the numbers and percentages of forms found at each individual site. The fauna from each site must, of course, be considered on its own, separate from the fauna derived from other sites. The fact that the combined fauna for this region at this time may be considered reasonably complete, while significant in general terms, gives only the broadest of implications concerning the fauna from each individual location.

7. BUKWA

Bukwa is an important site primarily because of the fossil fauna and flora which have been recovered there, but also for the K/ar dates obtained. Unfortunately there are no Proconsul forms in the Bukwa fossil fauna but the above factors make its inclusion relevant to the finds from other sites. The site of Bukwa is located on the slopes of Mount Elgon in Eastern Uganda (Lat. 0 58'N Long. 34 8'E).

7.1 GEOLOGY

Bukwa consists of two separate locations, Bukwa I and II. Bukwa I is a remnant of a paleosol lens that has yielded remains of Deinotherium (Walker 1969:592). The principal site, however, is Bukwa II which lies at the foot of Kwongori Hill.

The fossiliferous deposits at Bukwa II are bracketed by lava flows and other volcanic detritus (Bishop, Miller and Fitch 1969). The base of the fossiliferous strata lies at an elevation of 5,900 feet above sea level (Walker 1969). The principal fossil bearing horizon is composed of a green clay heavily laced with ostracods. Successive layers are made up of a sequence of tuffaceous deposits with horizons of sedge, grass and leaf fossils, capped by a small outcrop of nephelinite lava (Walker 1969, Brock and McDonald 1969). The ostracod clay represents deposition in a lacustrine environment of some sort but the precise depositional mechanism depends upon interpretation.

Chaney (1933) suggests that the fossils were deposited in a series of basins each showing lacustrine sands and other sediments, notably leaves, fruit and wood (Lind and Morisson 1974). VanCouvering and VanCouvering (1976) are essentially in agreement with this concept. They state that the preservation of fossils occurred in small mud ponds which were inter-bedded with Elgon lavas. It has also been suggested, however, that deposition was in a small lake rather than in ponds or small basins (Brock and McDonald 1969). A small lake as a depositional environment appears more likely as the fossil fauna contains crocodiles and medium size fish (Walker 1969), which would probably be more suited to a body of water larger than a mud pond. The lake itself was probably caused by faulting which disrupted the riverine system and led to the collection of water in low lying areas. Alternatively, locally deposited tuffs could also have blocked drainage (Brock and McDonald 1969).

In any event, a number of geological facts seem to be more or less certain, and agreed upon by most researchers, in regard to Bukwa II. First, the site occurred upon a lava flow and was eventually covered by a second flow. Second, the deposits were layered in a body of water of some size. Finally, the deposits occurred at a time of continuing volcanic activity in the area, a fact evidenced by tuff formation in the fossiliferous sequence.

7.2 DATING

The following K/ar dates have been obtained from the nephelinite lava at the base of the Bukwa II sequence, below the fossiliferous horizon.

1. 24.2 +/- 0.7 (Bishop 1972).
2. 24.3 +/- 0.7 (Pickford 1981).
3. 17.2 +/- 0.4 (Bishop, Miller and Fitch 1969).

The lava flow above the fossil bearing layer has also been dated:

1. 19.8 +/- 1.5 (Bishop, Miller and Fitch 1969).
2. 22.0 +/- 0.2 (Bishop, Miller and Fitch 1969).
3. 21.9 +/- 0.2 (Bishop, Miller and Fitch 1969).
4. 20.1 +/- 0.3 (Pickford 1981).

On the basis of this evidence the age of the Bukwa II fossils is estimated to be 22 m.y. (Brock and McDonald 1969), 23 m.y. (VanCouvering and VanCouvering 1976) or 20 m.y. (Lind and Morisson 1974). The most probable age of Bukwa II is 22-23 m.y.

The 17.2 +/- 0.4 date obtained from the lower flow is considered to be discrepant as the upper flow is clearly dated to be older than 17 m.y. (Walker 1969). The dating of Bukwa II is interesting as it seems to be considerably older (5-6 m.y.) than most of the East African Miocene sites (Pickford 1981).

7.3 ABUNDANCE OF PROCONSUL FORMS

None.

7.4 FAUNA

The following faunal list for Bukwa II was published by Walker (1969:592). Frequency data are from VanCouvering and VanCouvering 1976 (P indicates form is present but in unidentifiable quantities).

	FREQ. (M.N.I.)
1. INSECTIVORA	
a) *Myohyrax oswaldi* and others	P
2. PRIMATES	
a) *Limnopithecus legetet*	P
3. CARNIVORA	
a) small and medium sized carnivores	
4. PROBOSCIDEA	
a) (*Pro*)*Deinotherium hobleyi* and others	P
5. RODENTIA	
a) *Megapedetes pentadactylus* and others	P
6. HYRACOIDEA	
a) *Megalohyrax championi* (*Pachyhyrax*?)	P
b) *Meroehyrax bataeae*	1-10
7. PERISSODACTYLA	
a) *Chilotherium pattersoni*	P
b) *Dicerorhinus sp*.	P
8. ARTIODACTYLA	
a) *Brachyodus aequitorialis* (?)	
b) *Hyoboops africanus*	*

c) *Diamantohyus africanus*	*
d) *Bunolistriodon jeanelli*	P
e) *Dorcatherium parvum*	P
f) *Dorcatherium pigotti*	P
g) tragulid	*
h) *Paleomeryx sp.*	*

In the above list, species marked with a (*) are forms not cited as occurring at Bukwa by VanCouvering and VanCouvering (1976), thus there is no frequency data available. Additions to the above list were contained in VanCouvering and VanCouvering (1976). They are:

1. PROBOSCIDEA

a) *Platybelodon kisumuensis*	P
b) *Gomphotherium* (?)	

2. RODENTIA

a) *Paraphiomys stromeri*	P
b) *Paraphiomys pigotti*	P

3. ARTIODACTYLA

a) *Masritherium aequitorialis*	P
b) *Xenochoerus africanus*	1-10

7.4.1 FAUNAL ANALYSIS

7.4.2 Habitat Indicator Species

As might be expected from such a limited faunal sample, the habitat indicators are mixed. While *Megapedetes pentadactylus* is generally believed to have been associated with a savanna, or even drier, type of habitat (VanCouvering and VanCouvering 1976), the Tragulids, notably *Dorcatherium* may be considered as forest indicators (Nesbit Evans et al 1981). Likewise, the two species of *Paraphiomys*, *stromeri* and *pigotti* may be forest indicators as they are members of the Theridomyidae, an extinct group of the Anomaluroidea (Leakey 1967). In total, both forest and savanna type environments are indicated at Bukwa, but neither strongly.

7.4.3 Relative Abundances

Because of the limited sample, conclusions based on the relative abundance of the forms represented must be very speculative. However, 10 of the 24 species present are ungulates, representing 42% of the sample, a considerable portion. Small ungulates dominate the fauna in extant secondary forests in West Africa (Bourliere 1963), and such an environment might also have been present at Bukwa. There is no real evidence to support such a conclusion, however, and with a faunal list of only 24 forms relative abundance statistics cannot be relied upon.

7.4.4 Taxonomic Habitat Index

Not used here because of the limited faunal sample.

7.4.5 Ecological Diversity Analysis

The ecological diversity analysis has been calculated despite the incomplete nature of the Bukwa fauna (table 7.1). Unfortunately, such factors as exact size, locomotor adaptation and feeding adaptation cannot be assessed with certainty in a fossil form, and thus, this analysis must be, to a certain degree, speculative. Despite the above constraints, however, some broad ecological implications concerning the environment at Bukwa can be gained through this analysis.

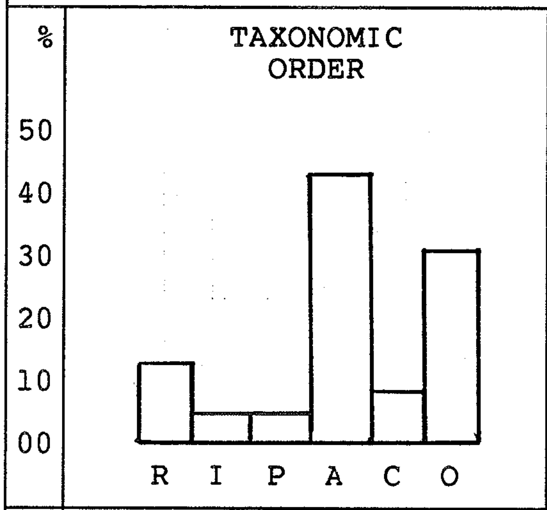
None of the ecological diversity analysis spectra from Bukwa match closely those from extant populations provided by Nesbit Evans et al (1981). Their closest analogues are, however, as follows:

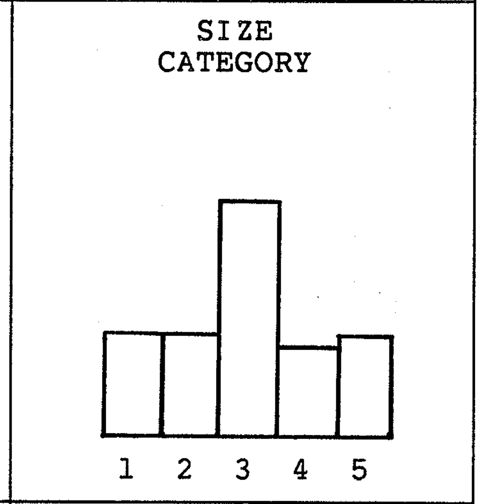
1. Taxonomic order - the Bukwa pattern is most similar to the extant floodplain and woodland-bushland patterns.
2. Size category - the Bukwa spectrum is most similar to the montane forest pattern.
3. Locomotor adaptation - is most similar to the extant woodland-bushland pattern.
4. Feeding adaptation - most closely resembles the extant woodland-bushland pattern.

In total, from the limited amount of information available, the ecological diversity analysis tends to indicate that the woodland-bushland biome was dominant at Bukwa.

TABLE 7.1

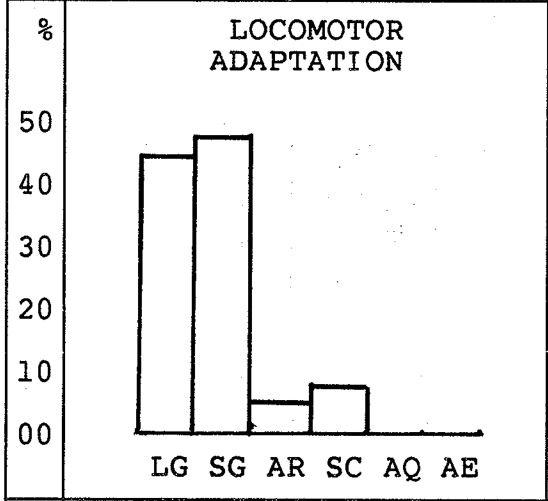
ECOLOGICAL DIVERSITY ANALYSIS-BUKWA

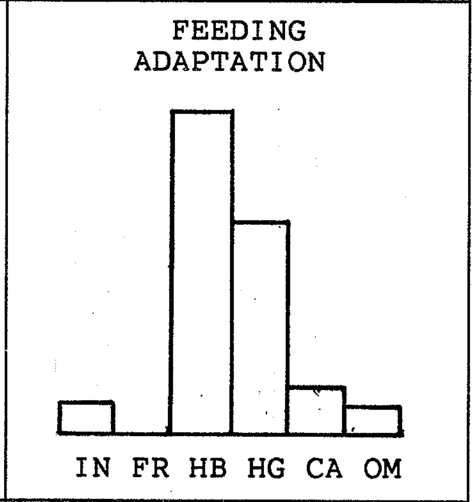




R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.





LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

7.4.6 Non-mammalian fauna

The Bukwa fauna is also rich in non-mammalian forms, which is somewhat uncommon in an East African Miocene site. Most of these forms reflect the obvious lacustrine deposition at Bukwa. This fauna includes: ciconiiform birds, crocodiles, trionychid and pelomedusid water tortoises, medium and tiny freshwater fish, ostracods (*Heterocypus sp.*), potamid crabs and some millipede fragments (Walker 1969).

A number of gastropods have also been recovered at Bukwa. These have been described by Andrews and VanCouvering (1975:82-83).

-------GASTROPOD----------	ECOLOGICAL INDICATION
1. *Maizania* (4 *sp.*)	evergreen forest
2. *Homorus* (*Subulona*)	wet evergreen forest
3. *Burtoa nilotica*	woodland
4. *Limicolaria* (2 *sp.*)	forest-bushland
5. *Thapsia*	forest
6. *Tayloria* (2 *sp.*)	drier evergreen forest & bush
7. *Gulella* (3 *sp.*)	forest and thicket

The obvious implication of the gastropods is that some kind of forest existed at, or near, Bukwa, but the exact character of the biome is less clear. The indications are divided between more open forest-woodland- bushland on one hand, and closed evergreen forest on the other.

7.5 FLORA

Bukwa has one of the best collections of fossil flora from the East African Miocene period. The following list (all are leaves, fruit or wood) has been compiled from: Chaney (1933), Philips (in Chaney 1933), Walker (1969), Palmer and Pitman (1972) and Lind and Morisson (1974).

------FLORA--------------------	DESCRIPTION
1. POLYPODIACEAE	
a) *Acrostichum sp.*	fern
2. LEGUMINOSAE	

a) *Bauhinia waylandi*	large shrub or sm. tree
b) *Berlina* (*2 sp.*)	small tree
c) *Cassia sp.*	(uncertain)
d) *Dahlbergia sp.*	tree, shrub or climber
3. OLEACEAE	
a) *Olea sp.* (*cf. africana*)	tree
4. ROSACEAE	
a) *Parinari sp.*	tree or shrub
5. PITTOSPORACEAE	
a) *Pittosporum* (*5 sp.*)	trees or shrubs
6. COMBRETACEAE	
a) *Terminalia sp.*	tree or shrub
7. MELIANTHACEAE	(uncertain)
a) *Bersama sp.*	(uncertain)
8. STERCULIACEAE	(uncertain)
a) genus and sp.	shrub or tree

Most of the trees and shrubs from Bukwa may be construed as indicators of tropical conditions as many of the families and genera listed are still extant in tropical Africa today (Chaney 1933). In addition to the trees and shrubs, grasses, sedges, *Truncellus* rhizomes and a herb *Jencellus laevigatus* have also been recovered (Walker 1969). The latter forms may indicate alkaline soil conditions caused by volcanic ash fall (VanCouvering and VanCouvering 1976). The fern, *Acrostichum* indicates fairly moist conditions, not surprising considering the lacustrine nature of the sediments (Chaney 1933).

The Bukwa flora indicates to Walker (1969) and Andrews and VanCouvering (1975) that an evergreen forest biome existed at, or very near, the site. VanCouvering and VanCouvering (1976) also suggest some kind of forest existed because of the number and kind of trees present. Chaney, however, states that the size of the leaves recovered is critical (1933:707). He believes that the leaf sizes from Bukwa are more consistent with those found in extant savanna or woodland biomes. Many of the Bukwa leaves are of small size while larger leaves would be more characteristic of a tropical rainforest. Thus, once again, both open and closed forest conditions are indicated, depending upon interpretation.

7.6 PALEOGEOGRAPHY

The site of Bukwa II lay on the slopes of Mt. Elgon and likely consisted of a small lake surrounded by forest of some character. The exact nature of the forest is debatable but neither the faunal nor the floral analysis strongly support the closed evergreen forest biome envisioned by Andrews and VanCouvering (1975). While many of the habitat indicator species are primarily forest dwelling forms, none are the clear cut forest oriented species such as *Rhynchocyon* or *Paranomalurus*. Both the relative abundance figures and the ecological diversity analysis tend to reflect a more open environment, perhaps some kind of woodland. The implications from the gastropods and the flora were evenly divided between open and closed forest conditions. In total, then, there seem to be more indicators pointing to a woodland-bushland or similar environment at Bukwa, as opposed to a rainforest or an evergreen forest biome.

8. KARUNGU

Lying under volcanic deposits from the Kisingiri volcano, 45 km. South of Rusinga Island, is the site of Karungu (34 12'E 00 52'S).

8.1 GEOLOGY

At the base of the fossil bearing lithologies of Karungu lies an arkose bedrock formation. The main fossiliferous strata itself is composed of red marl, limey arkosic grits and yellow sands (VanCouvering and VanCouvering 1976). The fossil beds contain no significant amounts of pyroclastic material and no detritus from lava flows, leading to the conclusion that the site preceds most of the volcanic activity at Kisingiri (VanCouvering and VanCouvering 1976).

The marl and sands indicate that the deposits were layered in water. Two differing interpretations suggest that the depositional medium was partly lacustrine (Andrews and VanCouvering 1975) or fluvatile (VanCouvering and VanCouvering 1976). The latter authors believe that Karungu lay on a floodplain which was broken by numerous fluvatile channels. Nesbit Evans et al (1981) agree with the floodplain/fluvatile setting, citing the fact that there is hydronamic sorting in the deposits, more likely in a riverine or flood channel depositional environment than in a lacustrine setting.

The fossiliferous deposits themselves are usually considered as a single unit although they do not all come from the same beds (Pickford 1981:87). The largest single fossil bearing location, containing only fifteen species, was uncovered by Oswald in 1914, and is named Bed 16. Subsequent investigations have added substantially to the Karungu faunal inventory.

8.2 DATING

Only one K/ar date has been obtained from Karungu, this being 22.5 +/- 0.4 m.y. (from biotite)(Bishop, Miller and Fitch 1969:697). This date has, however, been questioned by Pickford (1981). After analysing the Karungu fauna, he suggested that it was very similar to that from the Hiwegi horizon on Rusinga Island, dated quite securely at approx. 18.5 m.y. Since, Pickford believes, the fauna would not likely be so continuous over 5 million years, the two sites are probably contemporaneous. VanCouvering and VanCouvering, however, do not question the date and point out that the lithology of Karungu is similar to that from the Lower Kiahera Formation on Rusinga Island (dated at approx. 23 m.y.). Both these fossiliferous horizons overlie arkose formations and neither contain pyroclastics from the Kisingiri volcano (VanCouvering and VanCouvering 1976). The Hiwegi formation, on the other hand, is characterized by tuffaceous redbeds, at least partially volcanic in origin (VanCouvering and VanCouvering 1976). Thus, they are not likely to be contemporaneus with the Karungu deposits.

Pickford's argument does not have any geological basis but, nevertheless, must be considered. While it is not necessary, in evolutionary theory, that a fauna must show significant change over a considerable length of time, it is assumed that it will. The question, then, really revolves around how similar the two faunas are. As will be discussed below, while many of the species present, are, in fact, common to both sites, there are also considerable differences in the two faunas, which tends to weaken Pickford's contention. Since the K/ar date and the geological evidence both point to a date of approximately 23 m.y., this must be considered accurate, at least for the time being.

8.3 ABUNDANCE OF PROCONSUL FORMS

Proconsul nyanzae (M.N.I.=2) (Andrews 1978).

8.4 FAUNA

The following faunal list has been drawn from VanCouvering and VanCouvering (1976) and Wilkinson (1976).

1. MACROSCELIDEA	FREQ.
a) *Myohyrax oswaldi*	>100
2. PRIMATES	
a) *Dendropithecus macinnesi*	1
b) *Proconsul nyanzae*	2
3. CREODONTA	
a) *Anasinopa leakeyi*	11-100
b) *Metapterodon kaiseri*	1-10
c) *Pterodon africanus*	1-10

4. CARNIVORA	
a) *Metailurus africanus*	1-10
5. PROBOSCIDEA	
a) *Prodeinotherium hobleyi*	P
b) *Platybelodon kisumuensis*	P
c) *Gomphotherium sp.*	?
d) *Primelephhas lepersonnei*	?
6. LAGOMORPHA	
a) *Kenyalagomys rusingae*	11-100
7. RODENTIA	
a) *Paraphiomys stromeri*	1-10
b) *Paraphiomys pigotti*	11-100
c) *Diamantomys leuderitzi*	>100
8. HYRACOIDEA	
a) *Pachyhyrax championi*	P
b) *Pachyhyrax cf. pygmaeus*	1-10
9. PERISSODACTYLA	
a) *Chalicotherium rusingense*	P
b) *Aceratherium acutirostratrum*	1-10
c) *Dicerorhinus leakeyi*	1-10
d) *Brachypotherium heinzelini*	1-10
10. ARTIODACTYLA	
a) *Masritherium aequitorialis*	11-100
b) *Brachyodus africanus*	1-10
c) *Hyotherium dartevellei*	3
d) *Xenochoerus africanus*	6
e) *Dorcatherium crassum*	1-10

f) Dorcatherium pigotti	1-10
g) Dorcatherium parvun	1-10
h) Canthumeryx sirtensis	?
i) Walangania africanus	?

8.4.1 FAUNAL ANALYSIS

8.4.2 Habitat Indicator Species

The fauna is dominated by two forms, Myohyrax oswaldi and Diamantomys leuderitzi. Both of these species are characterized by extremely hypsodont teeth which suggest a grazing adaptation to coarse ground vegetation (Pickford 1981). The lagomorph Kenyalagomys rusingae is well represented, and may be considered as an indicator of non or lightly forested conditions. Possible indicators of forest conditions are the two species of Paraphiomys and the Tragulids. In total, however, the indicators more clearly point to an open biome as opposed to closed forest conditions.

8.4.3 Relative Abundances

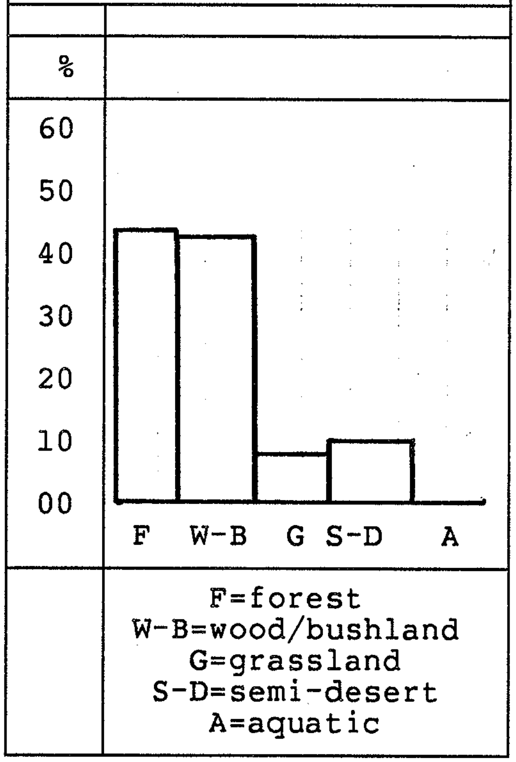
Although only three species of rodents are known from Karungu one form, Diamantomys leuderitzi is represented by over 100 individuals. This dominance by a single species of rodent is common in open woodland and grassland situations (Andrews and VanCouvering 1975). Furthermore, a high percentage of the Karungu mammalian species (42%), are ungulates, which also might be an indicator of non closed forest conditions.

8.4.4 Taxonomic Habitat Spectrum

Although this analysis must be considered suspect when computed using a small sample, it will be included here as it has been calculated by Nesbit Evans et al (1981).
This analysis points equally to both the forest and the more open woodland-bushland biomes.

TABLE 8.1

HABITAT SPECTRUM



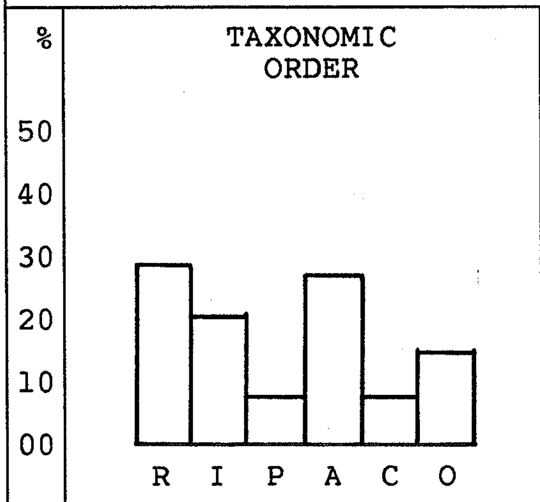
F=forest
W-B=wood/bushland
G=grassland
S-D=semi-desert
A=aquatic

8.4.5 Ecological Diversity Analysis

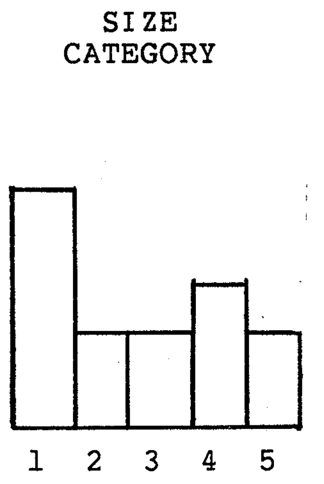
The Karungu ecological diversity analysis has also been calculated by Nesbit Evans et al (1981). As these authors point out, the percentages for Karungu (similarly for other sites) do not exactly match modern community structures, so the environment cannot be inferred with absolute certainty. Rather than comparing all four categories as a unit, it may be more revealing to assess the closest extant analogue in each category individually. In the Karungu sample, using this method, no clear pattern emerges. The taxonomic order spectrum most closely matches that from extant woodland-bushland biomes, size category - floodplain, locomotor adaptation category - grassland : the feeding adaptation spectrum does not resemble that from any modern environment. In total, while this analysis does not point to any particular environment, it does generally tend to point away from a closed forest biome.

TABLE 8.2

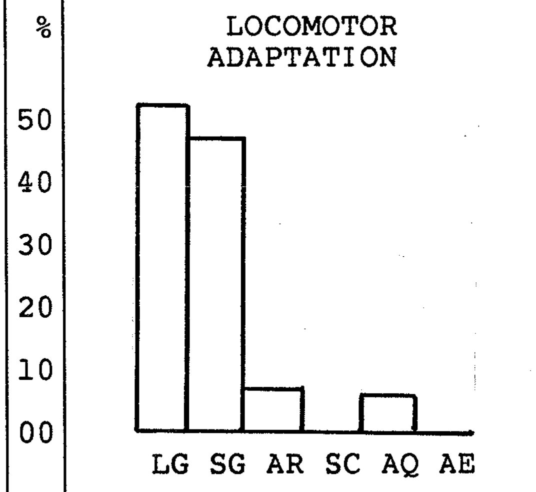
ECOLOGICAL DIVERSITY ANALYSIS-KARUNGU


TAXONOMIC ORDER

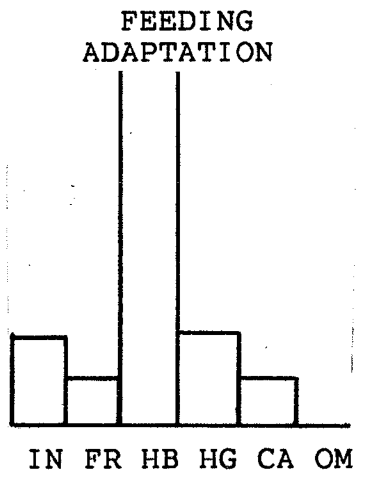
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER


SIZE CATEGORY

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.


LOCOMOTOR ADAPTATION

LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL


FEEDING ADAPTATION

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

There is no data available concerning non-mammalian fauna from Karungu.

8.5 FLORA

There are no published floral remains from Karungu.

8.6 PALEOGEOGRAPHY

It is probable that Karungu lay on a floodplain. The depositional environment was either lacustrine, or, more likely, riverine. The analyses of the Karungu fauna tend to suggest that the surrounding environment was quite open, not a closed evergreen forest, as has been suggested by Andrews and VanCouvering (1975). It is interesting to note that neither of the two East African sites dated @23 m.y. (Karungu and Bukwa) show strong indications of a fully developed forest biome. Since later sites, particularly those dated to @18-19 m.y., show strongly developed forest facies, it may be possible that the time of major forest development in this area was between 23-18 m.y., rather than before 23 m.y.

9. KIRIMUN OR KIRIMON

An Eastern Rift site (36 54'E, 00 43'N), Kirimon is one of the most poorly known Miocene African locations.

9.1 GEOLOGY

The only geological analysis thus far carried out at Kirimon was done by Shackleton in 1946. He placed the site in conjunction with "Rumuruti phonolite" which overlies the basal Samburu basalt. Shackleton's work is largely accepted by VanCouvering and VanCouvering (1976:170) although his Samburu basalt is now named Upper Turkana basalt (tvb2), with the Samburu basalt being considered much older. The depositional environment is a lakebed (VanCouvering and VanCouvering 1976).

9.2 DATING

There are no radiometric dates from Kirimon so estimates of its age are based upon geological and faunal grounds. Bishop (1967) placed Kirimon as a Late Miocene or Early Pliocene site while VanCouvering and VanCouvering (1976) date it to approximately 13 m.y., both estimates, presumably, based on the geology of the site. Pickford (1981:89) dates it at 17.5-18 m.y. because of similarities between the Kirimon fauna and those from other sites dated to this age.

None of the above estimates can be considered to be based on particularly solid grounds. VanCouvering and VanCouvering (1976:170) themselves point out that the geology of the Eastern Rift is very confused, which indicates that their placement of the site must be suspect. Similarly, the faunal list contains only 9 species so dating on faunal grounds is very uncertain. Nevertheless, the one specimen assigned to *Proconsul major*, if it does in fact belong to that species, would seem to indicate an earlier date than 12-13 m.y., as there is no corroborative evidence from other sites that *P. major* survived this long.

9.3 ABUNDANCE OF PROCONSUL FORMS

Proconsul major(?) - 1 individual (Pickford 1981).

9.4 FAUNA

The following faunal list is from Pickford (1981), there are no frequency figures available.

1. PRIMATES
   - a) *Proconsul major* (?)
2. PROBOSCIDEA
   - a) "Mastodon"
3. RODENTIA
   - a) *Diamantomys leuderitzi*
   - b) *Paraphiomys stromeri*
   - c) *Paraphiomys pigotti*
4. PERISSODACTYLA
   - a) *Aceratherium acutirostratrum*
   - b) *Chalidotherium pattersoni*
5. ARTIODACTYLA
   - a) *Dorcatherium parvun*
   - b) *Canthumeryx sp.* (?)

No faunal analysis will be carried out as the sample is too small to yield significant results.

9.4.1 Non-mammalian fauna

In addition to the mammalian fauna, two forms of gastropods are also known from Kirimon (Andrews and VanCouvering 1975). They are: *Ligatella* (2 sp.) and *Saulea*. Extant members of the former genus inhabit bushland areas while those from the latter are widely distributed (Andrews and VanCouvering 1975:82-83). Thus, no firm conclusions can be drawn from this information.

9.5 FLORA

There are no published floral remains from Kirimon.

9.6 PALEOGEOGRAPHY

The depositional environment at Kirimon is described by VanCouvering and VanCouvering (1976) as being lakebed, although, perhaps, a lake margin location is also possible. The surrounding paleoecology is basically unknown and even the dating is suspect.

According to Pickford (1981) the specimen of *P. major* has been reanalysed after new work at Kirimon, and may, in fact, not be primate at all. The new excavations have, however, yielded new fossils, and this will lead to an expansion of the Kirimon faunal list in the near future. If *Proconsul major* did live at, or near, this site, it may be possible to reconstruct the paleoecology of Kirimon using ecological parameters defined for this species from other sites.

10. KORU

Koru (35 16'E, 00 09'S) lies within the Tinderet volcanic sequence at the Eastern end of the Kavirondo Rift Valley. It has variously been treated, in regard to the fauna, as a single faunal unit (Andrews and VanCouvering 1975:77), three discrete units (Pickford 1981, Nesbit Evans et al 1981), four discrete units (Pickford and Andrews 1981), or a single unit together with the fauna from the Songhor sites (VanCouvering and VanCouvering 1976). In the interest of obtaining the maximum amount of ecological information available, the Koru fossils will be treated here as representing four different communities from four sites: Meswa Bridge, Koru, Legetet and Chamtwara.

10.1 GEOLOGY

The entire succession in the Koru area, centered on Legetet Hill to the West of Tinderet, has been analysed and mapped by Pickford and Andrews (1981) and drawn into a general stratigraphy of the area. This was necessary as the Koru sites are dispersed in a number of locations, rather than overlying one another in a single succession. Thus , in this case, the geology of the whole area must be known in order to assess the relationship between the separate sites.

In the Tinderet area a layer of coarse agglomerate called the Muhoroni conglomerates lies just above the basement granite and gneiss (VanCouvering and VanCouvering 1976). It is characterised by volcanic cobbles and lapilli tuff matrix which indicates nearby volcanic activity. Root casts and fossil wood are common, although as yet unanalysed, and fossil animals are rare except at Meswa Bridge (Pickford and Andrews 1981, Andrews et al 1981).

Overlying the Muhoroni agglomerates are the finer grained deposits of the Koru formation (Pickford and Andrews 1981). These deposits are stratified with paleosol horizons, weathering profiles and root casts present. The depositional medium throughout the whole formation is generally tuff. Gastropods are common in the paleosols, and, although the unit is not greatly fossiliferous as a whole, the Koru site is found in this horizon.

In some locations the Koru formation is succeeded by Legetet carbonates. The Legetet formation is comprised of six stratiform carbonate units separated by paleosols and weathering horizons (Pickford and Andrews 1981). The fossils composing the Legetet site are found in the paleosol lenses, the carbonates themselves being unfossiliferous. In some places the Legetet carbonates are succeeded by Walker's limestone composed of well bedded calcified tuff which is sparsely fossiliferous (Pickford and Andrews 1981).

Variously overlying the Walker's limestone deposits and the Legetet formation, sometimes to a depth of 200 m., lies the Kapurtnay agglomerates. These agglomerates are largely non-fossiliferous but towards the top of the formation in the Chamtwara area lies a horizon of well bedded calcified tuffs with intercalcated red marls. The Chamtwara fossil location as well as the site of Songhor are found here (Pickford and Andrews 1981).

There is some variation in the depositional environments at the various Koru sites. Meswa Bridge lies in a fluvatile channel cut contemporaneously into the volcanic ejecta. The Muhoroni agglomerates, from the gastropod and wood fossils as well as the root casts, appear to be subaerial in nature (Pickford and Andrews 1981). Similarly, the Koru formation, the Legetet carbonates and the Chamtwara member all appear, from the paleosols and weathering horizons, to have been deposited subaerially (Pickford and Andrews 1981). The above information, coupled with the fact that aquatically oriented forms are very uncommon in the faunas, leads to the conclusion that the majority of the Koru sites were buried under successive eruptions from the Tinderet volcano, or even some more distant cone (Pickford and Andrews 1981).

10.2 DATING

A number of radiometric dates were obtained by Bishop, Miller and Fitch (1969:677) from the Koru sequence, although their exact provenance is uncertain. The material used was mica, from tuff, and the dates obtained were:

1. 24.6 +/- 8.0 m.y.
2. 34.0 +/- 8.0 m.y.
3. 51.0 +/- 2.0 m.y.
4. 72.0 +/- 3.0 m.y.

None of these can be reasonably considered accurate, the first two because of their high +/- values, and the second two because they are aberrantly high when compared to other dates which have been obtained from this site.

These other dates are: 19.6 +/- 0.3 m.y. and 19.5 +/- 0.3 m.y., and they were obtained from samples of biotite (Bishop, Miller and Fitch 1969). These dates were also cited by Pickford and Andrews (1981), who say they probably come from the Koru formation. Other radiometric dates obtained by Pickford and Andrews are:

1. 23.6 m.y. from the Muhoroni agglomerate.
2. 23.5 m.y. from the Muhoroni agglomerate.
3. 19.6 m.y. from the Chamtwara member/Songhor.
4. 9.7 m.y. from the Kapurtnay agglomerates

The stratigraphic and absolute dating of Koru, as envisioned by Pickford and Andrews (1981) can be seen in table 10.1.

TABLE 10.1

KORU, STRATIGRAPHY AND DATING

FORMATION	SITE	K/ar DATE
Kapurtnay agglomerate		
Chamtwara member/Songhor	Chamtwara/Songhor	19.6
Kapurtnay agglomerate	Kapurtnay	19.7
Walker's limestone		
Legetet formation	Legetet	
Koru formation	Koru	19.5, 19.6
Muhoroni agglomerate	Meswa Bridge	23.5, 23.6

10.3 ABUNDANCE OF PROCONSUL FORMS

Because of the wealth of material which has only recently been uncovered at Koru the actual number of Proconsulines represented (M.N.I. analysis) is difficult to assess. The most recent excavations have yielded new material (Pickford and Andrews 1981) but this has been published only as number of specimens uncovered, rather than as minimum numbers represented. As of 1978 there was material representing three individuals each of _Proconsul africanus_ and _Proconsul major_ (Andrews 1978). The new specimens, and their descriptions, were listed by Martin (1981:141-146). The figures in table 10.2 have been calculated from his list.

TABLE 10.2

RECENT PROCONSUL FINDS FROM KORU

SITE	Proconsul africanus		Proconsul nyanzae	
	# specimens	M.N.I.	# specimens	M.N.I.
Koru	3	1	3	1
Legetet	4	1	11	1+1 im.
Chamtwara	12	1+1 im.	22	2+1 im.
Kapurtnay	1	1	0	0
Total	20	5	36	7

im. = immature individual.

Unfortunately, there appears to be some confusion regarding the number of specimens recovered in recent excavations as Pickford and Andrews's count (1981) differs considerably from Martin's (1981). The former authors list only 18 and 15 specimens attributable to _P. africanus_ and _P. major_ respectively, as compared to 20 and 36 listed by Martin. Martin's count will be accepted here because he has itemized each piece and described them in some detail.

Presumably, since the above are all referred to as new specimens they must be considered to be in addition to the six individuals recorded up to 1978 (Andrews 1978:208). It is unfortunate that these previously recorded individuals are listed only as coming from Koru. At the present time it is impossible to know which of the four Koru sites, if any, to which they should be assigned. The combined total of new and old finds can be seen in table 10.3.

TABLE 10.3

M.N.I. OF PROCONSUL FORMS FROM KORU

SITE	P.africanus	P.major	UNCERTAIN
KORU	1	1	-
LEGETET	1	3	-
CHAMTWARA	2	3	-
KAPURTNAY	1	-	-
MESWA BRIDGE	-	-	2
KORU (UNCERTAIN)	3	3	-
TOTAL	8	10	2

The Meswa Bridge site has yielded immature Dryopithecine remains which cannot be clearly attributed to any Proconsul species (Andrews et al 1981). Finally, Koru, Legetet and Chamtwara have produced many specimens of Limnopithecus legetet, Dendropithecus macinnesi and Micropithecus clarki (Harisson 1981). The most common of these is Limnopithecus legetet.

10.4 FAUNA

The following faunal list has been drawn from Pickford and Andrews (1981), Martin (1981) and Harisson (1981). There is no faunal list available for Meswa Bridge or Kapurtnay.

X= uncertain.

TABLE 10.4

KORU FAUNA (# of SPECIMENS)

ORDER	GENUS/SPECIES	KO	LE	CH
INSECTIVORA	Erythrozootes chamerpes	-	1	1
	Prochrysochloris miocaenicus	2	9	6
	Protenric tricuspis	-	1	9
	Geogale aletris	-	-	3
	Gymnurechinus leakeyi	-	6	1
	Amphechinus rusingensis	1	11	29
	Galerix africanus	5	1	15
	Rhynchocyon clarki	1	5	16
	Rhynchocyon sp.	1	1	2
	Myohyrax oswaldi	-	-	15
CHIROPTERA	Taphozous incognita	-	1	-
	Propotto leakeyi	1	1	7
	Hipposideras sp.	-	-	1
PRIMATES	Progalago dorae	-	X	X
	Progalago minor	-	X	X
	Progalago robustus	-	X	X
	Limnopithecus legetet	2	22	89
	Proconsul af. africanus and P. af. koruensis	3	4	12
	Proconsul major	3	11	22
	Dendropithecus macinnesi	-	-	19
	Micropithecus clarki	1	17	60
CARNIVORA	Teratodon spekei	3	6	7
	Hyaenodon andrewsi	-	2	3
	Hecubides eurydon	-	-	4
	Kichechia zamane	2	3	5
TUBULIDENT.	Orycteropus minutus	1	-	3
PROBOSCIDEA	Prodeinotherium sp.	1	-	-
	Gomphotherium sp.	-	3	-
RODENTIA	Diamantomys leuderitzi	4	89	57
	Paraphiomys pigotti	5	18	16
	Paraphiomys stromeri	1	4	7
	Epiphiomys corydoni	-	5	5
	Phiomys andrewsi	-	5	2
	Simonomys genovefae	-	11	-

	Kenyamys mariae	-	3	-
	Elmerimys woodi	-	-	1
	Paranomalurus soniae	-	5	6
	Paranomalurus bishopi	-	7	6
	Paranomalurus walkeri	-	3	14
	Afrocricetodon songhori	2	17	6
	Notocricetodon petteri	-	5	-
	Bathyergoides sp.	1	8	3
	Megapedetes sp.	-	-	1
	Vulcaniscurius africanus	-	-	1
HYRACOIDEA	Pachyhyrax championi	-	1	-
PERISSO.	Chalicotherium rusingense	3	1	4
	Dicerorhinus africanus	1	-	-
ARTIO.	Hyotherium kijivium	2	1	-
	Dorcatherium songhorensis	X	X	X
	Walangania africanus	1	X	X
	TOTAL # SPECIMENS	47	288	458
	TOTAL # SPECIES PRESENT	24	39	41

10.4.1 FAUNAL ANALYSIS

10.4.2 Habitat Indicator Species

1. KORU - The most ambiguous of the three sites under analysis, probably because the fauna is impoverished compared to the others. Neither forest nor non-forest indicators are strongly represented. The two species of Rhynchocyon would be good forest indicators except they are each represented by only a single specimen. Similarly, two species which probably preferred a more open habitat, Bathyergoides sp. and Orycteropus minutus are also poorly represented.

   It is interesting to note that clear forest indicators, the Anomalurids, fairly common at the other two sites, are completely absent from Koru. Thus, while it is by no means certain, it may be possible that the environment at Koru was more open than that at the other two sites.

2. LEGETET - The indicators of a forest environment are clear here. Three species of Anomalurids are represented as well as two species of Rhynchocyon, two species of Paraphiomys and a number of small pri-

mates: all which tend to indicate forested conditions prevailed at Legetet.

3. CHAMTWARA - Since the species represented at Chamtwara are almost exactly the same as those from Legetet, it appears likely that forest conditions prevailed here also.

10.4.3 Relative abundances

1. KORU - The faunal list, consisting of only 24 species is dominated by insectivores (5), rodents (5), and ungulates (5), each of which comprise 21% of the sample. Primates are also common, with 4 species known. On the basis of the number of specimens recovered none of the rodents apparently dominated the others numerically, although the reduced nature of the fauna makes such conclusions tenuous. In total, the relative abundances within the Koru fauna do not point to any particular environment.

2. LEGETET - The greatest number of specimens recovered indicates that rodents and small primates were common at Legetet. This is exactly the situation described by Bourliere (1963) as existing in the evergreen forests of West Africa today. Furthermore, rodents constitute 33% of the sample but the single most common species, Diamantomys leuderitzi constitutes less than 50% of the rodent specimens recovered, which may also be indicative of forest conditions (Nesbit Evans et al 1981, Andrews and VanCouvering 1975). Thus, a forest environment is again indicated at Legetet.

3. CHAMTWARA - The situation at Chamtwara is almost identical to that at Legetet, except that primates are even more common (20% of species, 44% of specimens recovered). As at Legetet, forest conditions likely prevailed here also.

10.4.4 Taxonomic Habitat Spectra

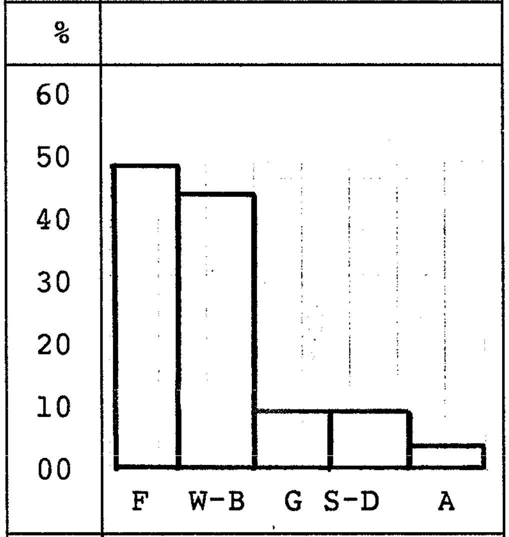
The taxonomic habitat spectra for all three of the major Koru sites have been calculated by Nesbit Evans et al (1981).

The taxonomic habitat spectra clearly demonstrate that the affinities of both the Legetet and the Chamtwara faunas lie with the forest biome. The Koru fauna again yielded an ambiguous result. Comparing the spectra from Legetet and

TABLE 10.5

HABITAT SPECTRUM

KORU



F=forest
W-B=wood/bushland
G=grassland
S-D=semi-desert
A=aquatic

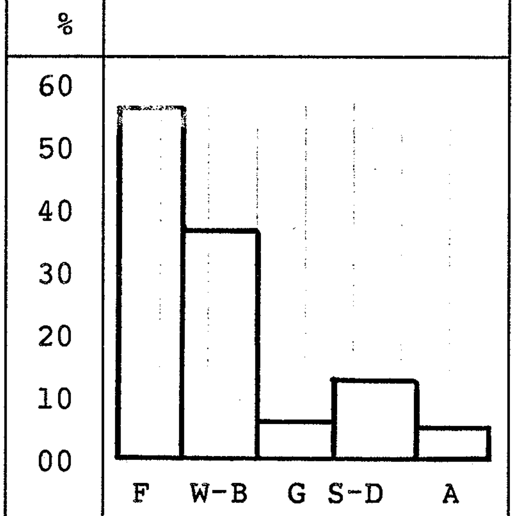
Chamtwara to those from extant environments (table 5.1) reveals that both are closest to semi-deciduous forest, evergreen forest and montane forest, in that order (Nesbit Evans et al 1981). Nesbit Evans et al believe that the fact that the semi-deciduous forest is strongly indicated is actually an artifact of the small samples and the nature of the calculations themselves (1981:109). They believe that the biome at these two sites was a lowland evergreen forest, the spectrum from which is also very similar to those from Legetet and Chamtwara. Both the fossil spectra are less similar to the spectrum from the extant montane forest biome.

The spectrum from Koru is not particularly similar to any of the spectra from table 5.1. It is closest, however to the semi-deciduous forest/woodland, and to the semi-decidu-

TABLE 10.6

HABITAT SPECTRUM

LEGETET



F=forest
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G=grassland
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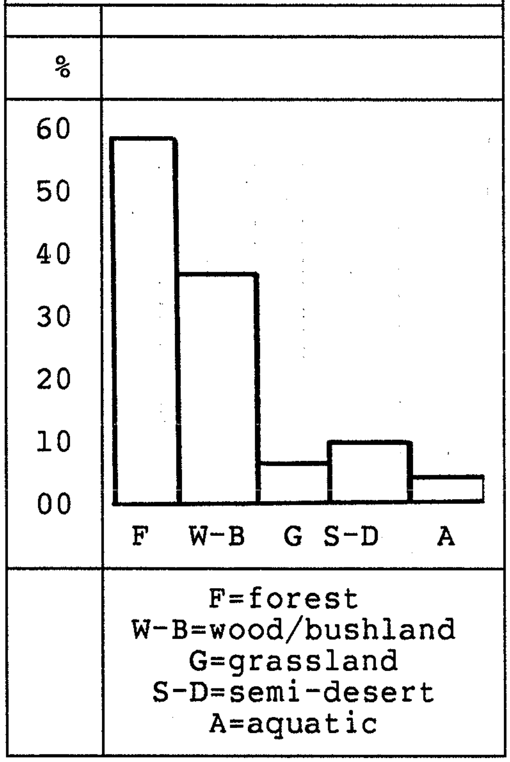
A=aquatic

ous forest spectra. Once again, there is no clear indication of the paleoenvironment at Koru.

TABLE 10.7

HABITAT SPECTRUM

CHAMTWARA



10.4.5 Ecological Diversity Analysis

The ecological diversity analysis has also been calculated by Nesbit Evans et al (1981:109).

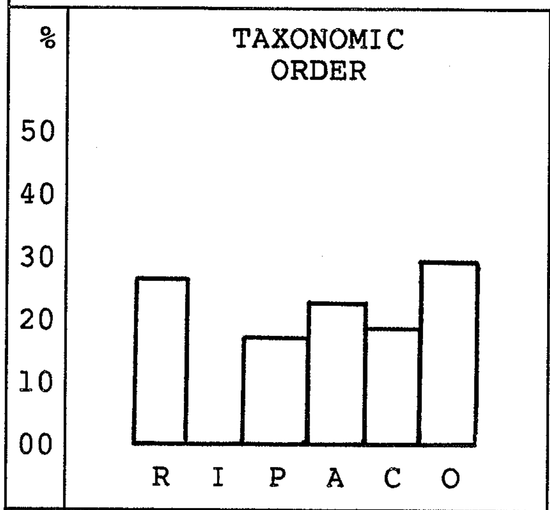
1. Taxonomic Order - Both the Legetet and Chamtwara spectra are similar to spectra from extant montane forest environments in Africa. The Koru spectrum is most similar to the lowland forest pattern.

2. Size Category - Both Legetet and Chamtwara approximate closely the lowland forest spectra while Koru is most similar to the floodplain pattern.

3. Locomotor Adaptation - In this category Legetet most closely resembles the lowland forest while Chamtwara

TABLE 10.8

ECOLOGICAL DIVERSITY ANALYSIS-KORU


TAXONOMIC ORDER

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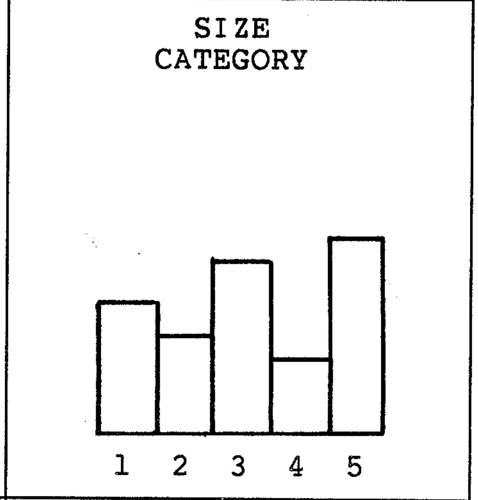
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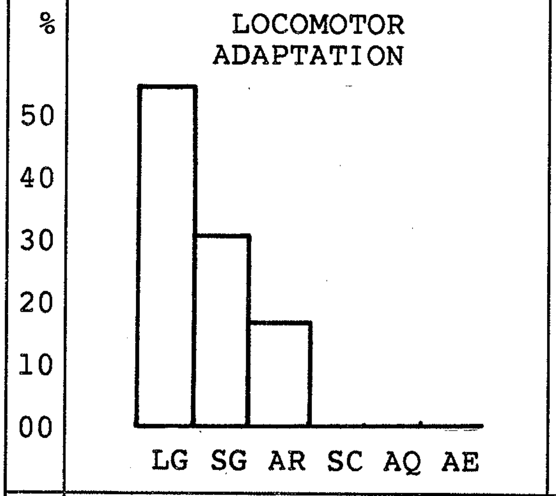
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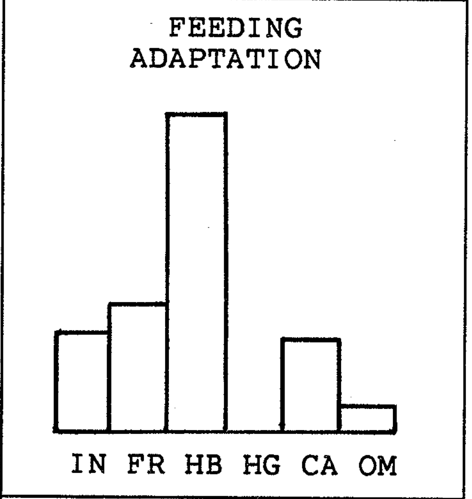
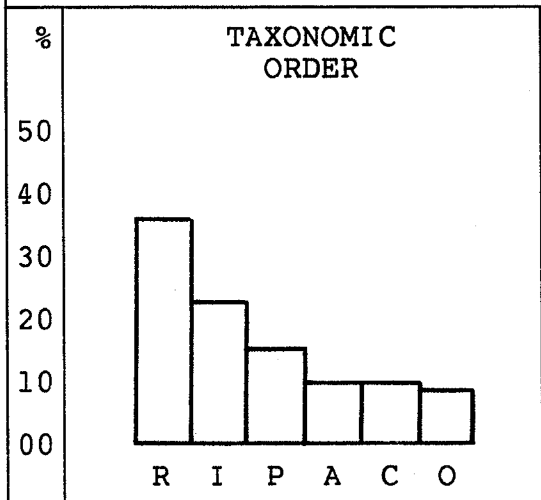

FEEDING ADAPTATION

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 10.9

ECOLOGICAL DIVERSITY ANALYSIS-LEGETET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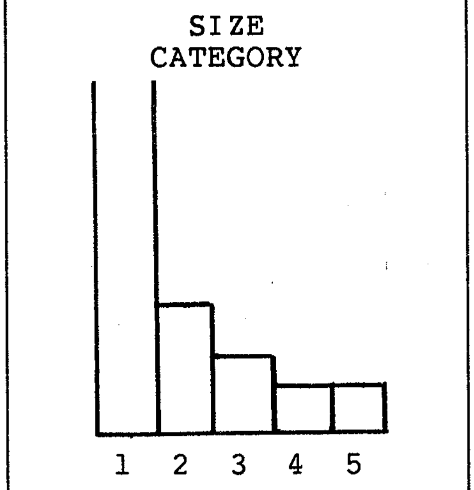
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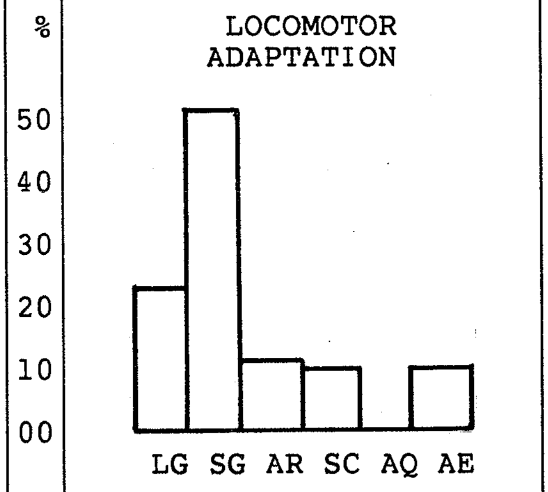
LOCOMOTOR ADAPTATION

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SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
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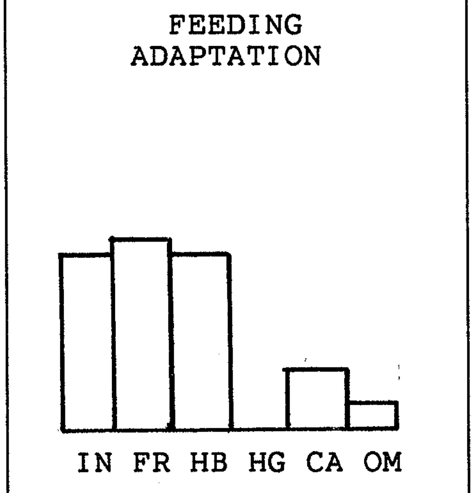
FEEDING ADAPTATION

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FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
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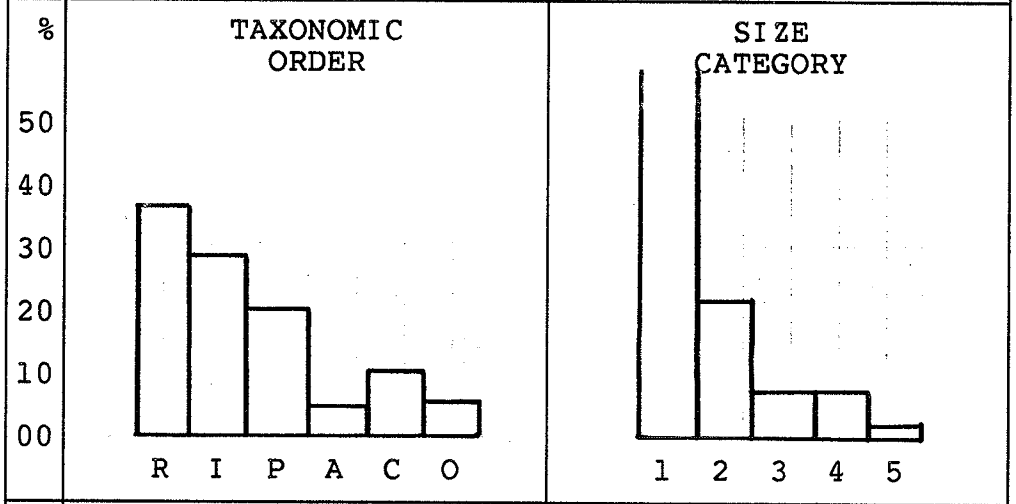
TABLE 10.10

ECOLOGICAL DIVERSITY ANALYSIS-CHAMTWARA



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P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

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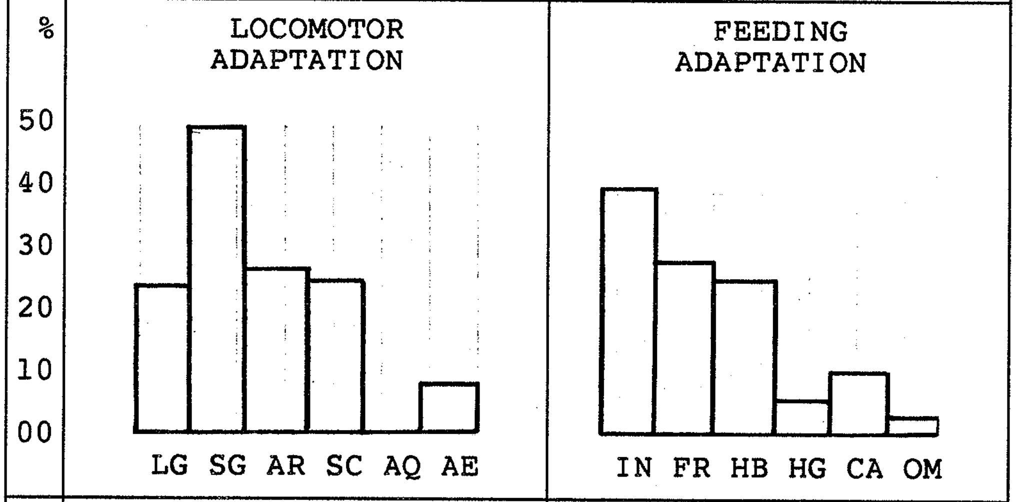
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

is most similar to the montane forest. Koru is most like the woodland-bushland pattern.

4. Feeding Adaptation - Legetet and Chamtwara are similar to the lowland forest spectra while Koru is most, but not very, similar to the woodland-bushland pattern.

In summary, the forest orientations of both Legetet and Chamtwara show through clearly, while the environment at Koru is more difficult to assess. While the Koru fauna shows some affinities to a savanna environment (i.e. locomotor adaptation) it is not consistent throughout the whole analysis (Nesbit Evans et al 1981).

10.4.6 Non-mammalian Fauna

The non-mammalian fauna from Koru at large has not as yet been thoroughly analysed. Meswa Bridge has yielded over 700 gastropods, including Maizania, but with the exception of Legetet non-mammalian fossils are rare from the other sites (Pickford and Andrews 1981). At Legetet molluscs are abundant, the most common being Homorus (Stenogyridae), Tayloria and Gulella (both Streptaxidae), Burtoa (Achatinidae) and Krapfiella (Streptaxidae) (Pickford and Andrews 1981).

In total, the family Streptaxidae is most well represented followed by Stenogyridae. According to Andrews and VanCouvering (1975) both of the above gastropod families indicate evergreen forest conditions. Homorus is considered to be associated with a wet evergreen forest biome (Andrews and VanCouvering 1975). Thus, the gastropod fauna supports the conclusion that the environment at Legetet, and probably at Chamtwara also, was forest.

There have also been finds of bird, reptile (including snake) and arthropod fossils from Legetet, but these have not yet been analysed in detail (Pickford and Andrews 1981).

10.5 FLORA

There are no published floral remains from any of the Koru sites.

10.6 PALEOGEOGRAPHY

The site of Koru consists of at least five separate fossil bearing locations. Meswa Bridge is the oldest (23.5 m.y.) while Koru, Chamtwara and Legetet all date from 19.5 to 19.7 m.y. radiometrically. Stratigraphically, Koru lies above Meswa Bridge and is in turn followed by Legetet and Chamtwara respectively. The fifth site, Kapurtnay, lies in the Kapurtnay agglomerates, probably contemporaneus with the Chamtwara Member. This site is poorly defined and published.

All indications suggest that the Meswa Bridge site consists of an infilled temporary channel (Andrews et al 1981). Because of its early date it will be interesting to see a detailed listing of the flora and fauna from this site, as other sites (Bukwa and Karungu) in the same time range seem to have had a fairly open environment.

Deposition at the other sites appears to have been subaerial in nature, as they all demonstrate roughly the same pattern of paleosols, tuffs and calcretes (Pickford 1981). At the time of their formation these sites were probably buried in volcanic ejecta from the nearby Tinderet volcano. Although the evidence from Koru proper is ambiguous, it seems almost certain that the area surrounding both Legetet and Chamtwara was a full evergreen forest. Since many of the clear forest indicators common to the latter two sites are missing from the Koru location it may be possible that Koru itself was located in a more open, perhaps woodland, environment.

11. LOPEROT

Located in Uganda (35 50'E., 02 20'N.) Loperot is an Eastern Rift site.

11.1 GEOLOGY

Stratigraphically, Loperot lies beneath the Lower Turkana Basalt formation (tvb 1), and , because of this, has been assumed to lie in what is called "Turkana Grit" (Hooijer 1971 in VanCouvering and VanCouvering 1976). The "Turkana Grit" is an unspecified sediment found beneath tvb 1 farther North; it has been dated to @21 m.y. (VanCouvering and VanCouvering 1976). VanCouvering and VanCouvering, however, believe that Loperot does not lie in the "Turkana Grit" because the site would then have to be older than other evidence indicates (perhaps @23 m.y.). They postulate that the basalts and other sediments become younger the farther South they lie from the Ethiopian eruptive centres. Therefore, they use "local" dates for tvb 1 rather than a general date for the whole area.

The fossiliferous deposits lie in limey coarse sandstone, the deposition of which indicates the presence of water at the site.

11.2 DATING

The tvb 1 just above Loperot has been dated radiometrically at 17.5 +/- 0.9 m.y. (Pickford 1981). This is fairly consistent with the date assigned to Loperot by VanCouvering and VanCouvering (1976), 18 m.y., based upon stratigraphic grounds. Pickford, on the other hand, feels it may be younger, perhaps >17 m.y., based on faunal correlates. Thus, while fairly closely braketed (17-19 m.y.) the exact dating of Loperot is open to interpretation.

11.3 ABUNDANCE OF PROCONSUL FORMS

While there have been finds from Loperot assigned to the genus Proconsul apparently no specific designation is possible (VanCouvering and VanCouvering 1976, Pickford 1981).

11.4 FAUNA

The following faunal list has been compiled from VanCouvering and VanCouvering 1976 and Pickford 1981.

	FREQ.
1. PRIMATES	
a) *Victoriapithecus sp.*	P
b) *Proconsul sp.*	1-10
2. CREODONTA	
a) *Metasinopa sp.*	
3. PROBOSCIDEA	
a) *Prodeinotherium hobleyi*	P
b) *Platybelodon sp.*	P
4. RODENTIA	
a) *Paraphiomys sp.*	?
5. HYRACOIDEA	
a) *cf.* *Prohyrax=Meroehyrax*	P
6. CETACEA	
a) Ziphiid gen. and sp. nov.	
7. PERISSODACTYLA	
a) *Chilidotherium pattersoni*	11-100
8. ARTIODACTYLA	
a) *Masritherium sp.*	P
b) *Gelasmodon sp.*	P
c) *Dorcatherium pigotti*	P
d) *Dorcatherium sp.*	P
e) *Walangania sp.*	?

11.4.1 FAUNAL ANALYSIS

11.4.2 Habitat Indicator Species

Since most of the above identifications have been made to the generic level only, it is apparent that the Loperot fauna is poorly preserved. One interesting feature, however, is the presence of a whale at this site. While this says nothing about the surrounding vegetation type, it does indicate that this site was obviously under or near water at the time of deposition, and must have been either coastal, estuarine or on the banks of a very large river.

The fact that one form, a perissodactyl, Chilidotherium pattersoni is much more abundant than any other species may be significant (Pickford 1981). In fact, the most notable feature of the Loperot fauna, apart from the whale, is the abundant and well preserved rhinocerous fauna. Rhinos today dwell in open areas and their appearance at Loperot in abundance may indicate non or lightly forested conditions.

11.4.3 Relative Abundances

Of the 14 listed forms only one is a rodent, which indicates that there has probably been some differential preservation on the basis of size here. This could also be the result of hydronamic sorting given the nature of the site. As would be expected, with almost no rodents present, almost 50% of the forms are ungulates, but this can have only limited, if any, significance.

11.4.4 Taxonomic Habitat Index

This has not been computed because of the sparse nature of the fauna.

11.4.5 Ecological Diversity Analysis

Taxonomic order - The Loperot pattern, largely because of the absence of rodents, is not particularly similar to any extant pattern. It is closest, however, to the floodplain spectrum.

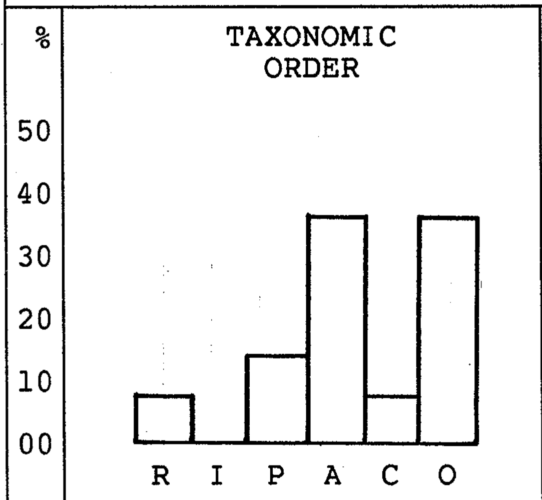
Size Category - The same situation applies in this category as in the taxonomic order.

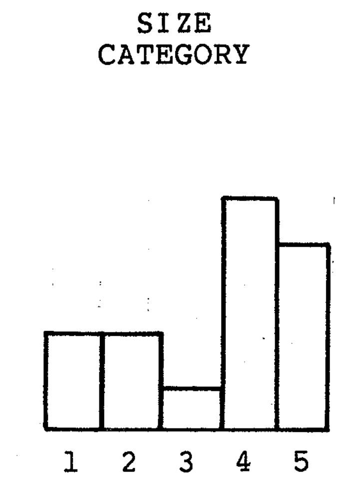
Locomotor Adaptation - Closest to, and in fact quite similar to, the floodplain pattern.

Feeding Adaptation - Not similar to any pattern.

TABLE 11.1

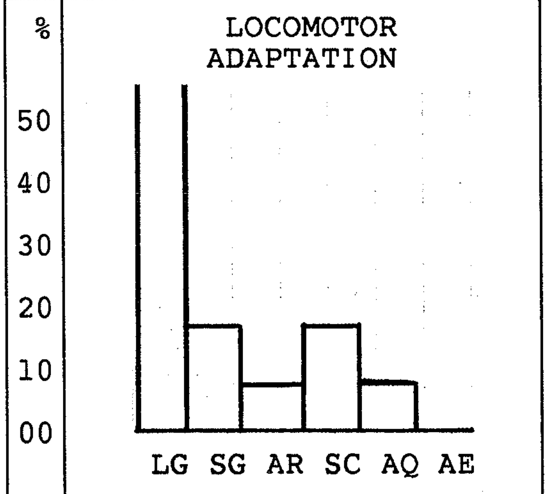
ECOLOGICAL DIVERSITY ANALYSIS-LOPEROT

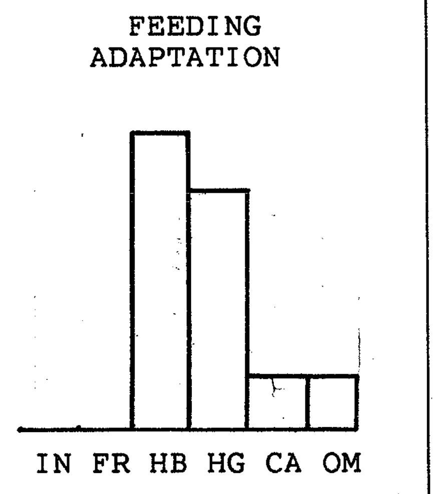

TAXONOMIC ORDER


SIZE CATEGORY

R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.


LOCOMOTOR ADAPTATION


FEEDING ADAPTATION

LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

11.4.6 Non-mammalian Fauna

There are no published non-mammalian remains from Loperot.

11.5 FLORA

There are no published floral remains from Loperot.

11.6 PALEOGEOGRAPHY

The presence of a whale poses some interesting questions concerning Loperot. If this was a coastal site it would be likely that there would be other sea going creatures in the fauna. An estuary site would also probably yield such forms as skates, sharks and sirenians (VanCouvering and VanCouvering 1976). It may be possible that the whale became incorporated into inland sediments after swimming upriver from the ocean (VanCouvering and VanCouvering 1976). The sediments and other fauna from Loperot tend to support the concept of an inland location for the site. It must be inferred, however, that this site would not have been far from the ocean, although it is a considerable distance from it today. This is consistent with VanCouvering and VanCouvering's notion that the Eastern coast of Miocene Africa may have lain as far West as what is today the Eastern Rift (1976).

Although the faunal analysis was largely inconclusive,it did tend to point to more open, not forested , conditions. Thus, it may be possible that Loperot lay on a floodplain. It has also been suggested that a coastal plain or delta may have been the site location (VanCouvering and VanCouvering 1976).

12. LOSIDOK-MORUAROT

Variously known as Losidok, Lothidok, Moruorot or Lothidok Hill, Losidok-Moruarot is an Eastern Rift site (35 45'E, 03 20'N).

12.1 GEOLOGY

The Losidok fossils are enclosed in the Lower Turkana Basalt "tvb 1", the same basalt which overlies Loperot. While the Loperot location lies beneath a single flow of tvb 1, Losidok is found between two flows of this basalt, the upper and the lower tvb 1 (VanCouvering and VanCouvering 1976).

The depositional medium is a series of tuffaceous sediments including red marl and siltstone, zeolitic volcanic sandstone and volcanic grit (VanCouvering and VanCouvering 1976). There are four fossiliferous levels which are usually lumped together to create a single Losidok-Moruarot fauna (Pickford 1981:90). Since both Pickford (1981) and VanCouvering and VanCouvering (1976) feel this is justified, the site will be treated here as a single unit. Further research may, however, necessitate the division of this site into its component faunas.

12.2 DATING

There are no radiometric dates from Losidok. Two age estimates have, however, been made on the basis of paleontological correlations. These are: 18 m.y. (Madden 1972) and 17-17.5 m.y. (Pickford 1981). Stratigraphically, it would appear as if Losidok, lying within tvb 1, would be younger than Loperot, which lies beneath it. VanCouvering and VanCouvering (1976), however, believe that the tvb 1 becomes locally younger the further South it is examined, which would make the two sites roughly contemporaneus (@ 17-19 m.y.).

Neither the paleontological nor the geological evidence can be considered conclusive, but in as much as they are largely in agreement, a range of 17-19m.y. or, more speculatively, a date of 18 m.y. can be assigned to this site.

12.3 ABUNDANCE OF PROCONSUL FORMS

There seems to be a certain amount of confusion regarding the exact nature of the species of *Proconsul* present at Losidok, and the frequency in which they have been found. For example:

1. Andrews (1978:208) lists 2 individuals of *Proconsul major*.
2. Andrews and VanCouvering (1975:94) list 1 *P.major* and 1 *P. nyanzae*.
3. Pickford (1981:90) lists an unspecified number of *P.nyanzae* only.
4. VanCouvering and VanCouvering (1976:200) list *P. africanus*, *P nyanzae* and *P. major*(?), although all (probably) in very low numbers.

It can only be assumed that identifications have been made on material which is not clearly diagnostic. Three of the above authors list *P. nyanzae*, so this form is likely present. Furthermore, the most recent paper (Pickford 1981), lists *P. nyanzae* as the only Proconsuline present. On the other hand, Andrews' 1978 monograph is very detailed, yet he lists only *P. major* as being present at Losidok. Until a further re-evaluation has been carried out this problem cannot be resolved, but on the basis of available information it must be assumed that both *P. major* and *P. nyanzae* are present at Losidok, in low frequencies.

12.4 FAUNA

The following faunal list has been drawn from Pickford (1981) and VanCouvering and VanCouvering (1976).

Apparently, there is also a considerable amount of confusion regarding the rest of the fauna as well as the *Proconsul* species. The list above was compiled from the two sources cited but the agreement between them concerning the species present at Losidok was very limited. The forms with an * before them, only 14/39 species listed, were cited as being present by both authors. Thus, although the fauna appears to be reasonably complete, it will be treated here as if it were incomplete for the purposes of faunal analyses.

TABLE 12.1

LOSIDOK FAUNA

ORDER	GENUS/SPECIES	FREQ.
MACROSCELIDEA	Myohyrax oswaldi	P
PRIMATES	Mesopithecus (?)	P
	Dendropithecus macinnesi	P
	* Proconsul nyanzae	1 (?)
	Proconsul major	1 (?)
CREODONTA	* Anasinopa leakeyi	1-10
	Leakitherium hiwegi	(?)
	Hyaenodon andrewsi	1-10
CARNIVORA	* Kichechia zamane	1-10
PROBOSCIDEA	* Prodeinotherium hobleyi	P
	Platybelodon kisumuensis	P
	* Zygolophodon sp.	(?)
	Mastodon	(?)
RODENTIA	* Paraphiomys stromeri	1-10
	Paraphiomys pigotti	1-10
	Diamantohyus africanus	(?)
HYRACOIDEA	Pachyhyrax championi	P
	Megalohyrax championi	(?)
PERISSODACTYLA	* Aceratherium acutirostratrum	1-10
	Brachypotherium sp.	(?)
	Chalicotherium rusingense	(?)
ARTIODACTYLA	* Masritherium aequitorialis	P
	Hyotherium dartevillei	1-10
	Hyotherium sp.	1-10
	Bunolistriodon jeanneli	(?)
	Hyotherine	1-10
	* Lopholistriodon moruoroti	1-10
	Xenochoerus sp.	1-10
	* Dorcatherium parvun	1-10
	Dorcatherium crassum	1-10
	Dorcatherium pigotti	1-10
	Dorcatherium chappuisi	(?)
	* Propaleoryx nyanzae	P
	* Canthumeryx sirtensis	P
	Paleotragus primevus	1-10
	Zarafa zeltini	1-10
	* Walangania africanus	1-10
	Libyochoerus jeanneli	(?)

12.4.1 FAUNAL ANALYSIS

12.4.2 Habitat Indicator Species

Clear habitat indicator species at Losidok are rare. The two species of *Paraphiomys* could represent forest conditions, while *Hyaenodon* would more likely be found in an open setting.

12.4.3 Relative abundances

It is readily apparent that the Rodentia are under-represented at Losidok. Despite this, however, there is a distinct emphasis upon Artiodactyls in the sample, which could be significant. The list agreed upon by both sources (Pickford 1981, Vancouvering and Vancouvering 1976), 14 species, contains 6 species of Artiodactyl (43%), while the entire sample listed by both, 39 species, contains 17 species of Artiodactyl (43.6%). From this evidence it would seem possible that Artiodactyls dominated the Losidok fauna.

When the Perissodactyls are added to the Artiodactyls, the combined ungulate group constitutes 50% of the sample in both cases. Such a high proportion of ungulates in the fauna may indicate more open, or lightly forested conditions (Bourliere 1963).

12.4.4 Taxonomic Habitat Index

Due to the nature of the fauna, this will not be calculated.

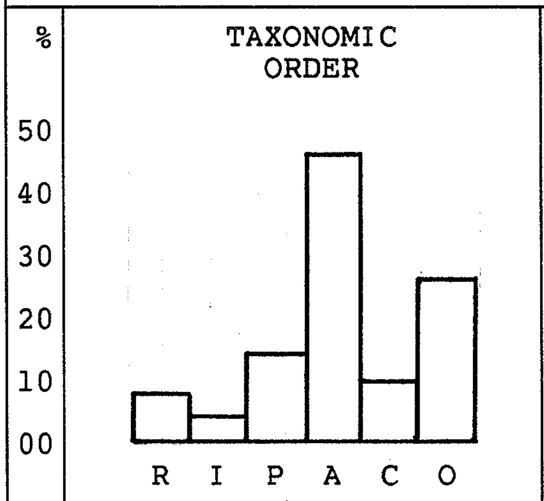
12.4.5 Ecological Diversity Analysis

The Losidok-Moruarot ecological diversity analysis has been carried out using only the agreed upon sample of 14 forms.

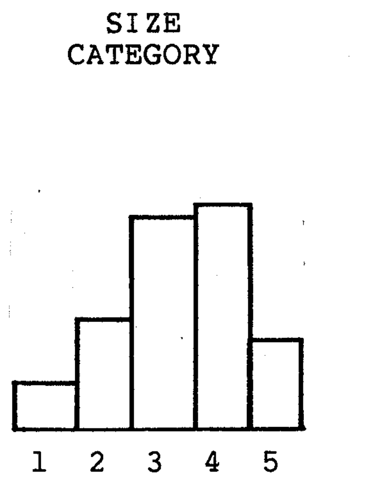
1. Taxonomic order - In this category the Losidok sample most closely matches the floodplain example, although the rodent population is far too low.
2. Size category - This does not resemble any extant pattern because of the dearth of animals in the smaller ranges.

TABLE 12.2

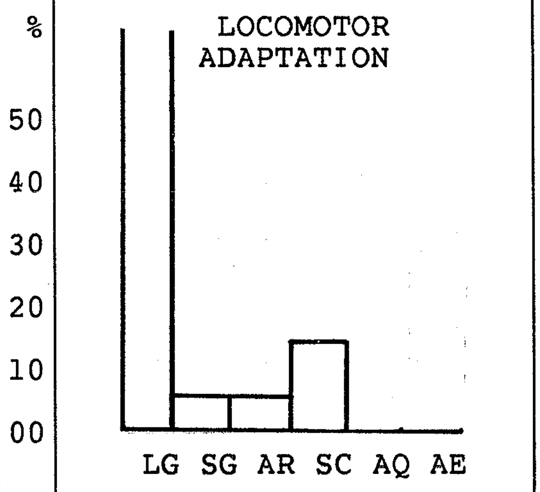
ECOLOGICAL DIVERSITY ANALYSIS-LOSIDOK



R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER



1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



LG=TERRESTRIAL
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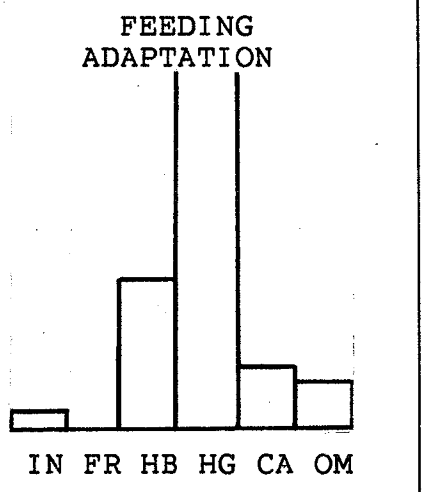


IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

3. Locomotor adaptation - The Losidok spectrum is most similar to the extant floodplain pattern.

4. Feeding adaptation - The Losidok spectrum is not similar to any extant pattern.

12.4.6 Non-mammalian Fauna

There is some additional fauna from Losidok, in the form of gastropods. There are two gastropods known, *Ampullaria ovata* and *Lanistes carinatus*. According to Andrews and VanCouvering (1975) *Ampullaria* represents a lakes and rivers habitat, while *Lanistes* is associated with rivers and swamps.

12.5 FLORA

There are no published floral remains from Losidok.

12.6 PALEOGEOGRAPHY

The depositional medium of red marl and siltstone indicates that there was probably a large body of water at Losidok at the time of sedimentation. VanCouvering and VanCouvering (1976) believe Losidok lay on a floodplain which was bisected by fluvatile channels. From the accumulation of marl, however, a lake environment cannot be ruled out, as marl is typically a lake bed sediment. The same is generally true of siltstone.

Arguing against a lake or lake margin site is the fact that there are no aquatic species in the fauna. This, coupled with the fact that small mammals are extremely rare means it is possible that this site has been hydronanically sorted, which generally implies a riverine location. It may well be possible that the surrounding environment at Losidok had both rivers and lakes.

Based on the evidence from gastropod fossils, Andrews and VanCouvering (1975) reached the conclusion that swampy lakes were the sedimentary environment at Losidok, which is largely in agreement with the above analysis. There is very little known about the surrounding vegetation but the ecological diversity analysis suggests a floodplain, non or lightly wooded, may have contained the site.

13. MABOKO

Maboko Island (34 30'E, 00 10'S) lies near the Western end of the Kavirondo Rift Valley, in a finger of Lake Victoria.

13.1 GEOLOGY

Maboko Island has a distinct saddle-shaped appearance, with flat-topped hills at the North-west and South-west extremities, and a smooth depression between (Andrews et al 1981). The hills are erosional remnants of phonolite flows which covered the fossiliferous site, now exposed in the saddle area (Andrews et al 1981). Some stratigraphic work was done by Kent (1944) and Owen (1934) which has been incorporated into a stratigraphy of Maboko recently completed (Andrews et al 1981).

In general, the sediments at Maboko are at least 40 m. thick, and fossils can be found throughout. Directly beneath the phonlite cap lies some 10 m. of deposits which are clearly volcanic in origin, composed of such sediments as tuff, volcanic agglomerate and marly conglomerate (Andrews et al 1981). The next 20-30 m. are sediments of clay, silt, siltstone, mudstone, limestone and marls, all of which show a lacustrine origin (Andrews et al 1981). Although bone has been found in these sediments, they are generally only sparsely fossiliferous.

The next horizon contains the two main collecting areas on Maboko, Owen's Quarry and Greensand Quarry (Andrews et al 1981). Owen's Quarry lies in brown, mottled orange and white crumbly clay not associated with, but lying beneath, primary pyroclastic material. The Greensand Quarry is a possible paleosol associated with a green clayey sand, variously coloured clays, and sandy marl (Andrews et al 1981). Andrews et al (1981) believe that these quarries (referred to as A and B respectively) are from the same level, and may indeed be the same sites discovered by Owen and Kent, but this, of course, is not certain.

Some volcanic pebbles, identified as nephelinites rather than phonolites, have been found throughout parts of the sediments. It has been suggested that these particles are not erosional features but rather were ejected into the sediments at the time of their formation, probably from Kisingiri which was a nephelinite volcano (Andrews et al 1981). These particles are significant in terms of the dating of the site.

13.2 DATING

The overlying plateau phonolite has been recently dated at @ 12 m.y. (Bishop, Miller and Fitch 1969). The volcanic tuffs lying below the phonolite yielded dates of 37 m.y. and 9.5 +/- 0.7 m.y., but both were considered discrepant by Andrews et al (1981). No radiometric dates are available from the fossiliferous sequence itself because the nephelinite cobbles included in the sequence are undatable by K/ar (Andrews et al 1981). These particles, however, must have been derived from a nephelinitic source, probably either Kisingiri (23-16 m.y.) or Tinderet (@ 15 m.y.)(Andrews et al 1981). Thus, a date of 23-15 m.y. would be suggested, but because the plateau phonolite is dated at 12-13 m.y. the underlying sediments are probably closer to the more recent end of the range (@ 15-16 m.y.)(Andrews et al 1981).

13.3 ABUNDANCE OF PROCONSUL FORMS

Only one Proconsuline is known fron Maboko, this being *Proconsul vancouveringi* (3 specimens, M.N.I.=1)(Andrews et al 1981). This listing differs considerably from Andrews' 1978 monograph in which he cited three individuals each of *P. nyanzae* and *P. vancouveringi*. Because the former report is more recent, and more comprehensive in regard to the Maboko site, it must be assumed to be correct. Although the *Proconsul* species may be lacking, it is interesting to note that a number of other important primates have been found at Maboko, notably *Ramapithecus wickeri* (6 specimens, M.N.I.=1) and *Sivapithecus africanus* (5 specimens M.N.I.=1)(Andrews et al 1981).

13.4 FAUNA

The following faunal list comes from Andrews et al 1981. There are four main areas from which collections have been assembled but only two of these, A and B have clear provenances. The other two collections are the fossils collected before 1973 by Owen and Kent, and the surface finds.

Because there are few differences between the mammalian faunas of the two quarry sites (A and B), Andrews et al (1981) group them together as a single fauna, which is justifiable given the information. Unfortunately, they also lump in all the other fossils because they are of uncertain provenance. There is, however, no certain stratigraphic information to base such a move upon, and certainly the composition of the faunas pre and post 1973 does not warrant them being put together. In fact, although Andrews et al (1981)

TABLE 13.1

MABOKO FAUNA (# OF SPECIMENS)

ORDER	GENUS/SPECIES	*1	*2	B	A	TOT MNI
INSECTIVORA	Amphechinus				1	1
PRIMATES	Victoriapithecus macinnesi	9	9	11	1	8
	Victoriapithecus leakeyi	3	5	3		4
	Victoriapithecus sp.	78	23	16	6	20
	Limnopithecus legetet	2	2	3	1	1
	Proconsul vancouveringi	2	1			1
	Ramapithecus wickeri	1	1	1		1
	Sivapithecus africanus	3				1
LAGOMORPHA	Kenyalagomys		1			1
RODENTIA	Phiomyidae		1			1
	Megapedetes sp.		1	1		1
	Zenkerella		1			1
CREODONTA	Anasinopa leakeyi		1			1
	Dissopsalis pyroclasticus	1				1
HYRACOIDEA	Pachyhyrax championi	4	1			1
PROBOSCIDEA	Prodeinotherium hobleyi	2	2	1		2
	Protanacus macinnesi	2				2
	Choerolophodon kisumuensis	67				10
PERISSO.	Dicerorhinus sp.		1			1
	Brachypotherium heinzelini		1			1
	Rhinocerotidae indet.	8				2
ARTIO.	Libychoerus khinzikebirus	3				2
	Listriodon akatikubas	10				1
	Lopholistriodon sp.	9				1
	Tayassulidae indet.	6				2
	Dorcatherium chappuisi		2	1	1	2
	Dorcatherium pigotti	45	1			5
	Canthumeryx sirtensis	1				1
	Climacoceras africanus	16	61	10	35	30
	Paleotragus primaevus	8				1
	Eotragus sp.	2				2
	Bovidae	10				4
	*1=Pre-1971 collections					

	*2=Surface collections					

feel that the locations of both the Kent and the Owen finds were in the same beds the 1973 collections came from, the earlier and later faunas differ to an amazing degree. Disregarding the surface collections, of the 32 mammalian species present in the entire sample, 19 of them (60%) are unique to either the earlier or the later group, leaving only 40% agreement between them. Thus, rather than treating the Maboko fauna as a single unit this paper will discuss the 1973 sample and the pre 1973 fauna as two distinct groupings.

13.4.1 Non-mammalian Fauna

Maboko has an excellent collection of non-mammalian fauna, and, as such, it must be considered when the various methods of faunal analysis are undertaken.

TABLE 13.2

MABOKO NON-MAMMALIAN FAUNA (# OF SPECIMENS)

PHYLUM/CLASS	FAMILY	*1	*2	B	A	TOTAL MNI
MOLLUSCA	Maizania				2	2
	Limicolaria				1	1
	indet.		255	90	74	5
VERTEBRATA TELEOSTOMATA	Siluriformes		1		1	1
	Perciformes ind.		1		1	1
	Cichlidae		3		3	1
AMPHIBIA	Anuran		26	2	24	5
	Nectridia		1		1	1
REPTILIA	Chelonia		1332	364	506	4
	Crocodylidae		382	34	231	2
	Lacertilia ind.		12	3	9	2
	Varanidae	1	1		1	2
	Amphisbaenidae		1		1	1
	Ophidia indet.		2		2	1
	Pythonidae		3	2		1
AVES	Ardeidae	1				1
	Phasianidae	1				1
	Burhinidae	1				1
	Bucerotidae	1				1
	*1=Pre-1971 collections *2=Surface collections					

13.4.2 <u>FAUNAL ANALYSIS</u>

13.4.3 Habitat Indicator Species

Pre 1973 Collections - The non-mammalian fauna is almost totally absent from these early collections, which is in direct contrast to the 1973 fauna dominated by non-mammalian remains. It must be considered that Owen and Kent may not have collected this type of fossil, as Andrews et al believe that both the 1973 and the pre 1973 samples come from similar areas (1981).

The most abundant genus, in terms of the number of specimens present, Victoriapithecus (macinnesi, leakeyi, sp.), may be a forest indicator but this is by no means certain (Nesbit Evans et al 1981). The next most abundant forms are a Proboscidean, Choerolophodon kisumuensis and two Artiodactyls, Dorcatherium pigotti, and Climacoceras africanus. Although none of these is a good habitat indicator species, together their appearance in abundance may suggest a more open environment at Maboko.

Eotragus, the bovid and Pachyhyrax may also be indicators of an open, perhaps woodland, environment (Nesbit Evans et al 1981).

Recent Collections - The recent collections obviously point to a very moist, probably swamplike environment. The mammalian fauna is dominated by Primates, and this may indicate that forest conditions prevailed in the surrounding area. Both Climacoceras and Megapedetes point to a more open, probably woodland biome.

13.4.4 Relative Abundances

Pre 1973 Collections - These are dominated by Artiodactyls (44% of species) and Primates (30% of species). This many species of Primate (7) would be found today only in a forest environment (Nesbit Evans et al 1981). The abundance of Artiodactyls does not necessarily imply non-forest conditions although they would more likely reflect a woodland ecotope rather than a full forest (Bourliere 1963).

Recent Collections - Not many interpretations can be made on the recent collections as only 10 species are represented. Of these five are Primate and, again, this might point to a forest environment.

13.4.5 Taxonomic Habitat Index

This has been calculated by Nesbit Evans et al (1981), but only using the entire sample of earlier and later collections as well as the surface finds. For this reason their results will not be used here. Furthermore, because the individual samples are too small the taxonomic habitat index will not be calculated on them.

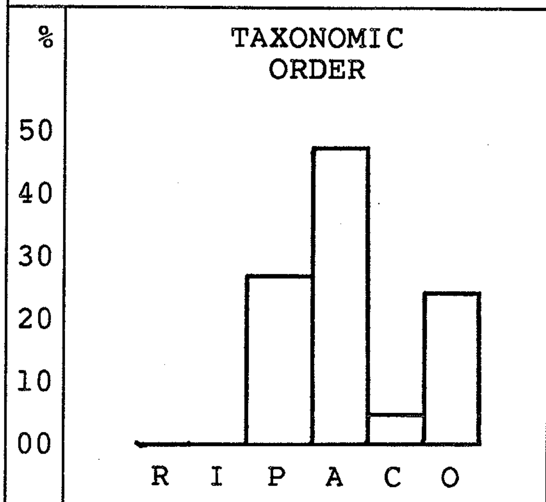
13.4.6 Ecological Diversity Analysis

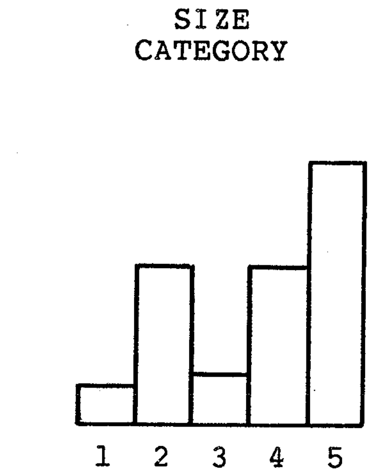
The ecological diversity analysis has been calculated on both the earlier and later collections from Maboko.

Unfortunately, none of the spectra from either the earlier or the later collections are comparable to the patterns of modern mammalian populations as set out by Nesbit Evans et al (1981) (table 5.2).

TABLE 13.3

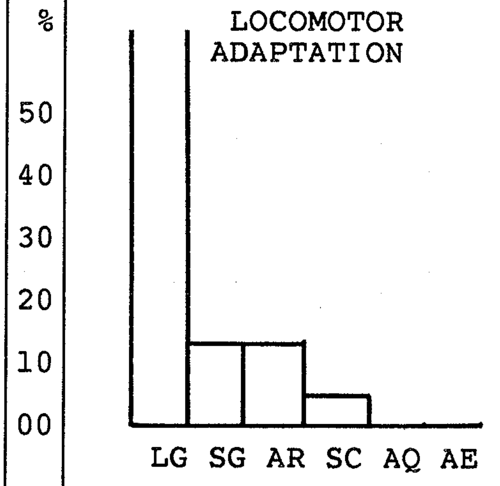
ECOLOGICAL DIVERSITY ANALYSIS-MABOKO PRE 1963 FAUNA

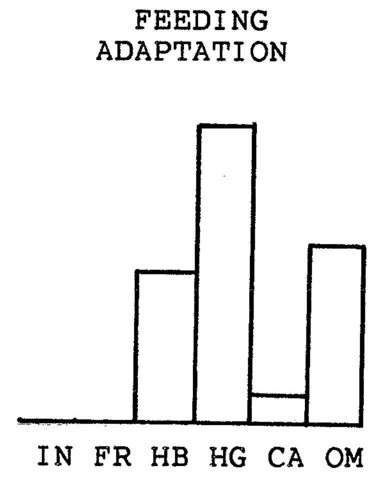




R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



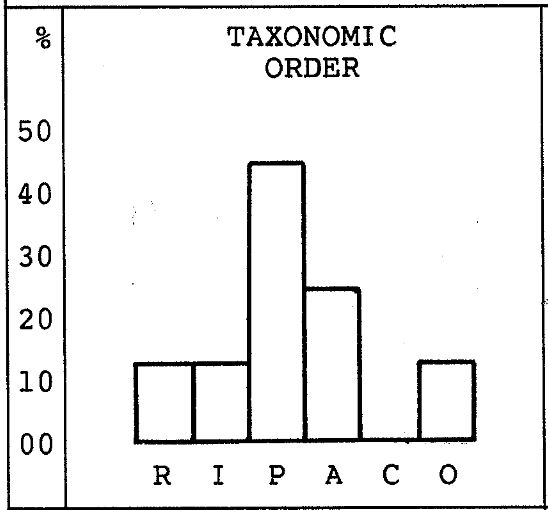


LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

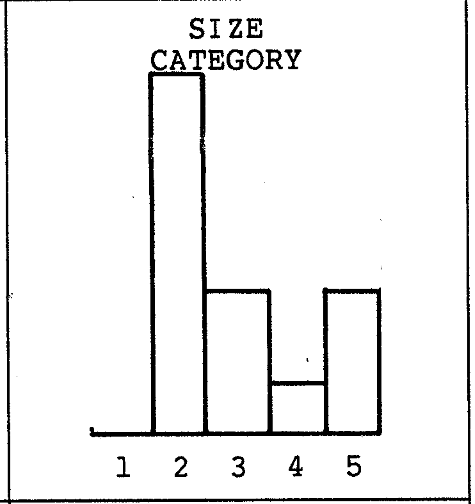
IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 13.4

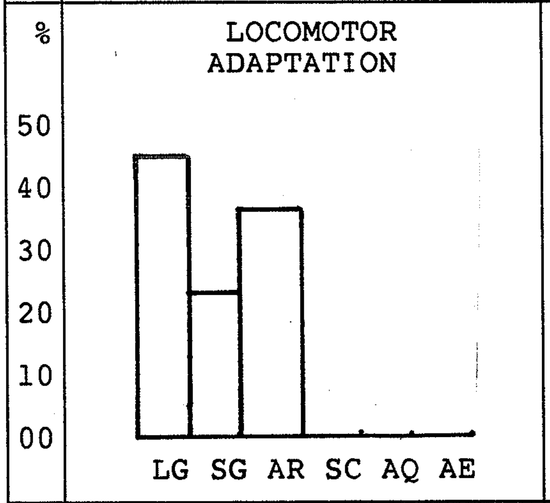
ECOLOGICAL DIVERSITY ANALYSIS-MABOKO 1973 FAUNA



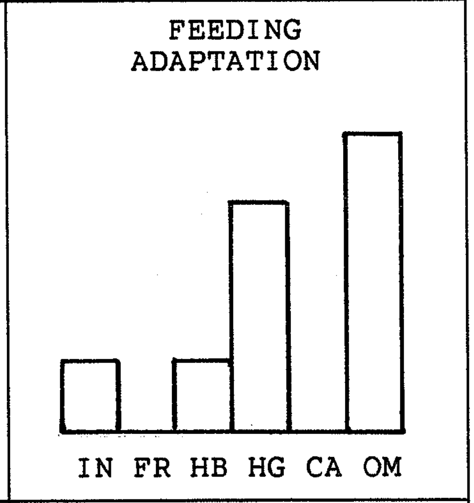
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER



1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL



IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

13.5 FLORA

There are no published floral remains from Maboko.

13.6 PALEOGEOGRAPHY

Recent Collections - There is fairly good evidence that both quarry sites excavated recently reflect a floodplain environment. The sediments of mud, marls and clays suggest this, as does the non-mammalian fauna which is largely composed of aquatic forms (Andrews et al 1981). Furthermore, the long bones found from these sites show a preferred orientation indicating that there was running water at both locations (Andrews et al 1981). Finally, the fact that many of these bones were oriented vertically, probably means that they were trampled into mud, or other soft sediments, by large animals (Andrews et al 1981).

All indicators, then, are of a floodplain, probably an extremely wet one. The surrounding vegetation, however, is more difficult to assess. There are no clear forest indicators in the fauna and it is possible that a woodland biome was present (Nesbit Evans et al 1981). The evidence is unclear, however, and thus the vegetation predominant at Maboko, at least as reflected in these two recent quarry sites, must remain uncertain.

Pre 1973 Collections - These are considered by Andrews et al (1981) to come from roughly the same provenance as the 1973 collections. Aside from the differences in the mammalian fauna documented above, these early collections are almost totally lacking in the type of remains most prevalent in the recent samples, those being fish, reptiles, molluscs and amphibians. It is, of course, possible that this is due to different sampling strategy or technigue, but it might also indicate that some levels at Maboko were deposited during drier periods. The sediments described by Owen (1934, Andrews et al 1981) and Kent (1944) seem, however, to be of a water lain nature, as were the sediments recently described by Andrews et al (1981). It can be postulated , then, that these samples reflect a floodplain also, but possibly a somewhat drier one.

Once again, as with the recent collections, the surrounding vegetation is difficult to assess. While it is by no means certain, the species present, as well as their relative abundances, may point to a woodland biome.

14. MFWANGANO

Located very close to Rusinga Island in Lake Victoria (33 57'E, 00 25'S), Mfwangano is usually correlated to the Rusinga stratigraphic sequence, and consequently, has largely been glossed over by East African Miocene researchers.

14.1 GEOLOGY

Fossiliferous material has been recovered from three discrete levels on Mfwangano. These levels are considered to be continuous with strata named on Rusinga Island (VanCouvering and VanCouvering 1976). The Kisingiri stratigraphic sequence from Rusinga is based upon the actual superposition of strata (VanCouvering and VanCouvering 1976), but it is unclear whether these beds are found in exactly the same order on Mfwangano, or if the Mfwangano situation is inferred from the Rusinga pattern.

A brief description of the Rusinga stratigraphic pattern may be found below. An * indicates that the Mfwangano level with the same name as a Rusingan horizon has yielded fossiliferous material. For the time being, it must be assumed that the lithologies of Rusinga and Mfwangano are directly comparable, and that features are continuous between them (VanCouvering and VanCouvering 1976).

1. 16 m.y. - Lunene lava.
2. 17 m.y. - Kiangata agglomerate.
3. ------- - Discontinuity
4. 18 m.y. - Sena beds.
5. 19 m.y. - Hiwegi redbeds *
6. ------- - Discontinuity
7. 19.5 m.y. - Rusinga agglomerate *
8. 20 m.y. - Discontinuity
9. 21 m.y. - Upper Kiahera tuffaceous redbeds *

The probable depositional environment for the three fossiliferous horizons has been listed by Andrews and VanCouvering (1975):

1. Upper Kiahera - depressions at the edge of the volcanic dome.

2. Rusinga agglomerate - narrow finger lakes.

3. Hiwegi redbeds - river floodplain.

14.2 DATING

There are no radiometric dates available from Mfwangano per se but many dates are available from the corresponding horizons on Rusinga Island (VanCouvering and Miller 1969). The relative ages of the horizons (as through the stratigraphy) and their absolute ages (K/ar) are as follows (VanCouvering and Miller 1969):

1. Hiwegi redbeds - 17-19 m.y.
2. Rusinga agglomerate - 19.6 m.y.
3. Upper Kiahera redbeds - 20 (?) m.y.

14.3 ABUNDANCE OF PROCONSUL FORMS

Andrews and VanCouvering (1975) list the following Proconsulines from Mfwangano:

a) *Proconsul africanus* M.N.I. = 5

b) *Proconsul nyanzae* M.N.I. = 2

c) *Proconsul gordoni* M.N.I = 1

d) *Proconsul vancouveringi* M.N.I. = 1

Andrews (1978) agrees with the above except for the M.N.I. of *P. nyanzae* which he places at 3.

14.4 FAUNA

There is no complete faunal list available for Mfwangano because the fauna is typically lumped in with that from Rusinga (as in VanCouvering and VanCouvering 1976). The proportions of the taxonomic orders from the Makeira series (Hiwegi) and the Walangani beds (Kiahera), constituting 80% of the Mfwangano mammalian fauna, have, however, been listed by Bishop (1967). They are (approximate values): Rodent 63%, Mastodon 4%, Artiodactyl 13%, Primate 8% and Other 12%.

The high proportions of rodent and Primate probably indicate a forest environment (Bourliere 1963). It is unfortunate that there is no breakdown of the rodent fauna by species, and so no way to tell if one form dominated over the others.

14.4.1 Non-mammalian Fauna

There is a rich gastropod fauna from Mfwangano, which has been listed by Andrews and VanCouvering (1975). Unfortunately, they do not divide it by level of occurrence, so it must be assumed that this fauna is a combined one from all Mfwangano fossil horizons.

TABLE 14.1

MFWANGANO GASTROPODS

GASTROPOD	ECOLOGICAL IMPLICATION
Ampullaria ovata	lakes and rivers
Maizania (4 sp.)	evergreen forest
Edouardia mfwangensis	arboreal (lowland habitat)
Homorus (Subulona)	wet evergreen forest
Burtoa nilotica	woodland
Limicolaria (2 sp.)	forest/bushland
Trochonanina (5 sp.)	lowland evergreen forest and bush
Gonaxis (Marconia) (9 sp.)	wet evergreen forest
Gulella (3 sp.)	forest and thicket
Ptychotrema usiforme	lowland evergreen forest

Six of the ten genera listed above are considered to be lowland or evergreen forest forms, so there is a clear implication that a forest biome existed on Mfwangano.

14.5 FLORA

There are no published floral remains from Mfwangano.

14.6 PALEOGEOGRAPHY

The three fossiliferous locations on Mfwangano may be separated chronologically by as little as 1.5 m.y. Unfortunately, because of the assumption that Mfwangano is simply an extension of Rusinga Island, in terms of stratigraphy and fauna, very little has been published about the Mfwangano sites. It is possible that two of the sites, Hiwegi and Rusinga agglomerate, may be associated with water, a floodplain in the former case and small finger lakes in the latter (Andrews and VanCouvering 1975). Since there appears to be, as will be seen later, a considerable difference between the Hiwegi and Kiahera faunas on Rusinga Island, it is unfortunate that there is no way to compare these faunas from Mfwangano.

Many indications point to a fairly heavily forested environment on Mfwangano, but there is no way to assess whether some of the individual sites diverge from this pattern. In total, it is obvious that a careful detailing of the stratigraphy, and a clear faunal list, are necessary here.

15. MOROTO

Moroto is an Inter-rift site in Uganda (34 35'E, 02 32'N).

15.1 GEOLOGY

Moroto is poorly known in terms of both stratigraphy and fauna. The two locations that comprise this site (Moroto I and II) lie near the volcano of the same name, and are associated with volcanic sediments. These sediments, lying above an arkose precambrian rock surface, are gritty (presumably composed of sands, silts and clays) (Bishop 1964:1327). Above the fossiliferous locations are levels of Kogole and Loitakero basalt. In general, because of the numerous discontinuities, the stratigraphy of Moroto is quite confused (VanCouvering and VanCouvering 1976).

15.2 DATING

There are three K/ar dates available from the overlying basalts. These are (Bishop, Miller and Fitch 1969):

1. 12.5 +/- 0.4 m.y.
2. 12.6 +/- 0.4 m.y.
3. 14.3 +/- 0.3 m.y.

The date cited for the overlying lava at Moroto is usually @ 14 m.y. (Pickford 1981, VanCouvering and VanCouvering 1976), a date which presumably refers to the basalt which directly supercedes the fossiliferous horizon, the Kogole basalt (VanCouvering and VanCouvering 1976). The other two dates appear to come from the Loitakero basalt, which overlies the Kogole (VanCouvering and VanCouvering 1976). Thus, the fossils themselves must date to earlier than 14 m.y., but their actual date is uncertain. VanCouvering and VanCouvering (1976) date the Moroto fossils at 16 m.y., but they themselves point out that the numerous discontinuities in the stratigraphy make the dating difficult. Dating the site by faunal comparison also yielded no clear results because of the sparse nature of the remains (Pickford 1981).

In summary, no date other than >14 m.y. can be assigned with certainty to Moroto, although @ 16 m.y. may be likely.

15.3 ABUNDANCE OF PROCONSUL FORMS

Proconsul major is the only Proconsuline known from Moroto but its frequency is uncertain. Bishop and Whyte (1961) list 1 individual at Moroto I, and 2 more at Moroto II, Bishop (1964) lists no primates from Moroto I but states that there are 64 specimens representing 3 individuals of P. major at Moroto II, and Andrews (1978) lists only 1 individual from the entire site. Thus, it must be assumed that P. major is represented here by at least 1, perhaps 2, individuals, probably from Moroto II.

15.4 FAUNA

The following faunal list is drawn from Bishop (1964) and Pickford (1981).

1. MOROTO I
    - a) CREODONTA
        - i) Dissopsalis pyroclasticus M.N.I. = 1
    - b) PROBOSCIDEA
        - i) uncertain M.N.I. = 1
    - c) ARTIODACTYLA
        - i) uncertain M.N.I. = 2
    - d) REPTILIA
        - i) unidentified M.N.I. = 5
2. MOROTO II
    - a) PRIMATES
        - i) Proconsul major M.N.I. = 2(?)
        - ii) Komba minor M.N.I. = 1
    - b) PROBOSCIDEA
        - i) Trilophodon angustidiens
        - ii) Deinotherium
        - iii) Rhinocerid

    iv) Anthrocothere (total Prob. M.N.I. = 16)

c) RODENTIA

    i) uncertain M.N.I. = 1

d) ARTIODACTYLA

    i) Masritherium aequitorialis M.N.I. = 3

e) REPTILIA

    i) CHELONIA M.N.I. = 9

f) AVES

    i) uncertain M.N.I. = 1

It is obvious that the fauna from Moroto is extremely poor. The abundance of Proboscideans must not be considered significant as the fauna is very poorly preserved (Bishop 1964) and the emphasis upon larger forms may simply be an artifact of this.

Very little faunal analysis can be carried out on such a small sample. At both sites, however, reptiles are present, the bulk of their remains consisting of chelonian scutes, which must be considered to indicate a waterside setting (Bishop 1964). The fauna does not yield any information concerning the probable vegetation type at this site.

15.5 FLORA

There are no published floral remains from Moroto.

15.6 PALEOGEOGRAPHY

Both sites are apparently of fluvatile origin (Bishop and Whyte 1962), and may have been situated in a valley (Andrews and VanCouvering 1975). In general, very little in known about this site and further research is necessary.

The second problem is that the fossils are not found in situ, per se, but rather in catchment areas where they collected after weathering out of the overlying banks (Bishop 1964, VanCouvering and VanCouvering 1976). Since Bishop states that the fossils in the catchment basins can satisfactorily be traced to their taphonomic origins, he is likely correct in his belief that they may be considered as a death assemblage (Bishop 1964)

As mentioned above, the division of the 10 sites into 2 groups, based on lithology and fauna, is widely accepted (i.e. VanCouvering and VanCouvering 1976). This grouping, however, should be one of age only, not ecology, as the various individual sites could show environmental differences.

16.2 DATING

The following dates have been obtained by K/ar (Bishop, Miller and Fitch 1969).

1. UPPER SITES
   - a) NAPAK I
     - i) 12.8 +/- 0.5 m.y. (nephelinite).
     - ii) 7.5 +/- 0.5 m.y. (nephelinite).
     - iii) 17.8 +/- 0.4 m.y. (mica tuff).
     - iv) 17.8 +/- 0.4 m.y. (mica tuff).
     - v) 17.8 +/- 0.4 m.y. (mica tuff).
   - b) NAPAX IX
     - i) 14.5 +/- 0.6 m.y. (mica tuff).
2. LOWER SITES
   - a) NAPAK II
     - i) 17.8 +/- 0.5 m.y. (mica tuff).

According to Bishop et al (1969), there have been an additional 13 radiometric dates obtained from Napak. Unfortunately, these have not been listed as per site, but rather simply designated Napak. These dates range from 6.7 +/- 1.5 m.y. to 31.3 +/- 1.0 m.y., with 8 of them over 23 m.y. in age.

16. NAPAK

Napak is an Inter-rift site in Uganda (34 14'E, 02 05'N) which has yielded faunal remains from a number of levels.

16.1 GEOLOGY

There are at least 10 distinct sites at Napak, numbered I-X (Bishop and Whyte 1962, Bishop 1964, Bishop 1967). These locations are divided into two groups on the basis of stratigraphy and faunal resemblance (Bishop and Whyte 1962, Bishop 1964, Pickford 1981).

Lying low in the succession, overlying basement rocks, are Napak II, III, VI, VII, VIII, the most significant of which, in terms of fauna, is Napak II (Bishop 1964). At Napak II the preservation is poor and the sedimentary environment consists of gritty deposits similar to those from Moroto I and II (Bishop 1964). This medium is considered by VanCouvering and VanCouvering (1976) to be a limey coarse sandstone.

There is then a break in the lithology which readily allows for the separation of these sites lower in the succession from those higher up (Bishop and Whyte 1962). The upper sites, Napak I, IV, V, IX, X, are in a more complicated lithological situation, and are considerably more complete, in terms of fauna, than are the lower sites.

In general, these upper sites were found in calcareous subaerial pyroclastic deposits, usually a medium to fine tuff (Bishop 1964). The various layers are separated by barren tuff which shows some degree of soil formation and frequent root casts (Bishop 1964)

The two most significant sites in this group, Napak I and IV, have, respectively, 6 fossiliferous horizons in 35' of deposits and 3 horizons in 25' of deposits. The preservation is excellent at all of the upper sites due to a high proportion of calcium carbonate in the soil (Bishop 1964).

Bishop (1964:1328) believes that the fossils represent a natural death assemblage, despite the realization that several factors are present that could possibly argue against this. First, traces of bone gnawing are common in the fauna. This would suggest that the fossils may have been scattered at, or after, death (Bishop 1964). While this must be considered as a possibility, there is really no reason to assume that the bones were moved far after death as bone gnawing does not have to imply transportation (as with rodents).

Based on faunal correlates, and the former group of dates, Pickford (1981) believes that the upper sites are @ 19 m.y. old. This would make the lower sites somewhat older than 19 m.y.

VanCouvering and VanCouvering (1976) place the upper sites at @ 18 m.y. and the lower at @ 19 m.y. These estimates, if even reasonably correct, tend to suggest that there are a high number of discrepant K/ar dates from Napak, notably the second group listed above. This could readily be due to contamination in the samples chosen for dating.

A date of 18 m.y. for the upper sites is probably reasonable and conservative. The lower sites could range anywhere from 18.5 - 23 m.y. The lithology, however, indicates that they are probably not greatly removed from the upper sites chronologically, and a date of 18.5 - 20.5 m.y. should be quite accurate.

16.3 ABUNDANCE OF PROCONSUL FORMS

There appears to be widespread agreement that only one Proconsuline, Proconsul major is present at Napak (Andrews 1978, Pickford 1981, VanCouvering and VanCouvering 1976). Bishop (1967), however, lists the presence of Proconsul nyanzae at Napak I as well as P. major. The more recent work, done by the former authors, makes it likely that a re-examination of the Napak fossils led to the conclusion that only P. major was present (M.N.I. = 8 (Andrews 1978).

All the Proconsul fossils have come from the upper sites, primates are apparently unknown from the lower sites (Bishop 1967, Pickford 1981).

16.4 FAUNA

Three faunal lists have been published for Napak (Bishop 1967, VanCouvering and VanCouvering 1976 and Pickford 1981). The total number of species listed varies somewhat: Bishop lists 31 species for the upper levels and 5 for the lower (Napak II), Pickford lists 33 and 6 for the upper and lower respectively, while VanCouvering and VanCouvering list 43 species in total. While the number of forms cited does not diverge greatly between the samples, the individual species listed digress considerably. The basic listing used here will be that of Bishop (1967) because this list was done by site, whereas the others are compiled lists for the entire Napak location. Additions, however, will be made from both other lists, on the following basis:

1. Where both Pickford and VanCouvering and VanCouvering agree that a species is present, but it is not listed by Bishop.

2. Small primates listed by Pickford but not the other authors (presumably these additions came after a restudy of the material).

3. From VanCouvering and VanCouvering, additional species of genera listed by Bishop, where the latter writer has not been specific.

It must be remembered that there appears to be a considerable difference of opinion regarding the species present at Napak, and this must be considered when further faunal analysis is attempted. The Napak faunal list can be seen in table 16.1.

x = presence * = presence in greater frequency.

TABLE 16.1

NAPAK FAUNA

ORDER	GENUS/SPECIES	I	IV	V	IX	II
INSECTIVORA	Erythrozootes chamerpes	x				
	Protenric tricuspis	*				
PRIMATES	Progalago dorae	*				
	Komba robustus	*				
	Komba minor	*				
	Micropithecus clarki	*				
	Proconsul major	x	x	x		
	Dendropithecus macinnesi	x	x			
	Limnopithecus legetet		x	x	x	
	Mioeuoticus bishopi	x	x			
CARNIVORA	Metasinopa napaki	x				
	Pterodon africanus	x				
	Hecubides euryodon	x	x			
	Kichechia zamane		x	x		
	Dissopsalis pyroclasticus	x				
	Kelba quadaemae		x			
	Pterodon nyanzae					x
	Stenoplesticid		x	x		
PROBOSCIDEA	Trilophodon angustidiens	x			x	x
RODENTIA	Diamantomys leuderitzi	x	x	x	x	
	Paraphiomys pigotti	x	x	x		
	Paraphiomys stromeri	*				
	Megapedetes pentadactylus	x		x		
	Bathyergidae		x			
	Bathyergoides neotartiarus	*		*	*	
	Afrocricetodon	x		x	x	
	Afrocricetodon songhori	*				
	Afrocricetodontine	*				
	Paranomalurus bishopi	*	*	*	*	
	Paranomalurus soniae	*				
	Paranomalurus walkeri	*				
HYRACOIDEA	Megalohyrax championi	x	x			
PERISSO.	Chalicotherium rusingense	x	x	x		
	Brachypotherium heinzelini					x
	Dicerorhinus leakeyi	x				

	Dicerorhinus sp.			x		x
	Acerath. acutirostratrum	x				
ARTIO.	Hyotherium darteveilei	x	x	x		
	Dorcatherium songhorensis	x	x	x		
	Dorcatherium pigotti			x		
	Paleomeryx africanus	x	x	x		
	Walangania africanus	*				
	Masritherium aequitorialis					x

16.4.1 Non-mammalian Fauna

In addition to the mammalian remains listed above, there are also non-mammalian fossils from Napak.

TABLE 16.2

NON-MAMMALIAN FAUNA

	I	IV	V	IX	X	II
REPTILE	10	65	35	2		359
BIRD		4	1	2		
FISH						3
MILLIPEDE	1	4			1	
GASTROPOD	5	74	49	29	5	1
COPROLITE						90

The non-mammalian faunal list comes from Bishop (1964) and refers to the number of specimens found.

The gastropod fauna has been analysed by Andrews and Van-Couvering (1975).

---------GASTROPOD-------------ECOLOGICAL IMPLICATIONS

1.	*Maizania* (4 sp.)	Evergreen forest
2.	*Homorus* (*Subulona*)	Wet evergreen forest
3.	*Limicolaria* (*2 sp.*)	forest & bushland
4.	*Trochonanina*	Evergreen forest & bush

16.4.2 FAUNAL ANALYSIS

16.4.3 Habitat Indicator Species

UPPER SITES - The indicators are relatively evenly divided between forest and non forest forms. Mole rats (Bathyergidae) are commonly found in non forest conditions and *Megapedetes pentadactylus* and the hyrax are generally seen to represent arid through savanna conditions (Bigalke 1972, VanCouvering and VanCouvering 1976). On the other hand, *Paranomalurus* is a strong forest indicator, especially since *Paranomalurus bishopi* is the only form listed with a frequency greater than 10 by VanCouvering and VanCouvering (1976). On this basis, a forest environment at the Napak upper levels is more strongly indicated.

LOWER SITES - There are no clear indicators from the lower sites.

16.4.4 Relative Abundances

UPPER SITES - The highest percentage of species are rodents (30%) followed by primates (22%) and artiodactyls (12%). Dominance by arboreal rodents and primates is common in forest environments, and thus, must be considered to indicate forested conditions here (Bourliere 1963). Furthermore, there are a number of rodent species represented (12) and none of them shows a clear dominance numerically over the others, as is often the case in open environments (Andrews and VanCouvering 1975).

LOWER SITES - The lower sites do not have enough fauna to calculate any reasonable relative abundance figures.

16.4.5 Taxonomic Habitat Index

The taxonomic habitat index has not been calculated because the highly specific nature of this test is not suited to a fauna in which there is a considerable amount of uncertainty concerning which fossil species are actually present.

16.4.6 Ecological Diversity Analysis

The ecological diversity analysis has been calculated for the upper sites only.

Taxonomic Order - This spectrum resembles most closely that from the lowland forest (Nesbit Evans et al 1981), although the percentage of primates from Napak is higher than would be expected, and those of rodents and artiodactyls are somewhat too low. Nevertheless, the match is still reasonably close, perhaps surprisingly so considering the temporal distance between the two samples.

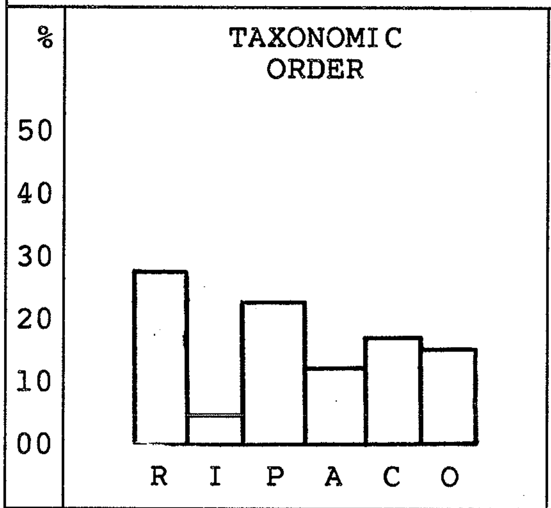
Size Category - The size category spectrum is ambiguous in that it resembles most of the published spectra to a certain degree, but matches none of them very closely. It is most similar to the woodland-bushland spectrum.

Locomotor Adaptation - The Napak spectrum does not closely match any of the published spectra. It is most similar to the floodplain sample but the S.G.M. and Aquatic classes are too low.

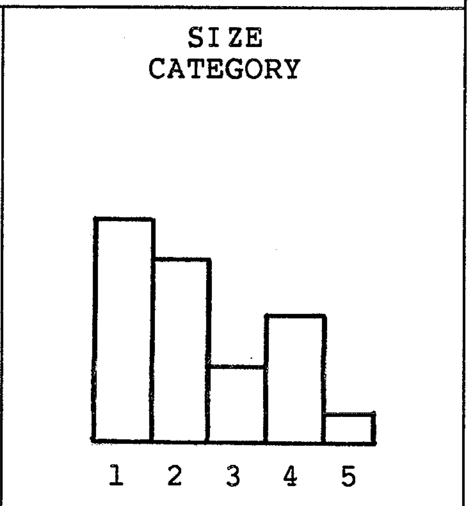
Feeding Adaptation - The Napak spectrum does not resemble any modern spectra at all.

TABLE 16.3

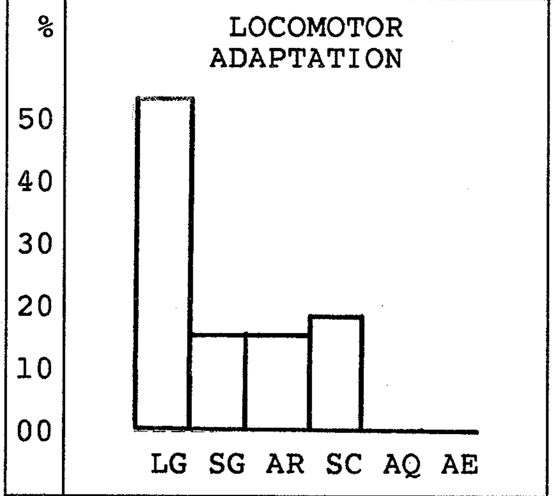
ECOLOGICAL DIVERSITY ANALYSIS-NAPAK


TAXONOMIC ORDER

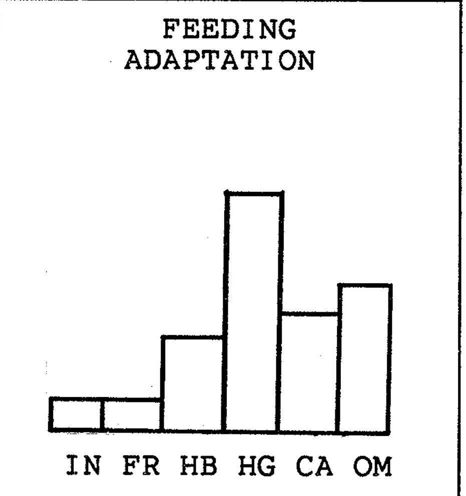
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER


SIZE CATEGORY

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.


LOCOMOTOR ADAPTATION

LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL


FEEDING ADAPTATION

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

16.5 FLORA

There are no published floral remains from Napak.

16.6 PALEOGEOGRAPHY

LOWER SITES

The lower sites are apparently not clearly associated with volcanic detritus. The sedimentary environment of gritty deposits, including sandstone, indicates deposition under wet conditions. This is substantiated by the faunal remains, much of which are non-mammalian, primarily reptile. No conclusions can be drawn regarding the surrounding vegetation type because of the sparsity of the fauna. Although 5 sites are generally considered to comprise the lower horizon only one, Napak II, has been published in any detail (Bishop 1964), and it is possible that the others may differ ecologically. It is, in fact, impossible to decide whether this grouping is justified on the basis of the available data.

UPPER SITES

The upper sites are much more well known. The faunal lists for Napak I, IV, V, IX, and X resemble each other quite closely. The species present at Napak IV, V and IX agree with those from Napak I (which has the longest faunal list) 76%, 69% and 83% respectively. Thus, it is reasonable to assume that these sites can be considered as a group.

In contrast to the lower levels, the upper sites are associated with pyroclastics, and the majority of the depositional medium is volcanic tuff. This argues for subaerial deposition at these sites although it should be noted that tuff can accumulate under water (Andrews et al 1981). The fauna, however, does not particularely support the notion of a water covered, or water margin, location as it did for Napak II. The non-mammalian fauna constitutes only 3% , 4.5%, 6%, and 1% of the fauna from Napak I, IV, V, and IX respectively. In total, the indications here are of subaerial deposition at the upper sites.

The surrounding vegetation pattern, from the faunal analysis, was probably forest. The relative abundance figures, the gastropod fauna and parts of the ecological diversity analysis, as well as some of the habitat indicator species all point to a forest biome.

The only *Proconsul* species present is *P. major* and it is not uncommon (M.N.I. = 8)(Andrews 1978). Since the environment at the upper levels is quite well known, this appears to be a case of a single *Proconsul* species associated with a particular habitat, the forest.

17. OMBO

Located on the North side of the Kavirondo Rift Valley (34 34'E, 00 04'S) Ombo lies mid-way between Kisingiri and Tinderet. Little information is available concerning Ombo, and no Proconsul remains have been found there, so it will not be discussed further.

18. RUSINGA

Rusinga Island, an erosional remnant of the North flank of Kisingiri mountain, lies in Lake Victoria, at the mouth of the Kavirondo Rift, just 15 km. North of Kisingiri (34 07'E to 34 13'E, 00 23'S to 00 27'S). Rusinga is the most studied East African Miocene site and has yielded the most information. Many facets of this site are, however, complex and confusing, especially the provenance of the component sites and faunal material.

18.1 GEOLOGY

Rusinga Island contains an immense number of fossiliferous localities. There are at least 77 numbered sites (listed discontinuously from R1 to R113) and an additional 18 or so named locations. Many of these sites are listed in groups (i.e. R30-40 Bishop 1967, Clark and Leakey 1951) and apparently have little fossiliferous material. The most significant sites, because of the fauna recovered, are: Gumba, Kalim (R74 and R75 at Gumba, Bishop 1967), Kathwanga (R5), R2 & 4, R105, Wakondu, Hiwegi, R1 and R3, R106, R107, Kiahera, R113, R10-19, Kiune, Sienga and Waynama (Pickford 1981). In addition to this list there are some sites that Pickford does not discuss in detail: Kathwanga Point (Andrews and VanCouvering 1975), and Kulu (VanCouvering and VanCouvering 1976). All of these sites can be fitted, with varying degrees of certainty, into the lithology of Rusinga Island as developed by VanCouvering and Miller (1969).

Finally, a group of sites which are significant in terms of fauna, R100-R112, cannot apparently be placed in the stratigraphy with accuracy (Bishop 1967), although some of them (R105-R107) have been placed in one of the formations by VanCouvering and Miller (1969) and Pickford (1981). A map of Rusinga Island may be seen below (Fig. 18.2) (from VanCouvering and Miller 1969).

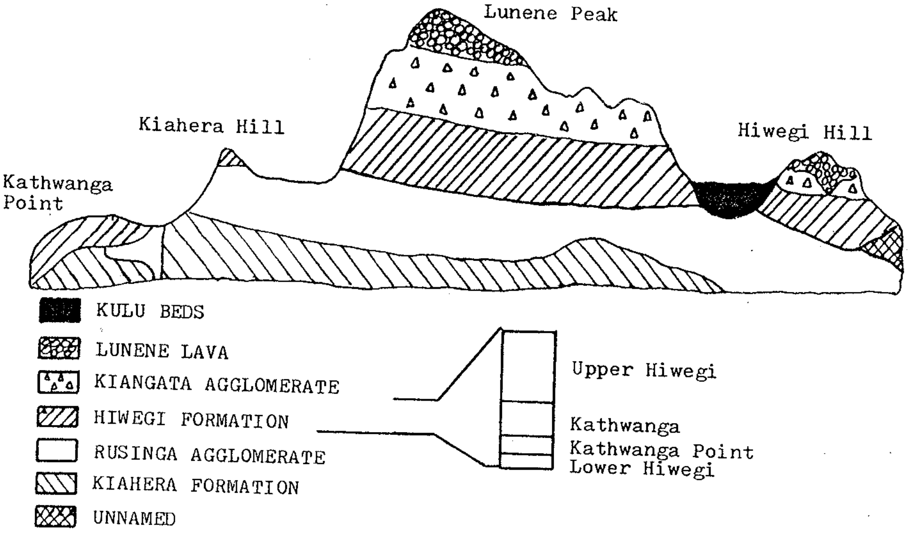


Figure 18.1: RUSINGA ISLAND - CROSS SECTION

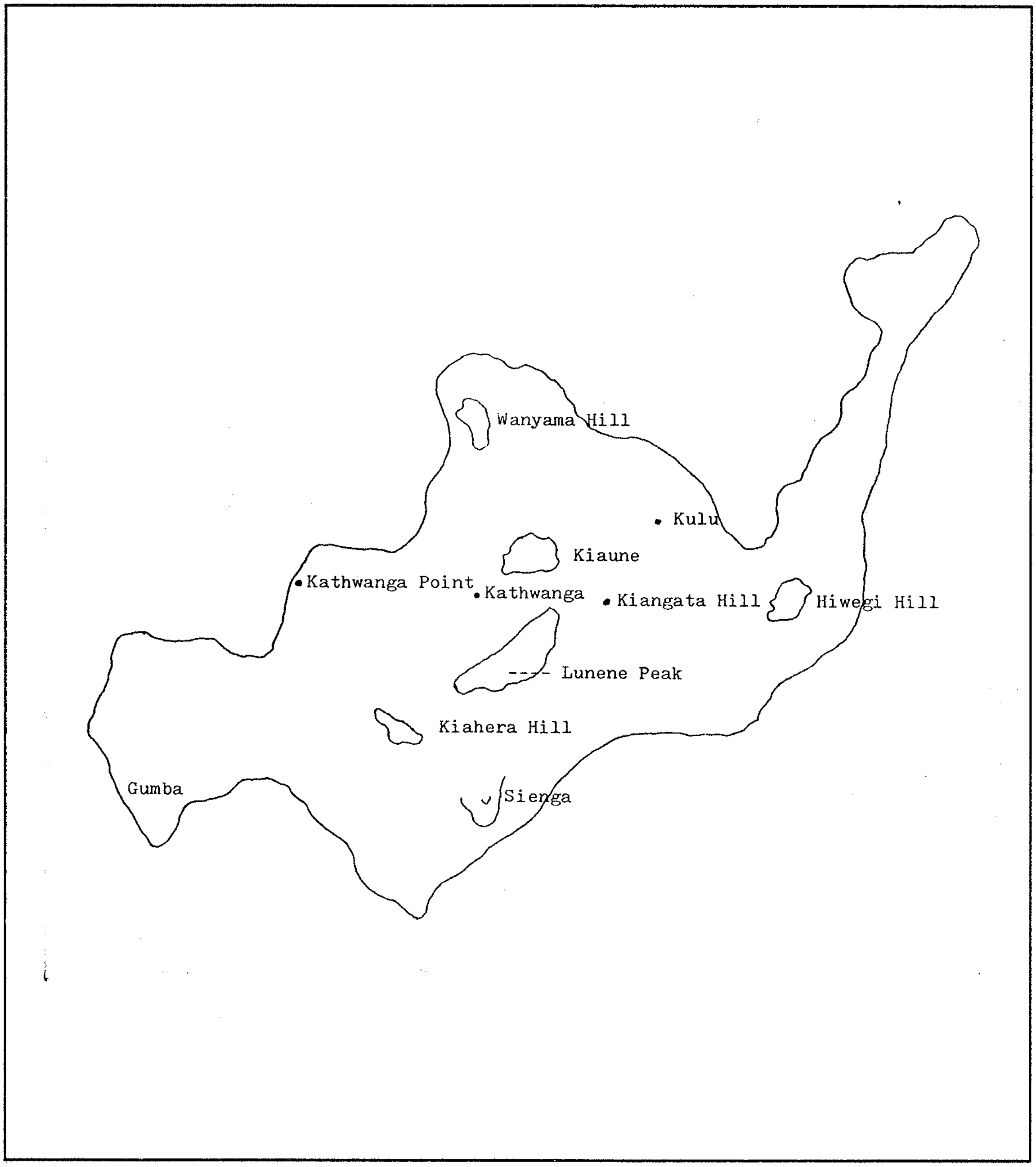


Figure 18.2: RUSINGA ISLAND

18.1.1 KIAHERA FORMATION

The lowest formation in evidence on Rusinga is the Lower Kiahera. This feature is composed of purely epiclastic conglomerates and sandstones, and, on this basis, is presumed to be pre-volcanic (VanCouvering and VanCouvering 1976). With the appearance of tuff, indicating volcanic activity, the Lower Kiahera becomes the Upper Kiahera. Besides tuff this horizon also shows the hyper alkaline rock alnoite, and numerous large mica flakes (VanCouvering and VanCouvering 1976).

There is no clear evidence that any of the Rusinga fossil localities can be assigned with certainty to the Kiahera series. Various authors, after studying the Rusinga lithology, have come to a variety of conclusions.

Bishop (1967) places R73, R76, R113, Kalim, and, possibly, R100-R112 in the Kiahera formation. Of the above, R73 (which may be part of Kalim) and R76 need not be discussed as they have very few fossils (Bishop 1967). R100-R112 could not be placed with certainty by Bishop and subsequently, several of this group have been dealt with separately (VanCouvering and Miller 1969, Pickford 1981). Andrews (1978), however, agrees with Bishop in the placement of R100-R112 which he puts in the Kiahera series, along with the site of Kiahera Hill. It is quite possible, or even probable, that at least some of these sites are located in either the Basal Hiwegi or the Kathwanga Point horizons.

Kalim was also placed in the Kiahera formation by Whitworth (1953) and Shackleton (1951) but VanCouvering (cited by Pickford 1981) could not place it lithologically and is unsure of its provenance. On faunal grounds, Pickford (1981) places it in, or near, the Hiwegi series. In an earlier report, however, VanCouvering and VanCouvering (1976) state that Kalim has no volcanic sediments, and may be considered older, or of the Kiahera series, on this basis. For the time being, Kalim should be retained in the Kiahera formation, at least until more lithological information becomes available.

The final site listed by Bishop as being of the Kiahera formation, is R113. This site, as were some of the above, is lithologically unclear (VanCouvering cited by Pickford 1981). Pickford (1981) places it in the Hiwegi formation on the basis of faunal similarities. There are uncertainties, however, regarding what material has actually come from R113 (Pickford 1981). While awaiting further data it seems best that R113, as was Kalim, should be retained in the Kiahera formation.

18.1.2 Rusinga Agglomerate

The Rusinga Agglomerate horizon consists mainly of a conglomerate composed of large stones in a calcium carbonate matrix. There are incorporated tuffs, alnoite is common, and large flakes of mica are present (VanCouvering and VanCouvering 1976). There are apparently no fossil sites from this horizon, although it is likely that some scattered fossils have come from here. The Rusinga agglomerate is often used as a marker to separate the Kiahera series from the Hiwegi.

18.1.3 HIWEGI FORMATION

The Hiwegi formation has produced almost all of the Hominoid material from Rusinga, and so is of great importence (VanCouvering and Miller 1969).

18.1.4 Basal Hiwegi

The basal Hiwegi consists of thick bodies of Rusinga melanite agglomerate and folded and faulted stratified rocks called "grey hards" (VanCouvering and Miller 1969). Bishop (1967) assigns the following sites to this formation: R1, R1A, R3, R10-R19 and Wanyama. Since, however, the stratigraphy of Rusinga Island was revised in 1969, it is possible that the sites listed above would now fall into the Kathwanga Point Series, which is generally more fossiliferous than the Lower Hiwegi (VanCouvering and Miller 1969).

The Basal Hiwegi series commonly lies directly on Rusinga Agglomerate, but in places (for example, at the base of Hiwegi Hill) the unit generally found above the Basal Hiwegi, the Kathwanga Point series, lies directly above the agglomerate with no intervening layer (VanCouvering and Miller 1969). In these locations the Kathwanga Point series is considered to be the Basal Hiwegi.

18.1.5 Kathwanga Point Series

Composed of greenish-grey and red brown highly micaceous flaggy volcanic siltstones and sandstones, the Kathwanga Point series represents a considerable (35') portion of the entire Hiwegi sequence. The sites listed above as Basal Hiwegi may, in fact, be of Kathwanga Point origin, as may be some of the R100-R112 group, notably R105-R107 (VanCouvering and Miller 1969).

18.1.6 Kathwanga Series

Lying above the Kathwanga Point series, the Kathwanga formation is the single most productive fossil horizon on Rusinga. Generally, the sediments are non-micaceous calcareous volcanic grits, but at the site of Kathwanga Point they grade into grey or brown clayey silts (VanCouvering and Miller 1969). The Kathwanga series contains the fossils from the important sites R105, R106 and R107 which represent more than one-third of the total Proconsul material from Rusinga (VanCouvering and Miller 1969 Leakey 1967). The Kathwanga Point site, described by Andrews and VanCouvering (1975), including the fossiliferous localities KB, KF, KG and KH, also lies in the Kathwanga series (VanCouvering and Miller 1969).

The Kathwanga series sediments are considered to be of lacustrine origin (Bishop 1967, VanCouvering and Miller 1969, Pickford 1981) and closely resemble those from the Kulu formation. Several authors have equated the two sequences and they may, in fact, be the same feature (Bishop 1967, VanCouvering and Miller 1969).

The principal fossiliferous beds from the Kathwanga Point site lie at an equivalent, or slightly lower, stratigraphic level as the site of Hiwegi on Hiwegi Hill (VanCouvering and Miller 1969). Thus, although the site of Hiwegi is considered to lie in the Upper Hiwegi sequence it may well be contemporaneus with the Kathwanga Point site from the Kathwanga series.

18.1.7 Upper Hiwegi

There is a general tendency in the entire Hiwegi series towards finer grained sediments moving from bottom to top (VanCouvering and Miller 1969). As would be expected, then, the Upper Hiwegi contains a considerable amount of sands and silts, with some conglomerate mixed in (Pickford 1981). The following sites are probably of Upper Hiwegi origin, although a Kathwanga series location must be considered possible: Hiwegi, Kiahera, Kiune and Sienga. The Upper Hiwegi sequence probably constitutes only one-half to one-third of the total Hiwegi formation, the bulk of this feature being contained in the Kathwanga/Kathwanga Point units (VanCouvering and Miller 1969).

18.1.8 Kulu Beds

A fairly localized feature West of Hiwegi Hill, the Kulu Beds are fine grained sediments of lacustrine origin (Pickford 1981). As well as mammal (including Proconsul) remains, there are fossil fish, plants, and non-mammalian forms represented. The following sites are considered to lie in the Kulu formation: Kulu, Wakondu, R20-R29, R2 and R4 (Bishop 1967). As mentioned previously, the Kulu series and at least part of the Hiwegi formation are probably contemporaneous, and may even be the same feature.

18.1.9 KIANGATA AGGLOMERATE

The first appearance of non-micaceous nephelinite lava occurs in the Kiangata agglomerate (VanCouvering and VanCouvering 1976). This lava is incorporated into the large grained agglomerate mixture.

18.1.10 LUNENE LAVA

True nephelinite lava from the Kisingiri volcano which today caps the two most prominant features on Rusinga Island, Hiwegi Hill and The Lunene Peak.

In summation, the stratigraphic sequence on Rusinga Island is now quite well documented. Unfortunately, the provenances of the many Miocene sites are not always clear. Even worse, the faunal samples have often been mixed, and, with the exception of recent samples, their exact origins can be problematic (Pickford 1981).

On the other hand, most of the faunal material comes from the Hiwegi formation, and the majority of this from the Kathwanga series. In addition to this, the fossils from the Kulu formation may be added to the Kathwanga series on the basis of similar lithologies. Thus, the bulk of the Rusingan faunal material may have a consistant origin.

18.2 DATING

Both VanCouvering and Miller (1969) and VanCouvering and VanCouvering (1976) have provided dates for the various Rusinga formations based on both K/ar dates and stratigraphic information. Those provided by VanCouvering and VanCouvering (1976) are:

1. 16.5 m.y. - Lunene Lava
2. 18.0 m.y. - Kulu Formation
3. 18.5 m.y. - Hiwegi Formation
4. 19.6 m.y. - Rusinga agglomerate
5. 21.0 m.y. - Upper Kiahera Formation
6. 23.0 m.y. - Lower Kiahera Formation

Those provided by VanCouvering and Miller (1969) are:

1. 16.5 m.y. - Lunene Lava
2. 17.0 m.y. - Kiangata Agglomerate
3. 17-18.6 m.y. - Hiwegi Formation (Kulu?)
4. 19.6 m.y. - Rusinga Agglomerate
5. 20-22.0 m.y. - Kiahera Formation

The following radiometric dates have been obtained from Rusinga Island: (unless otherwise referenced these dates have been drawn from VanCouvering and Miller 1969).

1. 16.8 +/- 0.6 m.y. (Lunene lava)
2. 16.3 +/- 0.5 m.y. (Lunene lava)
3. 16.5 +/- 0.7 m.y. (Lunene lava)
4. 16.6 +/- 0.7 m.y. (Lunene lava)
5. 15.3 +/- 1.5 m.y. (site R107, Kathwanga series) (Evernden et al 1964) (considered unreliable because of the high +/- figure)
6. 13.5 +/- 0.4 m.y. (lower Hiwegi)
7. 13.5 +/- 0.4 m.y. (lower Hiwegi) (both these last two dates are considered discrepant as they are younger than the lava overburden)

8. 19.6 +/- 0.2 m.y. (Rusinga agglomerate)

There are a considerable number of problems regarding K/ar dates from Rusinga. In addition to the discrepant dates cited above, there are other, more obviously incorrect, examples: 107 m.y. (site R1A), 167 m.y. (site unknown), 42 m.y. (site R107)(Evernden et al 1964).

The highly volcanic formations, Lunene lava and Rusinga agglomerate, are, however, consistently dated, and these provide the framework for the whole Rusinga sequence. The other formations are dated more clearly relative to one another by stratigraphy. VanCouvering and VanCouvering (1976) date the important Hiwegi formation at 18.5 m.y. which is largely consistent with VanCouvering and Miller's (1969) dates of 17-18.6 m.y. Within the Hiwegi formation, the Kathwanga series, with its significant fauna, lies near the mid-point. Following VanCouvering and Miller's stratigraphy, the dates for the Kathwanga series should be @ 17.8-18.2 m.y., which would agree, by and large, with the 18.5 m.y. date proposed by VanCouvering and VanCouvering (1976).

If the two most important fossiliferous series within the Hiwegi formation (Upper Hiwegi and Kathwanga) are taken together, they still constitute a reasonably limited time span of approximately one million years. Furthermore, the 18.0 m.y. date suggested for the Kulu formation (VanCouvering and VanCouvering 1976) falls within this time span. Thus, it is possible that the majority of the faunal remains from Rusinga Island come from a limited area, in both geographical and temporal terms.

18.3 ABUNDANCE OF PROCONSUL FORMS

The following distribution of *Proconsul* forms (table 18.1) was provided by Andrews (1978). His placement of sites in the various formations differs somewhat from that used here. Some sites were not placed in any formation by Andrews, and their locations, based on the evidence presented above, are listed in brackets: Kathwanga (Kathwanga series), Sienga (Upper Hiwegi), Wanyama (Lower Hiwegi), R114 (?), Gumba (Kiahera formation), R113 (Kiahera formation), and R73 (Kalim) (Kiahera formation).

Andrews' placement of R100-R112 in the Kiahera series is questionable, as it appears likely that at least R105-R107 are in the Kathwanga formation (Leakey 1967, VanCouvering and Miller 1969). For the time being R100-R104 and R108-R112 will also be placed in the Kathwanga series. Furthermore, based on the stratigraphy, it appears likely that the site of Kiahera Hill is in the Hiwegi formation, not the Kiahera formation as listed by Andrews (1978).

An examination of table 18.1 reveals that two species *P. africanus* and *P. nyanzae* dominate the *Proconsul* fossils from Rusinga. The appearance of the other Proconsulines is limited, and the significance of their occurrence is reduced by the fact the single specimens assigned to *P. major* and *P. gordoni* have no known provenance. It is also evident that the majority of the Hominoid fossils come from the Hiwegi formation. This unit contains 86% of the *P. africanus* individuals and 80% of the *P. nyanzae* individuals. If the Hiwegi and Kulu formations are grouped together they contain 88% and 86% of the *P. africanus* and *P. nyanzae* individuals respectively. Finally, the only specimens of *P. vancouveringi* come from the Hiwegi formation. Thus, it is obvious that the ecology of the Hiwegi formation is of paramount importence.

TABLE 18.1

DISTRIBUTION OF PRIMATES, RUSINGA

FORMATION	SITE	P. afr	P. nya	P. maj	P. gor	P. van
	Gumba	1				
	R113	3	3			
	Kalim		1			
KIAHERA TOTAL		4	4	-	-	-
	R1	3	8			
	R3	6	3			
	Wanyama		1			
LOWER HIWEGI OR KATHWANGA POINT TOTAL		9	12	-	-	-
	R100-R105	3	1			
	R106	6	6			2
	R107-R112	1	4			
	Kathwanga	13	13			1
KATHWANGA TOTAL		23	24	-	-	3
	Hiwegi	1	2			
	Kiahera Hill		3			
	Sienga	2				
UPPER HIWEGI TOTAL		3	5	-	-	-
	R2	1	2			
	R4		1			
	Wakondu					
KULU TOTAL		1	3	-	-	-
	R114	1				
	Unknown		3	1	1	
UNCERTAIN TOTAL		1	3	1	1	-
HIWEGI FORM. TOTAL		35	41	-	-	3
KIAHERA FORM. TOTAL		4	4	-	-	-

KULU FORM. TOTAL		1	3	-	-	-
RUSINGA TOTAL		41	51	1	1	3

18.4 FAUNA

The difficulty in analysing the fauna from Rusinga Island lies not in determining which species are present (as lists have been provided by VanCouvering and VanCouvering 1976 and Andrews and VanCouvering 1975), but rather in finding the provenance of the fossils. There are complete faunal listings for only Gumba, R113 (Pickford 1981) and Kathwanga Point (4 locations) (Andrews and VanCouvering 1975). Otherwise, there are listings only for Primates (Andrews 1978), insectivores and bats (Butler 1969) with appropriate specific site information. VanCouvering and VanCouvering(1976) have provided a complete faunal list for all of Rusinga Island, but with no detailed information.

As discussed earlier, few sites can clearly be placed in the Kiahera formation. In all likelihood these are: Gumba and/or Kalim, R76, and R113. The Gumba and R113 fauna has been listed by Pickford (1981) and will be used here as the Kiahera formation fauna.

Because most of the sites, and fossils, from Rusinga come from the Hiwegi formation, it will be assumed here that the forms specified by VanCouvering and VanCouvering (1976) have largely come from Hiwegi sites, and these will be used here as the Hiwegi faunal list. It must be remembered, however, that fauna from other levels has almost certainly been mixed into this sample.

Finally, a faunal list from the Kathwanga series (in the Hiwegi formation) will be provided (Andrews and VanCouvering 1975). Additional information for all of the above lists will come from Andrews (1978), Butler (1969) and Wilkinson (1976).

TABLE 18.2

KIAHERA FAUNA

ORDER	GENUS/SPECIES	R113	GUMBA
INSECTIVORA	Nasus rusingensis	x	x
PRIMATES	Progalago sp.		x
	Limnopithecus legetet		x
	Dendropithecus macinnesi	x	x
	Proconsul africanus	x	x
	Proconsul nyanzae	x	
CREODONTA	Metapterodon zadoki		x
	Anasinopa sp.		x
	Teratodon sp.	x	x
TUBULIDENTATA	Orycteropus africanus		x
PROBOSCIDEA	Prodeinotherium hobleyi	x	x
RODENTIA	Diamantomys leuderitzi	x	x
	Paraphiomys pigotti		x
	Diamantohyus africanus		x
	Simonomys genovefae	x	
	Megapedetes pentadactylus	x	
HYRACOIDEA	Megalohyrax championi	x	x
PERISSODACTYLA	Brachypotherium heinzelini		x
	Chilotheridium pattersoni		x
	Aceratherium acutirostratrum		x
	Chalicotherium rusingense	x	x
	Dicerorhinus leakeyi	x	x
ARTIODACTYLA	Masritherium aequitorialis		x
	Hyoboops africanus		x
	Nguruwe kijivium		x
	Libyochoerus jeanelli		x
	Dorcatherium pigotti	x	x
	Dorcatherium parvun		x
	Propaleortx nyanzae		x
	Walangania africanus	x	
	TOTAL SPECIES	14	26

TABLE 18.3

HIWEGI AND KULU FAUNA

ORDER	GENUS/SPECIES	FREQUENCY
LIPOTYPHLA	Protenrec tricuspis	1
	Geogale aletris	1
	Galerix africanus	1
	Gymnurechinus leakeyi	43
	Gymnurechinus comptolophus	8
	Amphechinus rusingensis	6
	Crocidura sp.	1
MACROSCELIDEA	Myohyrax oswaldi	11-100
	Rhynchocyon clarki	11
	Rhynchocyon rusingae	7
	Rhynchocyonid sp.	1
CHIROPTERA	Taphozous incognita	1
	Megadermidae sp.	1
	Propotto leakeyi	1
PRIMATES	Progalago dorae	1-10
	Progalago songhorensis	1-10
	Komba robustus	1-10
	Komba minor	1-10
	Mioeuoticus bishopi	1-10
	Limnopithecus legetet	6
	Dendropithecus macinnesi	43
	Proconsul africanus	35
	Proconsul nyanzae	41
	Proconsul vancouveringi	3
CREODONTA	Kelba quadaemae	1-10
	Anasinopa leakeyi	11-100
	Anasinopa sp.	1-10
	Dissopsalis pyroclasticus	P
	Metapterodon kaiseri	1-10
	Metapterodon zadoki	1-10
	Pterodon africanus	1-10
	Leakitherium hiwegi	1-10
	Hyaenodon andrewsi	1-10
	Hyaenodon metthewi	1-10
	Hyaenodon pilgrimi	1-10
	Megistotherium osteothalastes	1-10
CARNIVORA	Hecubides euryodon	1-10
	Hecubides macrodon	1-10
	Kichechia zamane	11-100

	Metailurus africanus Nimravine	1-10 P
TUBULIDENTATA	(My)Orycteropus africanus Tubulidentate (large)	1-10 1-10
PROBOSCIDEA	Prodeinotherium hobleyi Platybelodon kisumuensis	11-100 11-100
LAGOMORPHA	Kenyalagomys rusingae Kenyalagomys minor	100 11-100
RODENTIA	Phiomys andrewsi Paraphiomys stromeri Paraphiomys pigotti Epiphiomys coryndoni Diamantonys leuderitzi Kenyamys mariae Simonomys genovefae Myophiomys arambourgi Elmerimys woodi Bathyergoides neotartiarus Proheliophobus leakeyi Paranomalurus soniae Paranomalurus bishopi Megapedetes pentadactylus Megapedetes sp. Afrocricetodon songhori Protarsomys macinnesi Notocricetodon petteri Vulcanisciurus africanus Sciurid	1-10 11-100 100 1-10 100 1-10 1-10 1-10 1-10 1-10 1-10 11-100 1-10 11-100 1-10 1-10 1-10 1-10 11-100 1-10
HYRACOIDEA	Pachyhyrax championi Pachyhyrax cf. pygmaeus Meroehyrax bateae	11-100 1-10 1-10
PERISSODACTYLA	Chalicotherium rusingense Aceratherium acutirostratrum Chilotheridium pattersoni Dicerorhinus leakeyi Brachypotherium heinzelini	11-100 11-100 1-10 11-100 11-100
ARTIODACTYLA	Masritherium aequitorialis Brachyodus africanus Hyotherium dartevillei Hyotherium sp. Bunolistriodon jeanneli Listriodon sp. Xenochoerus africanus Dorcatherium crassum Dorcatherium pigotti Dorcatherium parvun Gelocus whitworthi	11-100 1-10 11-100 11-100 11-100 1-10 1-10 11-100 11-100 11-100 1-10

	Propaleoryx nyanzae Canthumeryx sirtensis Walangania africanus	1-10 1-10 11-100

TABLE 18.4

KATHWANGA SERIES FAUNA (FROM KATHWANGA POINT SITE)

ORDER	GENUS/SPECIES	KB	KF	KG	KH
LIPOTYPHLA	Gymnurechinus leakeyi		*	x	
	Lanthanotherium sp.		x		
	Lipotyphla indet	x	x		
MACROSCEL.	Rhynchocyon clarki	x	x	*	
PRIMATES	Progalago songhorensis	*			
	Komba robustus			x	
	Komba minor			x	
	Limnopithecus macinnesi		x	x	
	Proconsul africanus			x	x
CREODONTA	Anasinopa leakeyi			*	
	Hyainailourous sp.				x
CARNIVORA	Carnivora indet	x	x	*	
PROBOSCIDEA	Prodeinotherium hobleyi				x
LAGOMORPHA	Kenyalagomys rusingensis		*	*	x
RODENTIA	Diamantomys leuderitzi			*	x
	"Apodecter" stromeri	*		*	
	Megapedetes pentadactylus				*
	Anomalurid sp. A	*		*	
	Phiomyid sp. A	*	*	*	x
	Phiomyid sp. D	*	*		
	Phiomyid sp. indet	*	*	*	x
	(?)Bitis		*		x
	Rodentia indet vars	*	x	*	x
PERISSO.	Chalicotherium rusingensis			x	
	Chalicotherium sp. indet		x		
	Rhinocerotid indet				x
ARTIO.	Dorcatherium pigotti		x	x	x
	Dorcatherium parvun		*	x	x
	Masritherium aequitorialis				x
	Suidae indet				x
	Artiodactyla indet		x	x	x

	TOTAL SPECIES PRESENT	10	16	19	16
NON-MAMMAL. FAUNA	Crocodylus niloticus		*		x
	Crocodyla indet			x	
	Chelonia indet		*		
	Squamata indet	x	x		
	Lacertilia indet			x	
	Chamelionid indet			x	
	Serpentes indet		x		
NON-MAMMAL.	SPECIES PRESENT TOTAL	1	4	3	1

18.4.1 FAUNAL ANALYSIS

18.4.2 KIAHERA FAUNA

In addition to the mammalian fauna listed above (table 18.2), some non-mammalian material has been recovered from Gumba (Pickford 1981). These are: Aetheria elliptica, Aspatharia triangulata and Iridina (Pliodon) moharensis (fish), crabs, crocodyles and large turtles. These provide a strong suggestion that the habitat at Gumba was a lake margin or lacustrine location (Pickford 1981).

18.4.3 Habitat Indicator Species

The single species of Progalago can likely be seen as a forest indicator (Andrews and VanCouvering 1975). On the other hand Tubulidentates are today primarily savanna dwelling forms (Bigalke 1972), and Megapedetes pentadactylus is believed to have preferred arid through savanna type locations (Bigalke 1972, VanCouvering and VanCouvering 1976). As a whole the habitat indicators seem to point to a more open, non closed forest, environment during the Kiahera times.

18.4.4 Relative Abundances

The indicators here are unclear. While primates and rodents are both quite common (17% each), the ungulates are more frequent (perissodactyls = 17%, artiodactyls = 27% total = 44%). The rodents are not clear forest dwellers (i.e. anomalurids), so the predominance of ungulates may indicate a secondary forest, or more open, environment (Bourliere 1963). There is no frequency data available for the individual rodent forms so it is impossible to tell if one species dominated the others.

18.4.5 Ecological Diversity Analysis

1. Taxonomic Order - This spectrum from the Kiahera formation (table 18.5) does not match any obtained from modern environments. It is closest, however, to the floodplain and woodland-bushland spectra although the values for primates and "others" are too high, and the rodent percentage is too low.

2. Size Category - This spectrum does not resemble any of the modern spectra.

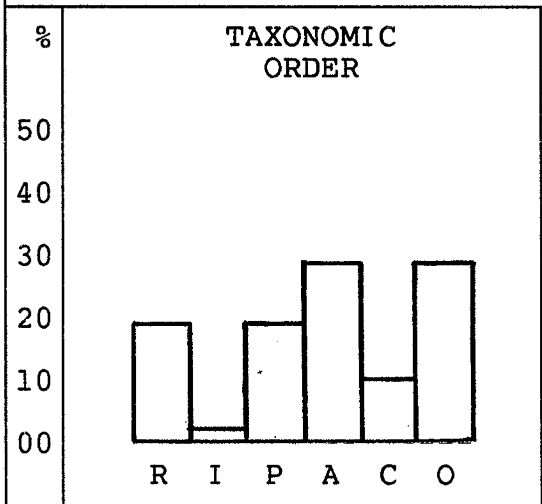
3. Locomotor Adaptation - This spectrum resembles most closely those from extant floodplain environments.

4. Feeding Adaptation - The Miocene spectrum resembles both the short grass plains and the floodplain spectra in terms of overall distribution of forms in the various classes, but the actual values diverge considerably.

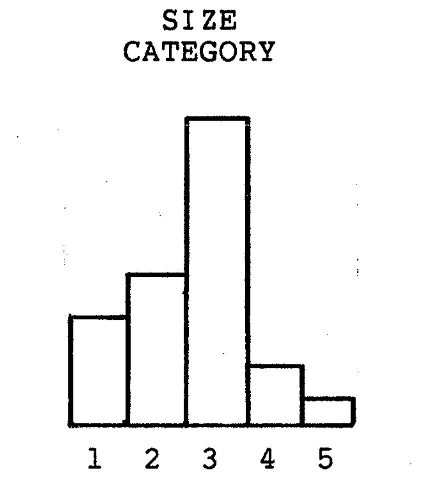
In total the ecological diversity analysis from the Kiahera horizon points towards a floodplain, or similar habitat. Taken together with the non-mammalian fauna: fish, crocodyles, crabs and turtles, a lacustrine/riverine/floodplain environment is indicated. The relative abundance and habitat indicator species analyses were inconclusive, but neither indicated strongly the presence of closed forest nearby. The predominant vegetation type could have been a savanna/woodland, which might help explain the mixed forest/non-forest indicators.

TABLE 18.5

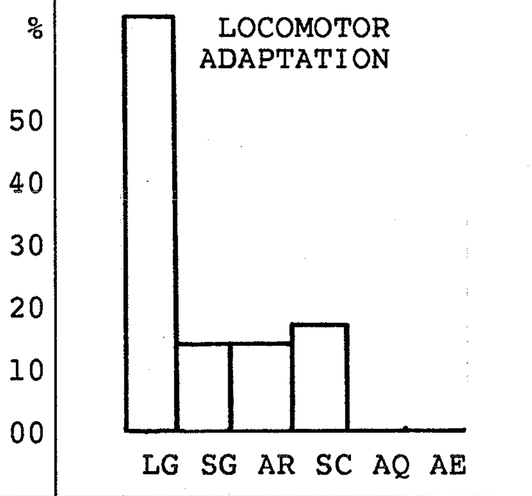
ECOLOGICAL DIVERSITY ANALYSIS-KIAHERA


TAXONOMIC ORDER

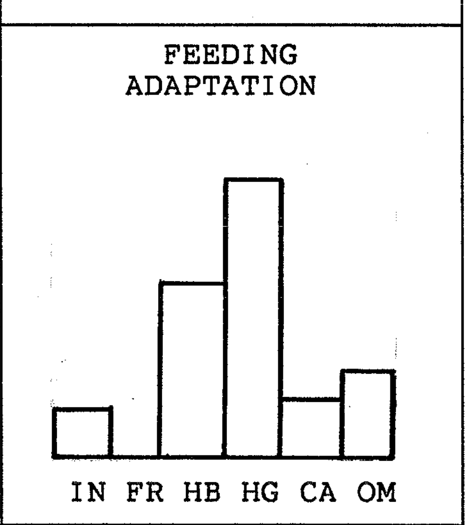
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER


SIZE CATEGORY

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.


LOCOMOTOR ADAPTATION

LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL


FEEDING ADAPTATION

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

18.4.6 HIWEGI FAUNA (excluding Kathwanga Point site)

18.4.7 Habitat Indicator Species

As with the Kiahera fauna, the habitat indicators are mixed in the fauna from the Hiwegi formation (table 18.3). Those that may be considered to be forest indicators are as follows

1. *Rhynchocyon* - There are three species present in the Hiwegi fauna, one, *R. clarki* is moderately frequent while the other two are less so.

2. *Paraphiomys* - Two species are present, *P. pigotti* is highly frequent, while *P. stromeri* is moderately frequent (Leakey 1967).

3. *Paranomalurus* - Two species are present, *P. bishopi* is rare, while *P. soniae* is moderately frequent.

4. Tragulidae - There are three species of *Dorcatherium* present and *Walangania africanus*: all are moderately frequent.

The non-forest indicators in the Hiwegi fauna are equally, or even more, impressive. They are:

1. *Myohyrax oswaldi* - moderately frequent.

2. *Hyaenodon* - Three species are present, all infrequent.

3. Tubulidentata - There are two forms of tubulidentate present, both are uncommon.

4. Lagomorpha - There are two species of *Kenyalagomys* present: *K. minor* is moderately frequent while *K. rusingae* is frequent.

5. *Bathyergoides* - One species is present, it is rare.

6. *Megapedetes* - two species are present, *M. pentadactylus* is moderately frequent while *M. sp.* is infrequent.

7. Erinaceidae - There are four species of hedgehog from the Hiwegi formation. *Gymnurechinus leakeyi* is frequent, *G. comptolophus* is moderately frequent, *Amphechinus rusingensis* is infrequent and *Galerix africanus* is rare (Leakey 1967).

8. Artiodactyla - Several artiodactyls may be considered woodland browsers, including: *Hyotherium darteveil-*

lei (moderately frequent), H. sp (moderately frequent), Bunolistriodon jeanneli (moderately frequent) and Listriodon sp. (infrequent) (Cooke and Maglio 1978).

There are more good habitat indicator species from the Hiwegi series on Rusinga Island than from any other Miocene site from East Africa. Unfortunately, the same problem of conflicting indicators that exists at the other sites exists here also, only magnified to a greater degree. Although the Hiwegi fauna is treated here, out of necessity, as a single fauna, it is highly likely that there were ecological differences between the great number of sites from which the fossils were derived. While the sites assigned to the Hiwegi formation are consistent lithologically, and were probably roughly contemporary (within approximately 1 m.y.), the habitat indicators point towards both forest and non-forest conditions. Thus, rather than searching for a dominant vegetation type, it may be possible that during a fairly restricted period of time there were at least two differing biomes existing side by side in the Rusinga area. which may have existed side by side.

18.4.8 Relative Abundances

The highest proportion of the Hiwegi fauna consists of rodents (22%), followed by carnivores (19%), artiodactyls (16%) and primates (11%). The abundance of rodents may indicate forest conditions as no one form dominates over the others numerically (Andrews and VanCouvering 1975, Pickford 1981). With precise faunal listings from each Hiwegi site, however, it might be seen that one of the forms found in great frequency (ie. Paraphiomys pigotti, Diamantomys leuderitzi, or Kenyalagomys rusingae) dominated the rodent population at any particular location.

The abundance of carnivores (Carnivora + Creodonta = 19%) is interesting, higher than at other East African Miocene sites. In extant environments, corresponding percentages of carnivores are found in quite open environments (N. American steppe = 18%, S. African savanna = 18%) (Walker 1975).

The high percentage of primates has been seen as an indication of a forested environment (Pickford 1981).

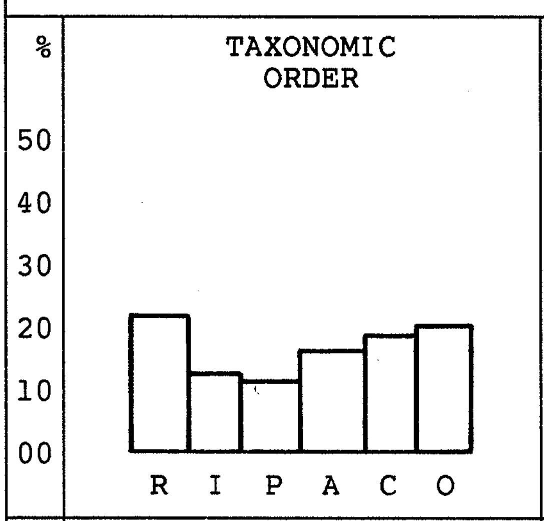
18.4.9 Ecological Diversity Analysis

1. Taxonomic Order - The Hiwegi spectrum does not match any spectra from modern environments. This is largely due to the number of species falling into the "other" category.
2. Size Category - The Hiwegi spectrum matches fairly closely the extant African woodland-bushland spectrum. The only significant deviation from this latter pattern lies in the >180 kg. class, in which the Miocene sample is less than is found today.
3. Locomotor Adaptation - There is a fairly close match between the Miocene spectrum and those from extant woodland-bushland environments.
4. Feeding Adaptation - The Miocene spectrum matches the spectra from extant woodland-bushland environments quite closely.

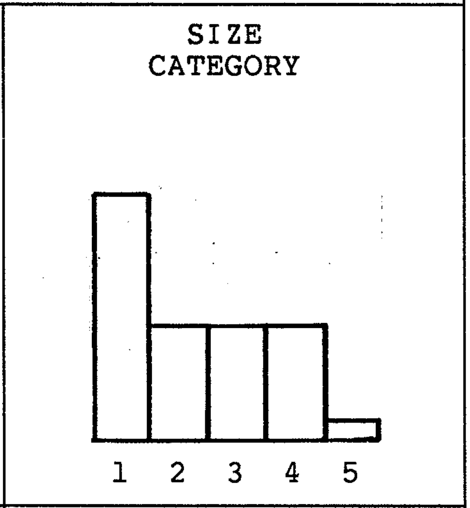
In total, the ecological diversity analysis reflects a strong woodland-bushland component in the fauna. This is especially clear in the size and feeding adaptation categories. None of the categories strongly reflect a forest environment.

TABLE 18.6

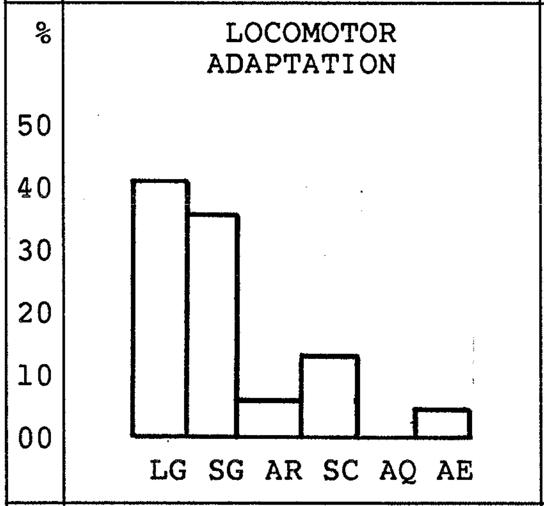
ECOLOGICAL DIVERSITY ANALYSIS-HIWEGI



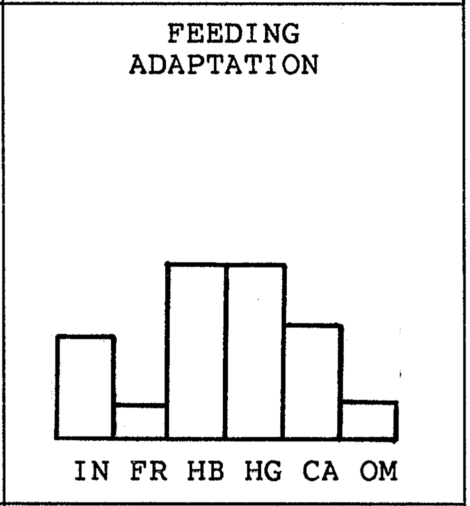
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER



1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL



IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

18.4.10 Non-mammalian Fauna

A number of gastropods have been recovered from the Hiwegi formation on Rusinga Island. The following come from site R3A (Lower Hiwegi) (Andrews and VanCouvering 1975).

TABLE 18.7

HIWEGI GASTROPODS

GASTROPOD	ECOLOGICAL IMPLICATION
Ampullaria ovata	lakes and rivers
Maizania (4 sp.)	evergreen forest
Ligatella (2 sp.)	bushland
Homorus (Subulona)	wet evergreen forest
Burtoa nilotica	woodland
Limicolaria (2 sp.)	forest/bushland
Trochonanina (5 sp.)	lowland evergreen forest and bush
Cerastua miocenicus	wide distribution
Tayloria (2 sp.)	drier evergreen forest and bush
Edentulina rusingensis	green forest

The implications of the gastropod fauna are mixed in the same manner as they were from the mammalian fauna.

There has undoubtably been a considerable amount of additional non-mammalian fauna recovered from Rusinga. Unfortunately, this has not as yet been analysed or published except for brief mentions of a cichlid fish (Andrews and

VanCouvering 1975), some terrestrial isopods (not ecologically specific), insects and myriapods (Morris 1979). A further analysis of the non-mammalian fauna could prove to be revealing, especially if done by site.

18.4.11 Hiwegi Summary

As mentioned earlier, it is likely that the individual sites from the Hiwegi formation differed ecologically to a significant degree. Thus, when using a combined fauna, it is possible only to obtain a general impression of the ecology of the whole area over a period of time. This situation will exist until such time as each site, and its component fauna, is listed individually.

While there are a considerable number of forest indicators in the Hiwegi fauna, the overall implications seem to be of a more open, perhaps woodland-bushland biome. There are more good habitat indicators for the latter type of environment than for the former. Furthermore, in the ecological diversity analysis, the woodland-bushland component of the Hiwegi fauna was clearly demonstrated. Notwithstanding this, however, the indicators of a forest biome are also clearly present.

Since there was a considerable amount of standing/flowing water on Rusinga Island at this time, as evidenced by the sediments which are largely lacustrine/fluvatile in origin, it is possible to speculate that the forest biome existed in well watered areas, such as the margins of lakes and rivers. Apart from these moist areas, the prevailing environment on Rusinga may have been a more open woodland or savanna. The concept of a gallery or riverine forest was first proposed by Chesters (1957) after an analysis of the flora from Rusinga, but has recently been contested by Andrews and VanCouvering (1975). These authors believe that the floral remains indicate a more extensive lowland forest.

It is obvious that the Rusinga flora can be interpreted in a number of ways (as will be discussed under FLORA), so the faunal evidence must be largely considered when trying to assess the paleoenvironment at Rusinga. While some of the faunas closely studied and discussed by Andrews and VanCouvering (Kathwanga Point site - Kathwanga series) have a strong forest component, this component is certainly not as clear in the larger Hiwegi formation fauna.

Thus, it seems reasonable to propose that on Rusinga Island, the Hiwegi formation, spanning approximately one million years, showed a number of differing environments. This leaves more latitude for analysis than simply stating that

Rusinga, over a million year period, was all forested or all savanna like.

18.4.12 KATHWANGA SERIES FAUNA

Although part of the Hiwegi formation, the Kathwanga fauna (table 18.4) from the site of Kathwanga Point will be treated separately here for a number of reasons.

1. The site was excavated fairly recently (1971) (Andrews and VanCouvering 1975).
2. There is a clear faunal list of both mammalian and non-mammalian forms.
3. The fauna has been listed for each of the four fossiliferous localities which comprise this site.

Andrews and VanCouvering (1975) carefully analysed the fauna from the four individual fossiliferous locations and reached the following conclusions: a) site KF - streamside with forest (?) affinities, b) sites KB and KG - forest, c) site KH - possibly open or bushland environment.

18.4.13 Habitat Indicator Species

KF - Andrews and VanCouvering (1975:89) list Rhynchocyon (rare) as a forest indicator. In addition to this the two species of Dorcatherium (one species common) may be forest indicators. On the other hand, Gymnurechinus leakeyi (common) and Kenyalagomys rusingensis (common) may reflect a savanna type of environment. Thus, the habitat indicator species are mixed.

KB - Andrews and VanCouvering list the following forest indicators: Progalago, Rhynchocyon, Paranomalurus. There are no clear indicators of non-forest conditions.

KG - The forest indicators are: Rhynchocyon, Paraphiomys, an Anomalurid and two species of Dorcatherium. The first three of the above are all common. Gymnurechinus leakeyi and Kenyalagomys rusingensis, indicating more open conditions, are present, but both are uncommon.

KH - A possible indicator of open conditions, Megapedetes pentadactylus, is present. In addition to this are: Hyainailourous and Kenyalagomys both which may be considered indicators of non-forest conditions. Furthermore, the only commonly occurring species at KH is Megapedetes. The only form that might indicate forest is Dorcatherium, represented by two species.

18.4.14 Relative Abundances

KB - 60% of the KB sample is composed of rodents but the entire list from this site consists of only ten species so the high percentage of rodents could easily be artifactual. Ecological Indication = none.

KF - The most dominant groups here are Rodentia (31% and Insectivora (25%). Most of the rodent forms are common and none dominates over the others numerically as would be typical in a savanna situation (Andrews and VanCouvering 1975). The high percentage of insectivores is unusual but not necessarily indicative of any particular environmental type. Ecological Indication = Probably forest.

KG - The dominant orders at KG are Rodentia (32%) and Primates (21%). This is exactly the situation found in many modern forests (Bourliere 1963). In addition to this, most of the rodent species are common, an even distribution typical of forest ecosystems (Andrews and VanCouvering 1975). Ecological Implication = forest.

KH - Only Rodentia (38%) and Artiodactyla (31%) are present in significant percentages at KH. This might be indicative of open conditions. Megapedetes pentadactylus is more common than the other rodents which may be suggestive of a non-forest environment. Ecological Implication = woodland/ savanna.

18.4.15 Taxonomic Habitat Index

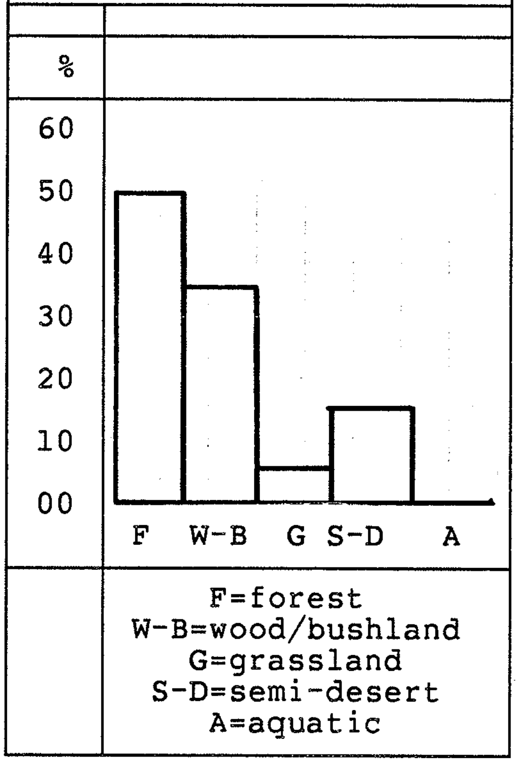
The individual sites do not have enough fauna to calculate the taxonomic habitat index. Nesbit Evans et al (1981), however, computed the THI for the combined Kathwanga Point fauna.

The taxonomic habitat index points to both forest and woodland- bushland components in the fauna, with the emphasis on forest oriented species. This is consistent with the notion that sites KB and KG reflect a forest environment while only KH was apparently more open.

TABLE 18.8

HABITAT SPECTRUM

KATHWANGA POINT



18.4.16 Ecological Diversity Analysis

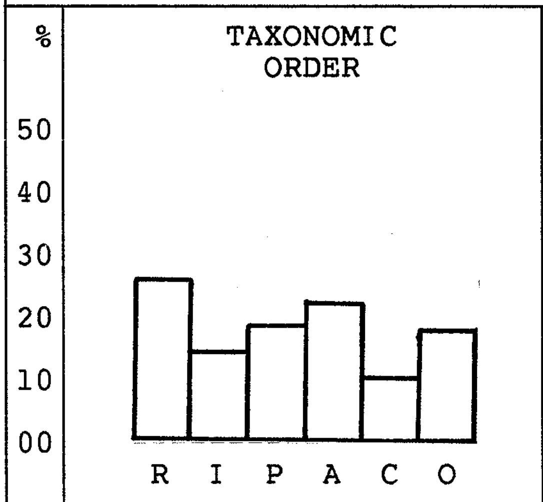
The ecological diversity spectrum for the combined fauna was calculated by Pickford (1981). This analysis has not been computed for site KB because there are so few species represented there.

KF - The taxonomic order and size category spectra do not match the spectra from any modern environments. The locomotor adaptation spectrum most resembles the spectra from extant woodland-bushland biomes while the feeding adaptation spectrum most resembles the spectra from the lowland forest of East Africa. Ecological Implication = mixed.

KG - The spectra from KG do not closely resemble the spectra from any extant environment. Ecological Implication = none.

TABLE 18.9

ECOLOGICAL DIVERSITY ANALYSIS-COMBINED FAUNA



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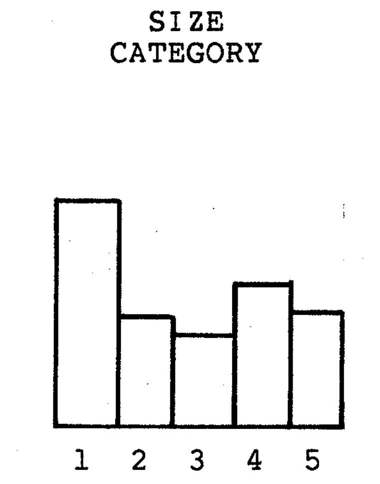
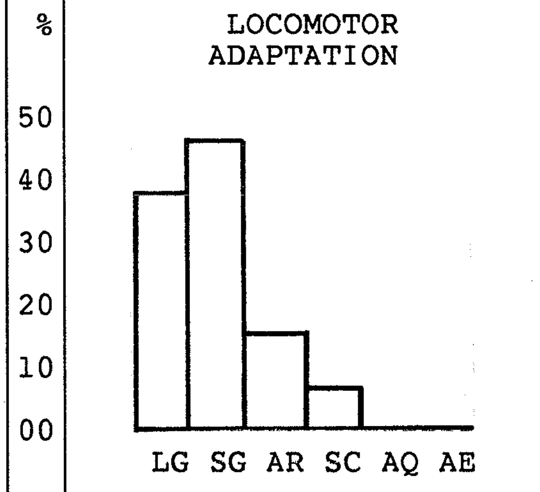
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER



1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



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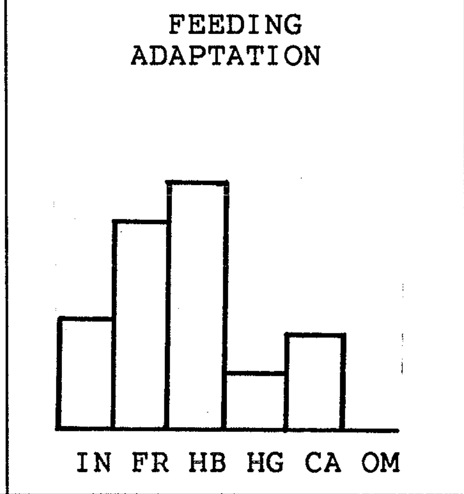
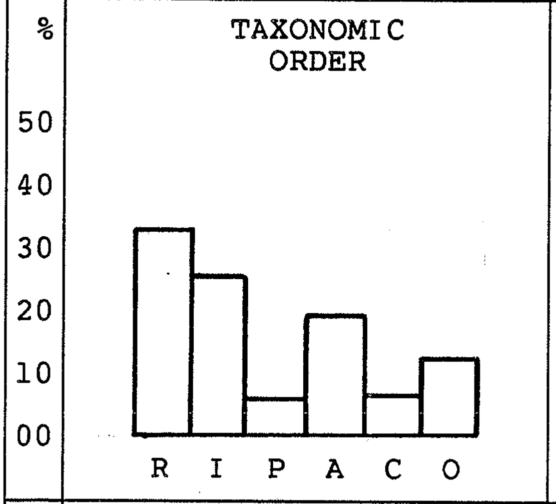
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL



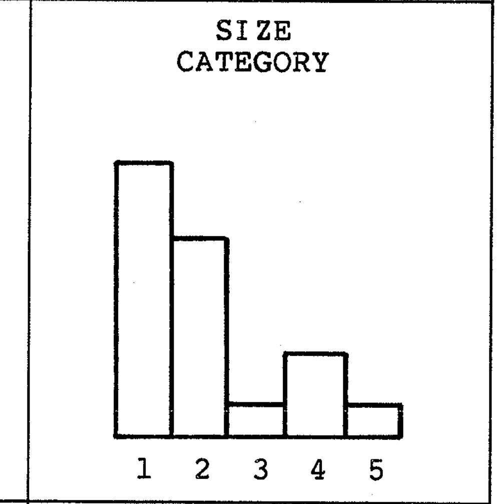
IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 18.10

ECOLOGICAL DIVERSITY ANALYSIS-KF


TAXONOMIC ORDER

R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER


SIZE CATEGORY

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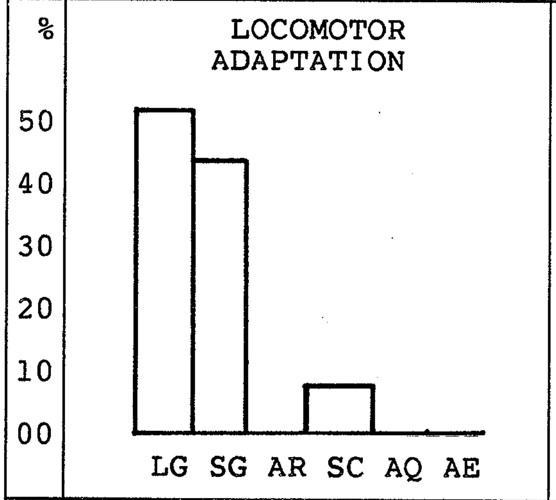
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.


LOCOMOTOR ADAPTATION

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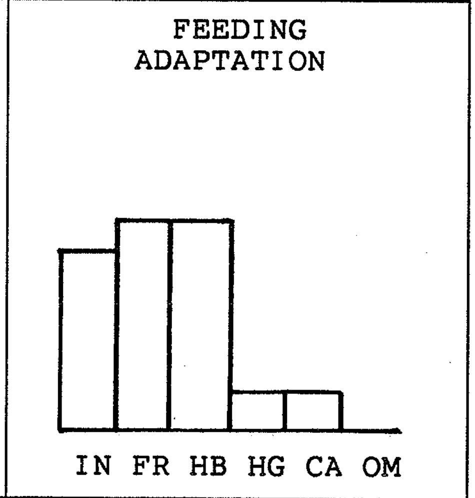
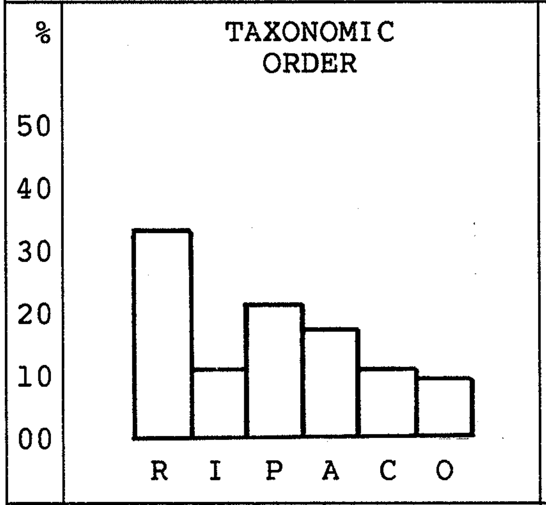
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

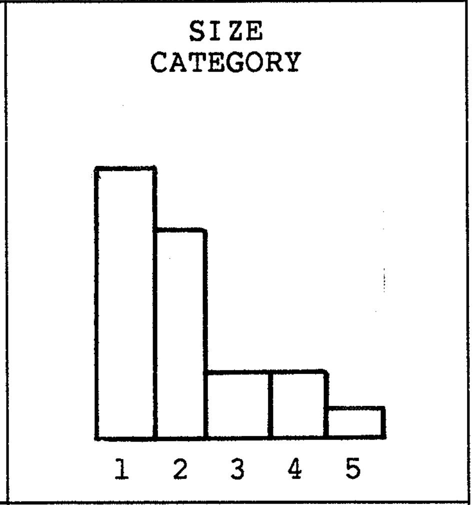

FEEDING ADAPTATION

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 18.11

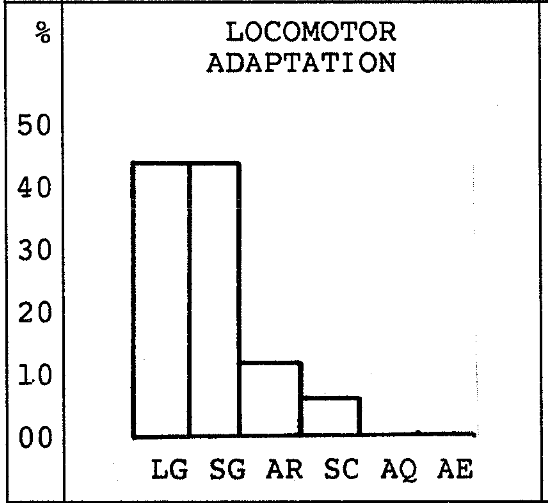
ECOLOGICAL DIVERSITY ANALYSIS-KG

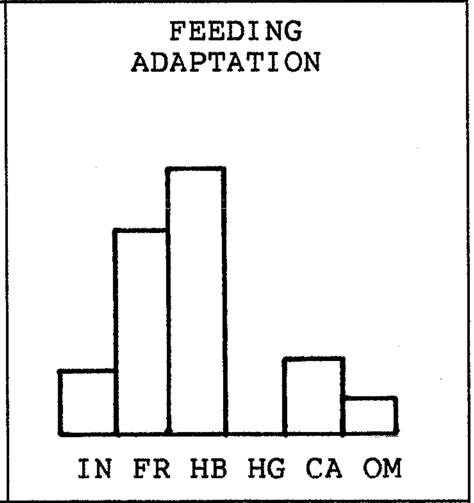




R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



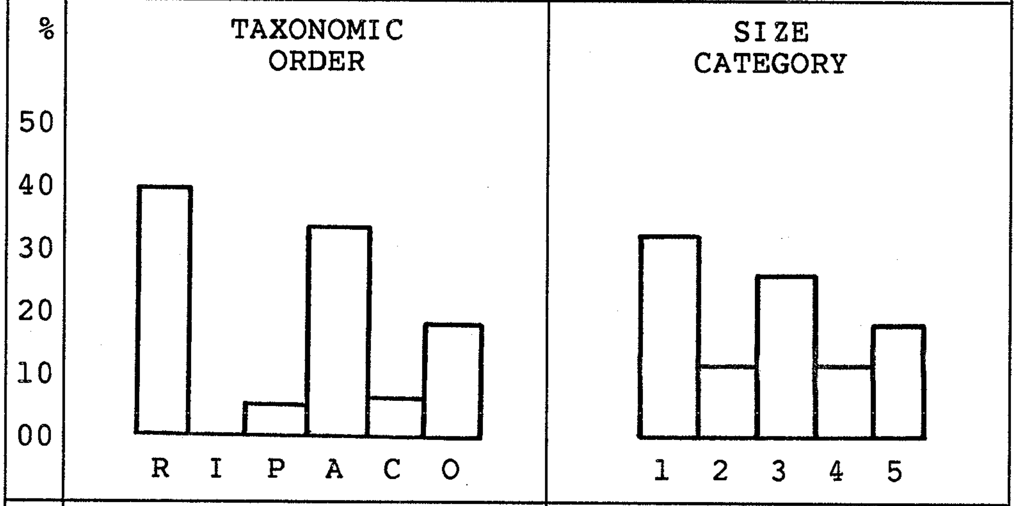


LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL

IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

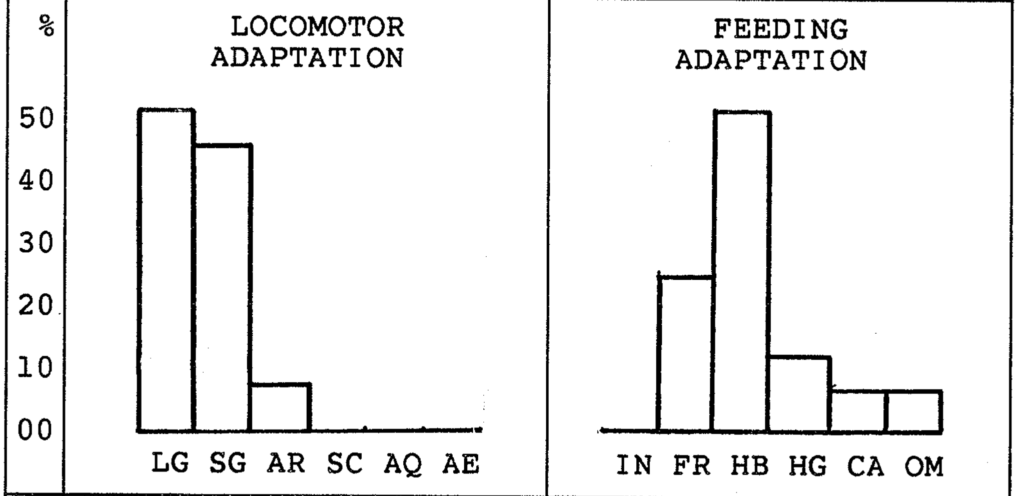
TABLE 18.12

ECOLOGICAL DIVERSITY ANALYSIS-KH



R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER

1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
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IN=INSECTIVORE
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CA=CARNIVORE
OM=OMNIVORE

KH - The taxonomic order spectrum resembles that from extant floodplain environments except in that KH has no insectivores. The locomotor adaptation spectrum is closest to that from the short grass plains. The other two spectra do not resemble those from extant environments. Ecological Implication = open conditions.

COMBINED FAUNA - The spectra from the combined fauna resembles the lowland forest spectra in both the taxonomic order and locomotor adaptation categories. Ecological Implication = forest.

18.4.17 Non-mammalian Fauna

A number of gastropods have been recovered from the Kathwanga Point site but from different levels than the mammalian fauna described above (Andrews and VanCouvering 1975).

The gastropods reflect both the forest and lacustrine/riverine conditions suggested by the fauna. They are, however, more clearly forest oriented forms than those from the Hiwegi formation (lower), described above. In total, the gastropods reflect forest conditions at the Kathwanga Point site.

TABLE 18.13

KATHWANGA POINT GASTROPODS

GASTROPOD	ECOLOGICAL IMPLICATION
Ampullaria ovata	lakes and rivers
Maizania (4 sp.)	evergreen forest
Edouardia mfwanganensis	lowland arboreal habitat
Homorus (Subulona)	wet evergreen forest
Gonaxis (9 sp.)	forest
Limicolaria (2 sp.)	forest/bushland
Trochonanina (5 sp.)	lowland evergreen forest and bush
Cerastua miocenicus	wide distribution
Gulella (3 sp.)	forest and thicket
Ptychotrema usiforme	lowland evergreen forest

18.4.18 Kathwanga Point Summary

The faunal indicators are all in agreement for three of the Kathwanga Point locations. KB and KG (as suggested by Andrews and VanCouvering) both show a strong forest orientation while there are few, if any, clear forest indicators from KH. KH apparently reflects a savanna or woodland biome. Site KF has features suggestive of both forest and more open environments. The fossils from KF show a preferred orientation when presented on a rose diagram (A rose diagram is a chart produced to determine if there is a preferred orientation to the long axes of fossil material from a site. If such an orientation exists, it is an indication that deposition took place in flowing water, or that the site has been hydronamically altered.). Thus, the whole site may have been altered by flowing water. The nature of the fauna and the sediments indicates that a streamside location is possible (Andrews and VanCouvering 1975).

The only Proconsuline present, Proconsul africanus, occurrs at both KG (forest) and KH (savanna/woodland (?), which adds little to the notion of a preferred environment for this species.

18.5 FLORA

Rusinga has the largest fossil flora from the East African Miocene. The following floral list and descriptions have been compiled from Chesters (1957), Palmer and Pitman (1972), Lind and Morisson (1974) and Andrews and VanCouvering (1975).

Five of the genera listed above are apparently gallery or canopy forest trees. Entandrophragma (mahogany) is fairly abundant and it has been suggested that this form is an indicator of evergreen forest (Chesters 1957). Celtis (Ulmaceae) (elm) is seen as a lowland form, as species from the same genera today are mid-canopy trees in the East African lowland forest (Andrews and VanCouvering 1975). The above are fairly clear indicators of a forest environment on Rusinga sometime during the Miocene, but it must be remembered that the exact site locations of the fossil flora are apparently unknown (due to the poor stratigraphic recording of the earlier expeditions) (Andrews and VanCouvering 1975).

Two genera are seen as forms more likely to be common in a woodland-bushland environment. These are: Odina (tree, mango family) and Berchemia (Brekthorn family, small thornless tree or shrub).

There are six genera of trees or shrubs present which are ambiguous ecologically in that they can be found in environments ranging through bushland to forest.

Seven of the genera and twelve of the species listed are woody climbers or lianas. Furthermore, many of the specimens of fossil wood bear the impressions of twining stems, indicating that climbers were common (Lind and Morisson 1974:190). Chesters (1957) concluded that one-half of the fossil flora from Rusinga was composed of climbers. He suggested that this was an indication of riverine forest, his conclusion presumably based on the amount of sunlight required for this type of plant to grow, and on extant riverine forest analogies. At any rate, climbers require trees, and so they can all be seen as indicators of at least woodland conditions, and probably forest.

TABLE 18.14

RUSINGA FLORA

FAMILY	GENUS/SPECIES	DESCRIPTION
ANACARDIACEAE	Antrocaryon sp. Odina sp.	forest tree bush or woodland tree
ANNONACEAE	5 sp.	trees or shrubs
APOCYNACEAE	Leakeyia sp.	riverine trees
BURSERACAE	Canarium sp.	trees or shrubs
CONNARACEAE	Cnestis sp.	shrubs or climbers
CUOURBITACEAE	Lagenaria sp. 2 sp.	climber (?) may be climbers
EUPHORBIACEAE	4 sp.	variable
LEGUMINOSAE	Pterocarpus sp. 3 sp.	tree forest/woodland unknown
MELIACEAE	Entandrophragma or Paleocarpus	tree or shrub canopy tree
MENISPERMACEAE	Cissampelos sp. Stephania sp. Syntrisepalum sp. Triclisia sp.	woody climbers "" "" ""
OLEACEAE	Schreberoidea sp.	forest tree/shrub
RHAMNACEAE	Berchemia sp. Ziziphus sp.	bushland tree or shrub forest/bush tree or shrub
RUTACEAE	sp.	tree or shrub
SAPINDACEAE	Sapindospermum sp. 4 sp.	climbers (?) climbers (?)
ULMACEAE	Celtis sp.	mid-canopy

		forest tree

Thus, both forest and more open conditions are indicated by the flora, the former more strongly. Furthermore, the concept postulated above, that the Rusinga forest was primarily riverine in nature, is not refuted by the fossil floral evidence.

18.6 PALEOGEOGRAPHY

Like the other East African Miocene sites apparently older than 20 m.y. or so (Karungu and Bukwa), the Kiahera formation (20-23 m.y.) seems to represent a non-forested environment. The sediments at Kiune and R113 consist largely of sands, silts and marls, and are considered to represent deposition on a floodplain (Pickford 1981). The non-mammalian fauna, consisting of such forms as crabs and crocodiles, agrees inasmuch as it points to wet conditions also. The mammalian fauna, when analysed, does not show any clear forest affinities. The ecological diversity analysis tended to reflect patterns similar to those found under extant floodplain conditions. During Kiahera times, then, it is possible that the predominant geographical feature was a, or several, large floodplain(s). The vegetation pattern on this floodplain appears to have been quite open, perhaps a woodland or bushland biome.

While there is no clear evidence of forest conditions from the Kiahera formation, there are ample forest indicators from the Hiwegi formation sites. Unfortunately, there are also ample indicators which point to non-closed forest conditions and, in general, these are just as convincing, if not more so.

The lithologies of the sites from the Hiwegi formation vary, but they all indicate the presence of nearby water. The sites placed here in the Basal Hiwegi (R1, R1A, R3, R10-19, Wanyama) are all considered to reflect a floodplain depositional environment by Pickford (1981); their sediments being largely sheet conglomerates, silts and sands. The other divisions of the Hiwegi formation, the Kathwanga, Kulu and Upper Hiwegi sites, lie in sediments described as lake margin and swamp (silts and marls) through lacustrine in location (silts and shales) (Pickford 1981).

The mammalian fauna from the Hiwegi formation seems to indicate that both forest and non-forest environmental conditions were present. Since, in Hiwegi times, the geography of Rusinga Island was variable, divided by lakes, rivers and swamps, there is no reason to assume that there was a singular vegetative pattern. It has been suggested, however, that the whole of the East African area, in Miocene times, was forested, part of a great lowland forest that stretched from the Congo Basin to the East coast (Andrews and VanCouvering 1975, Andrews 1981a). In regard to the Hiwegi formation on Rusinga, at least, this notion appears to be simplistic. While the forest face is well developed, there are also many species more likely to have been derived from a more open environment. It seems unlikely that any single environmental type would contain all of the diverse fauna found at Rusinga.

Thus, while it would be advantageous to state that the two Proconsulines common at Rusinga, P. africanus and P. nyanzae, were clearly associated here with a single environmental type, it is not possible to do so. More work, particularely the re-evaluation of material collected years ago, and more work on the provenances of many of the sites, is necessary.

19. SONGHOR

Lying at the Western end of the Kavirondo Rift Valley is the site of Songhor Hill (35 13'E, 00 02'S.). This important fossil locality is 17 km. NW. of the summit of Tinderet Mountain and 15 km. North of the site of Legetet Hill.

19.1 GEOLOGY

The geology of the Tinderet area has already been discussed in detail in regard to the Koru sites. Only a breif review of the overall sequence will be provided here, with a more detailed analysis of the geology and stratigraphy of the Songhor site. The Tinderet stratigraphy, as described by Pickford and Andrews (1981) is shown below.

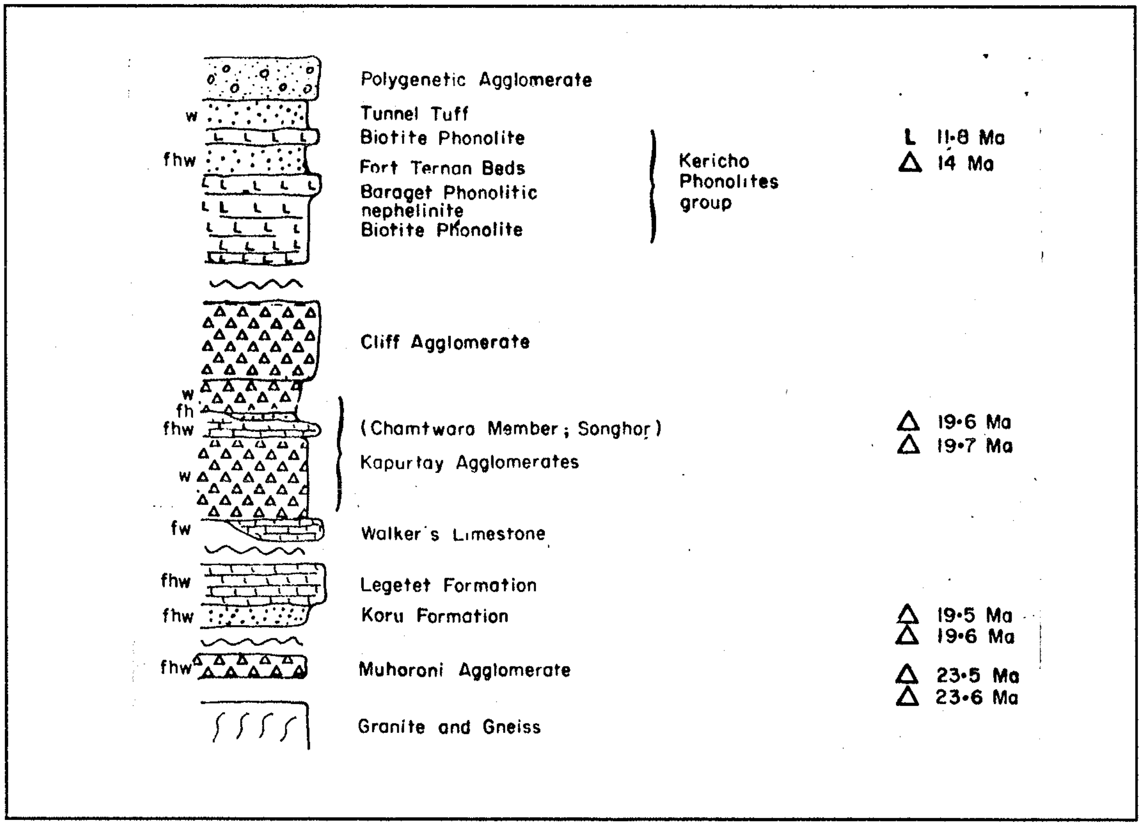


Figure 19.1: TINDERET FOSSIL SEQUENCE

The Songhor fossiliferous locality lies within the Kapurtnay agglomerates. These agglomerates are composed of coarse nephelinite agglomerates poorly sorted and bedded, with lenses of well bedded silty to sandy tuffs, red marls and bedded calcified tuffs (Pickford and Andrews 1981).

A bedded calcified tuff facies, similar to that found at the Chamtwara member in the Chamtwara areas, marks the base of the fossiliferous sediments at Songhor (Pickford and Andrews 1981). This is also the lowest of the four recognized sedimentary units in the main Songhor gullies.

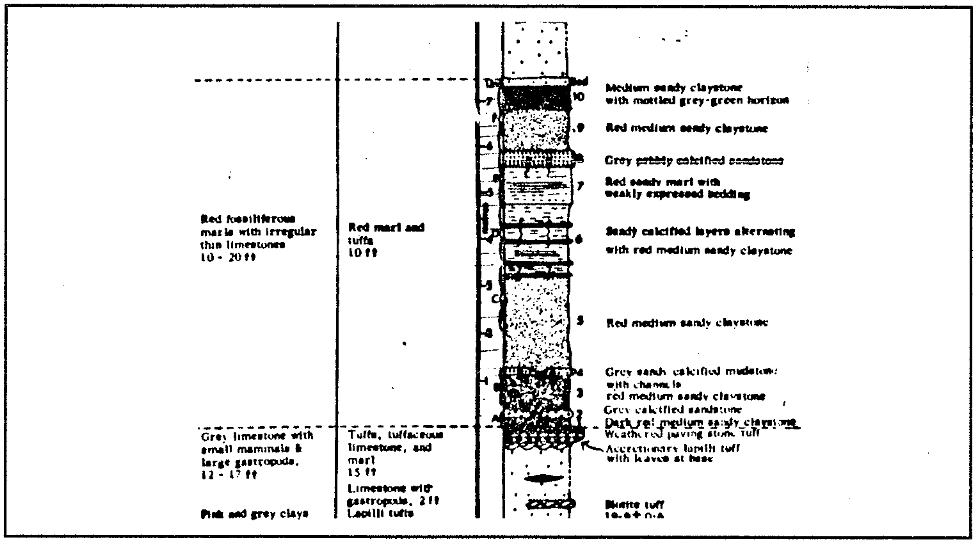


Figure 19.2: SONGHOR STRATIGRAPHIC SEQUENCE

CALCIFIED TUFF MEMBER - Composed largely of agglomerates and a variety of tuff formations, some with lenses of red marly silt (Pickford and Andrews 1981). These red marly silts are often fossiliferous and are very similar lithologically to those from the succeeding red bed member. The fauna from these lenses is also similar to that from the red bed levels (Pickford and Andrews 1981).

One lens of grey tuff has been dated, but the orientation of leaves found within it indicates that the tuff may have been reworked, possibly influencing the date (Pickford and Andrews 1981).

THE RED BED MEMBER - Composed of ten beds, the red bed member lies conformably on the calcified tuff member, and is the most fossiliferous sequence at Songhor. The ten beds are divided into five units, with a sharp stratigraphic contact between each pair. The five couplets are basically identical, each composed of a lower red marl horizon grading upwards into a slightly coarser calcified grey horizon (Pickford and Andrews 1981). The red marl horizons are generally more fossiliferous than the grey calcified sediments although faunal material has been recovered from each.

Figure 19.3 (after Pickford and Andrews 1981) shows the stratigraphy of the red bed member at Songhor. The most significant beds, in terms of fauna, are beds 5 and 9, the latter of which has yielded several complete skulls and mandibles of rodents and insectivores (Pickford and Andrews 1981).

BED #	
10	pink to red medium grained sandy clay, poorly fossiliferous
9	brick red medium to coarse sandy claystone, fossiliferous
8	grey to red sandy and pebbly calcified sandstone
7	red to grey sandy marl
6	4-8 resistant horizons=sandy calcified layers, o/w brick red medium fine to medium sandy clay, mod. fossiliferous
5	mottled red medium sandy claystone, richly fossiliferous
4	light grey medium to coarse sandy calcified mudstone
3	brick red medium sandy claystone
2	red to grey calcified sandstone, rounded limestone pebbles
1	brick red medium sandy claystone, mod. fossiliferous

Figure 19.3: THE RED BED MEMBER - SONGHOR

GREY TUFF MEMBER - This unit is generally composed of grey tuff with a few lenses of red marl. A discontinuous bed of grey to red marl lying midway in the member has yielded a few fossils (Pickford and Andrews 1981).

TUFF AND AGGLOMERATE MEMBER - Overlying the grey tuff, this member is composed of coarse tuff with lava fragments. It is fossiliferous in patches, yielding gastropods and rodents (Pickford and Andrews 1981).

19.2 DATING

Three K/ar dates from the Songhor sequence have been published by Bishop et al (1969). Two of these are very similar, 19.7 +/- 0.5 m.y. from the calcified tuff member and 19.9 +/- 0.6 m.y. from an unidentified source. The third date was obtained from the overlying basanite lava - 9.9 +/- 0.5 m.y.

Additional radiometric dates have been provided by Pickford and Andrews (1981) for the Muhoroni agglomerates (23.5 and 23.6 m.y.), the Koru formation (19.6 m.y.), the Legetet formation (@ 19.5 m.y.) and the Kapurtnay agglomerates (19.7 m.y.). The interesting feature of these dates is that all of the fossiliferous sites from the Tinderet sequence, with the exceptions of Meswa Bridge and Ft. Ternan, date to almost exactly the same age @ 19.6 m.y. Either all the fossiliferous sediments were deposited in a very narrow time period or some factor is influencing the K/ar dates, resulting in uniform values. Thus, the relative dating supplied by the stratigraphy is very important. Fortunately, the stratigraphy of Tinderet in general, and Songhor particularly, is well documented (Pickford and Andrews 1981).

19.3 ABUNDANCE OF PROCONSUL FORMS

Songhor is rich in *Proconsul* fossils and four species have been recovered from this site. The distribution of *Proconsul* forms can be seen seen in table 19.1 (number of specimens drawn from Pickford and Andrews 1981, M.N.I. figures from Andrews 1978).

The most common form is *P.* (*R.*) *gordoni* with 17 individuals. Also common is *P. major* (M.N.I. = 15), but less so are *P.africanus* (5) and *P. (R.) vancouveringi* (3). All of the *Proconsul* material from the 1971-1972 collections, with the exception of a single specimen of *P. gordoni* which came from the red bed member. Some of the earlier material excavated by Leakey (1948 and 1966 excavations) also was from the red bed member (Pickford and Andrews 1981), but the largest portion of Leakey's material was surface collected, and hence has no provenance. These specimens, however, are apparently similar in colour, fossilization and proportions of forms found, to those from excavations in bed 5 of the red bed

TABLE 19.1

PROCONSUL DISTRIBUTION, SONGHOR (# of specimens)

SPECIES	1971-1972	TOTAL	M.N.I.
P. africanus	3	12	5
P. major	6	44	15
P. (R.) gordoni	6	71	17
P.(R.) vancouveringi	1	3	3
L. legetet	13	94	19
D. macinnesi	2	29	12

member (Pickford and Andrews 1981). It is possible, then, that the vast majority of the Proconsul material, and the fauna at large, can be assigned to the red bed member. Within the red beds themselves, a provenance of either bed 5 or bed 9 for the Proconsul material is probable, as, in the 1971/2 collections, 65.5% of the Proconsul fossils came from these areas (Pickford and Andrews 1981). If bed 6 forms a unit with bed 5, as is suggested by Pickford and Andrews, then 95% of the Proconsul material is contained in these three horizons (beds 5, 6 and 9). Thus, it may be possible that the origin of most of the Proconsul fossils is restricted to quite specific areas.

19.4 FAUNA

The following faunal list (after Pickford and Andrews 1981) contains all the material collected at Songhor to the end of 1978.

TABLE 19.2

SONGHOR FAUNA

ORDER	GENUS/SPECIES	FREQUENCY
INSECTIVORA	Erythrozootes chamerpes	2
	Prochrysochloris miocaenicus	6
	Protenric tricuspis	21
	Gymnurechinus songhorensis	17
	Amphechinus rusingensis	2
	Galerix africanus	13
	Rhynchocyon clarki	23
	Rhynchocyon sp.	14
	Myohyrax oswaldi	3
CHIROPTERA	Taphozous incognita	1
	Propotto leakeyi	4
	Hipposideras sp.	5
PRIMATES	Progalago dorae	10
	Progalago minor	7
	Progalago robustus	6
	Limnopithecus legetet	94 MNI=19
	Proconsul gordoni	71 MNI=17
	Proconsul vancouveringi	3 MNI=3
	Proconsul africanus	12 MNI=5
	Proconsul major	44 MNI=15
	Dendropithecus macinnesi	29 MNI=12
RODENTIA	Diamantomys leuderitzi	529
	Paraphiomys pigotti	51
	Paraphiomys stromeri	44
	Epiphiomys coryndoni	1
	Phiomys andrewsi	12
	Simonomys genovefae	42
	Elmerimys woodi	2
	Paranomalurus soniae	34
	Paranomalurus bishopi	62
	Paranomalurus walkeri	19
	Zenkerella wintoni	2
	Afrocricetodon songhori	58
	Notocricetodon petteri	29
	Bathyergoides sp.	105
	Megapedetes sp.	14
	Vulcaniscurus africanus	5
	Goniodon songhori	1
	Protarsomys macinnesi	1
	Andrewsimys parvus	2
	Proheliophobus leakeyi	1

CARNIVORA	Teratodon enigmae	2
	Teratodon speki	2
	Hyaenodon andrewsi	1
	Hyaenodon pilgrimi	2
	Hecubides euryodon	1
	Kelba quademaae	1
	Mustelidae indet	2
	Metailurus africanus	1
	Kichechia zamane	4
PERISSODACTYLA	Chalicotherium rusingense	3
	Dicerorhinus leakeyi	4
HYRACOIDEA	Bunohyrax sp.	3
PROBOSCIDEA	Gomphotherium sp.	3
TUBULIDENTATA	Orycteropus minutus	2
ARTIODACTYLA	Hyotherium kijivium	6
	Masritherium sp.	1
	Dorcatherium songhorensis	151
	Gelocus whitworthi	4
	Walangania africanus	222
	TOTAL NUMBER OF SPECIES =	60

19.4.1 Habitat Indicator Species

There are a number of good forest indicators in the Songhor fauna. These are: 3 species of *Paranomalurus* (one frequent and two moderately frequent), 2 species of *Rhynchocyon* (both moderately common), three species of *Progalago* (all uncommon), two tragulids - *Dorcatherium* and *Walangania* (both common), *Paraphiomys* (two species both moderately frequent) and a single species of *Prochrysochloris* (*rare*).

There are also some forms present that tend to indicate more open conditions. The number of species falling into this class is fewer, however, only 8 as compared to 13 forest oriented forms. Furthermore, only one of this latter group of indicators, *Bathyergoides*, is common, the others being infrequent or rare. The others are: *Gymnurechinus*, *Amphechunus*, *Galerix*, *Megapedetes*, *Hyaenodon* (2 sp.) and the tubulidentate *Orycteropus*.

In total, the faunal indicators are quite clearly forest oriented, as was noted by Pickford (1981).

19.4.2 Relative Abundances

TABLE 19.3

RELATIVE ABUNDANCES

ORDER	NUMBER OF SPECIES	% OF TOTAL SPECIES PRESENT
RODENTIA	20	33
INSECTIVORA	9	15
PRIMATES	9	15
CARNIVORA	9	15
ARTIODACTYLA	5	8
CHIROPTERA	3	5
PERISSODACTYLA	2	3
HYRACOIDEA	1	2
PROBOSCIDEA	1	2
TUBULIDENTATA	1	2

Rodents constitute the highest percentage at 33% followed by insectivores primates and carnivores, all at 15%. The abundance of rodents and primates is a common pattern in extant African forests (Bourliere 1963). Within the Rodentia, Diamantomys leuderitzi constitutes 52% of the specimens recovered. This amount, coupled with the "moderately high percentages of several other rodent species" is considered a pattern characteristic of modern forest communities by Nesbit Evans et al (1981). This conclusion, however, might be arguable as Diamantomys, constituting as it does greater than 50% of the rodent remains, may be considered to have dominated numerically over the other rodents at this site. This would be more characteristic of a savanna setting (Andrews and VanCouvering 1975). Furthermore, the next most common rodent forms, in terms of numbers of specimens recovered, are not highly frequent. *Bathyergoides sp.* represents just 10.5% of the rodent specimens recovered, *Paranomalurus bishopi* 6%, and *Afrocricetodon songhori* 5.5%.

On the other hand, the dominant form in extant grassland and savanna situations often reaches 80-90% of the total rodent population, which is considerably more than 50%. Also, the number of specimens can hardly be directly equated between species. A minimum numbers analysis is required before such comparisons can be regarded as highly significant.

In total, the percentages of the various rodent species cannot be seen as indicative of a particular environment, as was suggested by Nesbit Evans et al (1981). In the overall sample, however, the high percentages of rodents and primates do seem to point towards a forested environment.

Two additional points of interest are the relatively high frequencies of insectivores and carnivores, both 15% of the total. The percentage of carnivores may be accurate as it is comparable to frequencies from some extant environments (Walker 1975) and there are definite traces of predator activity in the fossils (Pickford and Andrews 1981). Nesbit Evans et al (1981) cite the high proportion of insectivores as being puzzling, but not indicative, necessarily, of any particular environment. None of the modern environments listed by Walker (1975) show such a high percentage of insectivores, so no ecological conclusion can be readily drawn from their abundance here.

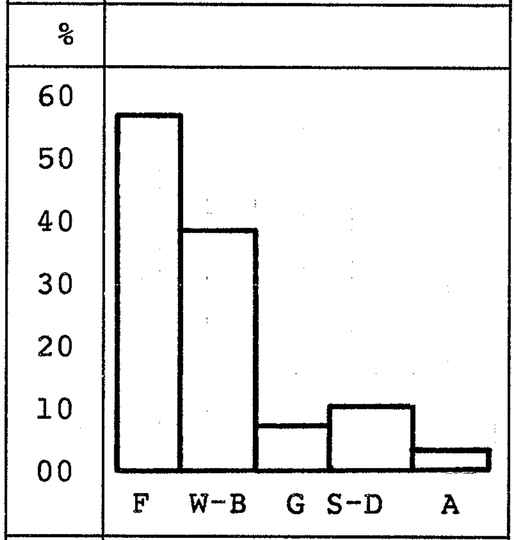
19.4.3 Taxonomic Habitat Index

The taxonomic habitat index for Songhor has been computed by Nesbit Evans et al (1981). The highest value is for forest, followed by woodland-bushland. The other categories are insignificant. Once again the forest component of the Songhor fauna is strongly reflected.

TABLE 19.4

HABITAT SPECTRUM

SONGHOR



F=forest
W-B=wood/bushland
G=grassland
S-D=semi-desert
A=aquatic

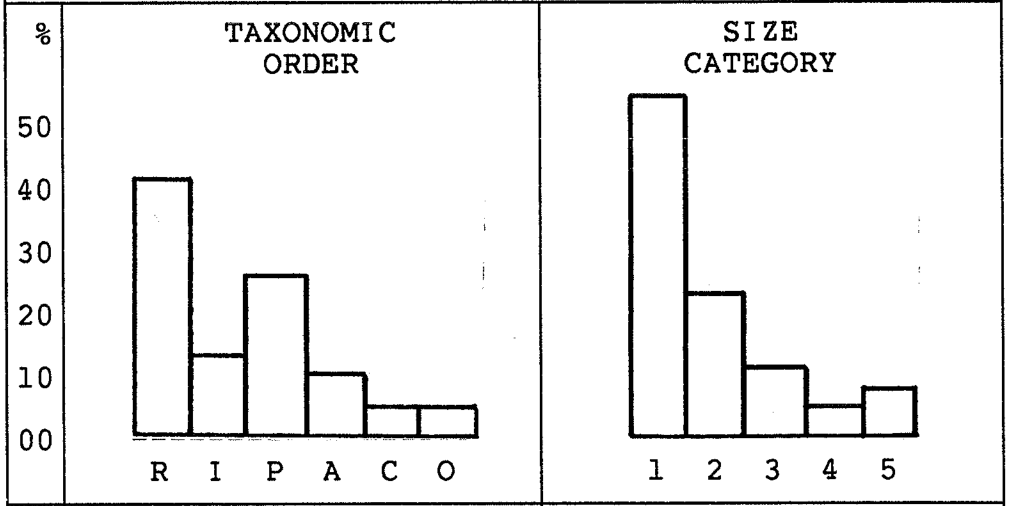
19.4.4 Ecological Diversity Analysis

This analysis has also been computed by Nesbit Evans et al (1981), both for the 1972 fauna in total, and for the 1972 fauna from the red bed formation, bed 5 only. A further analysis has been calculated here using the total fauna recovered from Songhor, pre and post 1972.

The 1972 total collection spectra are similar to spectra from extant forests. In fact, correlation coefficients between the Songhor and modern lowland forest spectra are statistically significant (p=0.05) in three of the four categories (Nesbit Evans et al 1981). The bed 5 pattern is similar to the 1972 spectra at large.

TABLE 19.5

ECOLOGICAL DIVERSITY ANALYSIS-SONGHOR-1972 FAUNA



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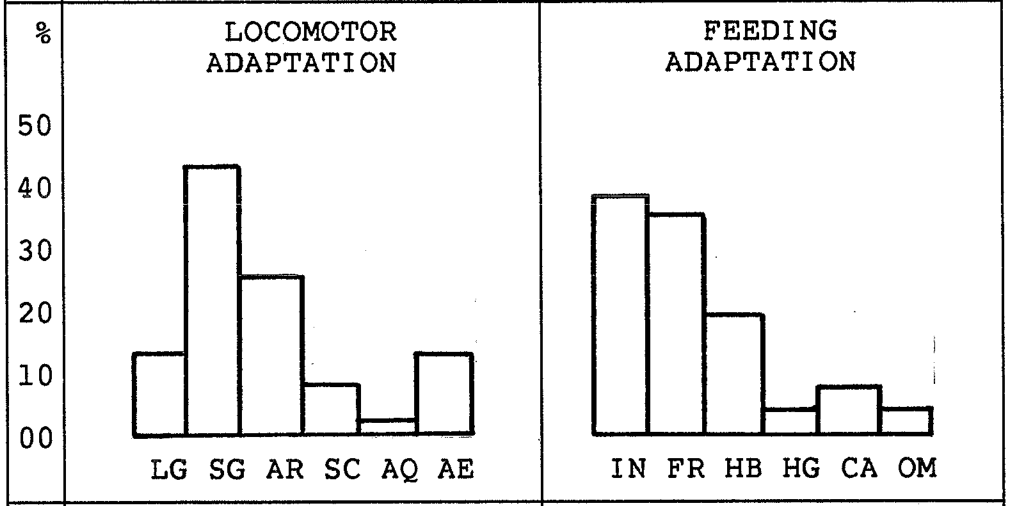

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AR=ARBOREAL
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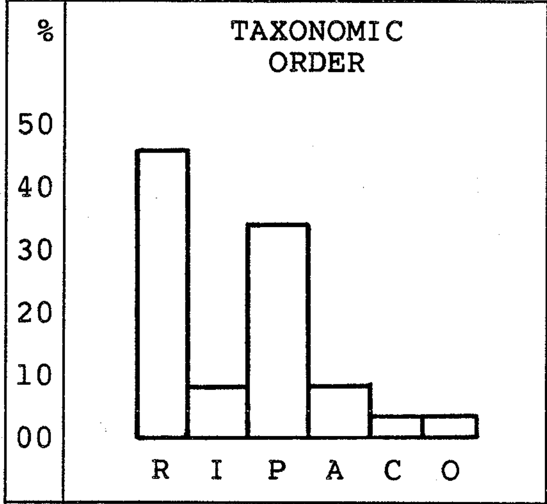
AQ=AQUATIC
AE=AERIAL

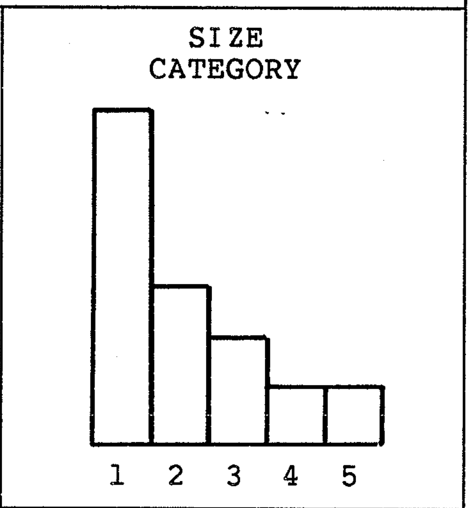
IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 19.6

ECOLOGICAL DIVERSITY ANALYSIS-SONGHOR BED 5


TAXONOMIC ORDER

R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER


SIZE CATEGORY

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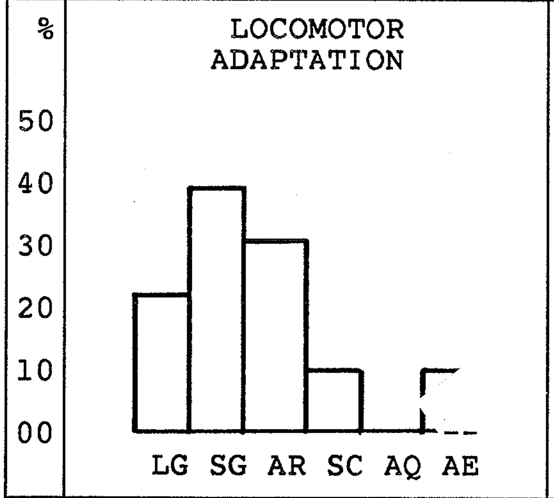
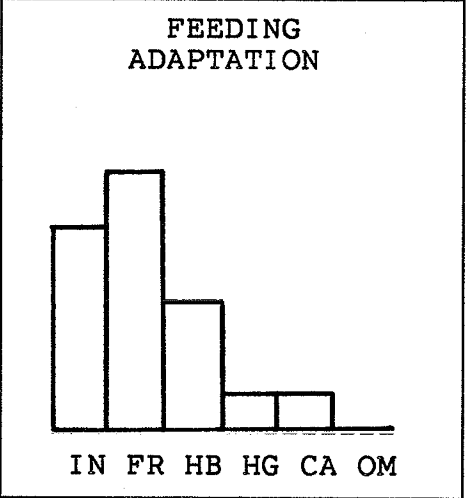
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.


LOCOMOTOR ADAPTATION

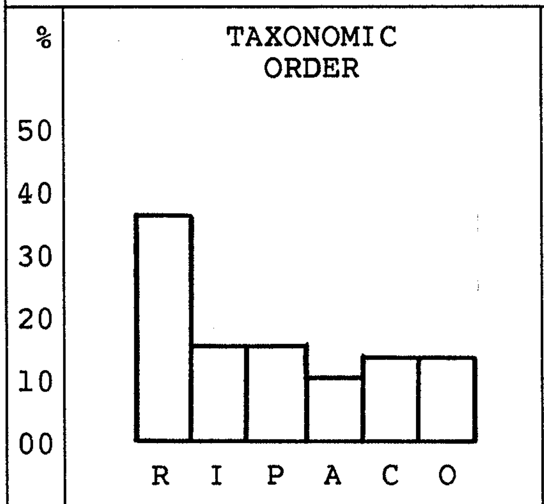
LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL


FEEDING ADAPTATION

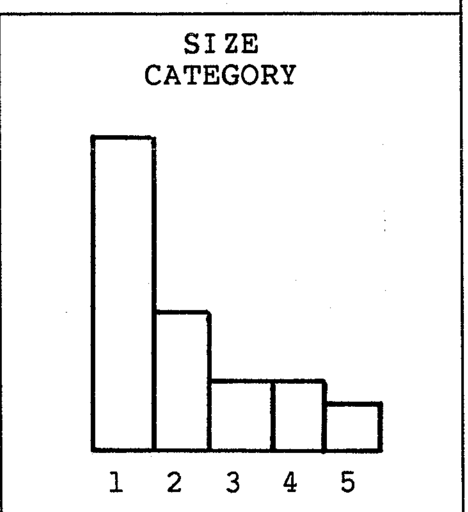
IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

TABLE 19.7

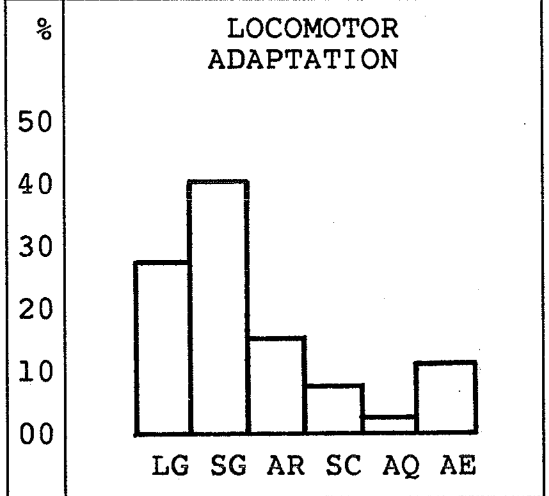
ECOLOGICAL DIVERSITY ANALYSIS-SONGHOR TOTAL FAUNA



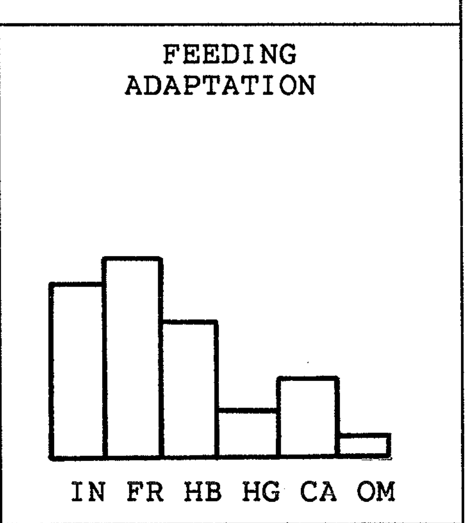
R=RODENT
I=INSECTIVORE
P=PRIMATE
A=ARTIODACTYL
C=CARNIVORE
O=OTHER



1=0-1.0 KG.
2=1.1-10 KG.
3=10.1-45 KG.
4=45.1-180 KG.
5=180+ KG.



LG=TERRESTRIAL
SG=MAINLY TERRESTRIAL
AR=ARBOREAL
SC=SCANSORIAL
AQ=AQUATIC
AE=AERIAL



IN=INSECTIVORE
FR=FRUGIVORE
HB=HERBIVORE-BROWSER
HG=HERBIVORE-GRAZER
CA=CARNIVORE
OM=OMNIVORE

The addition of the pre 1972 fauna changes the overall pattern only slightly. The only significant difference lies in the taxonomic order category, in which the total Songhor collections have a much lower percentage of primates than does the 1972 collection alone. This is due to the fact that, for some reason, the earlier expeditions uncovered a greater diversity of forms, thus making the percentage of primates, of the total forms, lower.

19.4.5 Non-mammalian Fauna

In addition to the mammalian fauna there are a number of non-mammalian forms, most gastropods, from Songhor. The following list comes from Andrews and VanCouvering 1975.

Of the above, six forms are forest oriented while only two are non-forest (bushland) forms. This is consistent with the mammalian fauna which also pointed to a forest biome at Songhor.

The 1971/1972 excavations yielded remains of only two other non-mammalian forms, Chelonia and Python (Pickford and Andrews 1981). There were, however, only 9 and 5 specimens respectively recovered of these genera and no firm conclusions can be reached from their presence here.

TABLE 19.8

SONGHOR GASTROPODS

GASTROPOD	ECOLOGICAL IMPLICATION
Bloyeta	arid/bushland
Thapsis	forest
Ligatella (2 sp.)	bushland
Homorus (Subulona)	wet evergreen forest
Gonaxis (9 sp.)	wet evergreen forest
Limicolaria (2 sp.)	forest/bushland
Trochonanina (5 sp.)	lowland evergreen forest and bush
Gulella (3 sp.)	forest and thicket
Tayloria (2 sp.)	drier evergreen forest and bush
Krapfiella angusta	montane evergreen forest
Primigulella	montane affinities

19.5 FLORA

There are no published floral remains from Songhor.

19.6 PALEOGEOGRAPHY

It has been suggested in the past (Kent 1944, Shackleton 1951) that the limestone in the Tinderet sequence indicates that this area was flooded, at least periodically. Citing work by James (1956), however, Pickford and Andrews (1981) postulate that the limestone in the Koru/Songhor sequence was formed, not in a lacustrine setting, but rather by rainfall and groundwater acting upon the tuff extruded from the tinderet carbonatite volcano. The carbonatite nature of the tuff allows for rapid calcification when water is added, and limestone can be formed in this manner (Pickford and Andrews 1981). Thus, with this method of limestone formation there is no need to postulate any lacustrine influence in the Tinderet sequence. Support for this notion lies in the nature of some of the beds that show weathering, paleosols and rootcasts (Pickford and Andrews 1981).

The red bed horizon in the Songhor sequence is seen by Pickford and Andrews to reflect complete to partial calcification and alteration by mechanical and biologic processes on the surfaces of several successive horizons. This would explain the cyclic nature of the red bed member, with only the upper portion of each successive extrusion of tuff brcoming altered before being buried (Pickford and Andrews 1981).

The fauna from Songhor tends to support the notion of terrestrial deposition of limestone as there are abundant terrestrial mammals but aquatic forms are extremely rare.

It is almost certain that Songhor, at the time of deposition and therefore at the time of occupation by the _Proconsul_ forms, lay in a forest, probably one that was evergreen and fairly dense in nature. It is probably significant that while four _Proconsul_ species are known from Songhor, two apparently were much more frequent than the others. Together, _P. major_ (38%) and _P. gordoni_ (42%) constitute 80% of the _Proconsul_ individuals thus far found at Songhor. The other two species, _P. africanus_ (12%) and _P. vancouveringi_ (8%), are considerably less significant. Thus Songhor appears to be a good example of a particular environment (forest) being associated with particular species, notably _P. major_ and _P. gordoni_.

20. FORT TERNAN

Part of the Tinderet sequence, the Fort Ternan beds (35 21'E, 00 13'S) lie above both the Koru and the Songhor levels. Because of the unique nature of the Fort Ternan fauna, and the site's relatively late date, it is dealt with here after the other East African Miocene sites.

20.1 GEOLOGY

The geological sequence at Tinderet has already been described from the basement granite through the Kapurtnay agglomerates under the Koru and Songhor headings. Above the Kapurtnay agglomerate lies a resistant, coarse grained, non-fossiliferous nephelinite agglomerate, often of considerable depth, called the Cliff agglomerate (Pickford and Andrews 1981). Above the Cliff agglomerate, the Tinderet sequence becomes more confused and has to be interpreted from a number of outcrops over a fairly large area.

There are a variety of lavas, given the blanket name of the Kericho Phonolites Group, occurring between the agglomerate and the Ft. Ternan fossil beds (Pickford and Andrews 1981). Three separate lavas are recognized in this group by Pickford and Andrews (1981), biotite phonolite, nephelinite and baraget phonolite. None of these contain fossils.

Superseding these lavas is a sequence of tuffs which show ripple marks and have been re-worked by water (Andrews and Walker 1976). These tuffs have yielded radiometric dates. Above the water worked tuffs are two groups of tuffaceous sediments, separated by a layer of phonolite, called the Fort Ternan A and B group beds (Shipman et al 1981). The lower group, A, is largely unfossiliferous, but the upper group, B, contains two fossiliferous paleosol horizons (Shipman et al 1981). The depositional environment in the tuffs surrounding the paleosol horizons is generally considered to be subaerial although some lacustrine elements can be defined (Andrews and Walker 1969).

Above the fossiliferous deposits are fine grained and sorted sediments, probably riverine in origin (Andrews and Walker 1976). Finally, to top the sequence, further volcaniclastic material has yielded additional K/ar dates.

20.2 DATING

Andrews and Walker (1976:293) have provided the following K/ar dates from Ft. Ternan:

1. 14.7 +/- 0.7 m.y. - from crystal lithic tuff (below paleosols).
2. 14.0 +/- 0.2 m.y. - ""
3. 14.0 m.y. ""
4. 11.8 +/- 0.2 m.y. - from top of Ft. Ternan succession.
5. 11.8 +/- 0.3 m.y. - ""
6. 12.6 +/- 0.7 m.y. - ""
7. 12.5 +/- 0.4 m.y. - ""

There seems to be a general concensus that the Ft. Ternan fossils can be dated from 12.5 - 14.0 m.y. (Andrews and Walker 1969, Pickford 1981, Pickford and Andrews 1981). The above authors have even suggested that more specific dating is possible, and that the Ft. Ternan fauna likely dates to 13.5 - 14.0 m.y.

20.3 ABUNDANCE OF PROCONSUL FORMS

Proconsulines represented in the Fort Ternan fauna are: P. nyanzae (7 specimens) and P. africanus (3 specimens) (Andrews and Walker 1976). M.N.I. figures calculated by Andrews (1978) are: P. nyanzae=3 and P. africanus=2 although Shipman (et al 1981) lists only one individual of each. Ramapithecus wickeri has also been recovered from Ft. Ternan which is an unusual occurrence (Andrews and Walker 1976).

It is possible, or may even be likely, that the Proconsul remains, which show evidence of rolling and water transport, may have been derived from other areas, and thus may not in fact be part of the natural death assemblage from Ft. Ternan (Nesbit Evans et al 1981). Until this is ascertained definately, if possible, these elements should be considered part of the Fort Ternan fauna. While these fossils probably were transported by water, there is no way of telling how far they were moved or their exact origin, so it is prudent to retain them with the rest of the faunal assemblage, but further analysis involving the Proconsul material should be conducted with caution.

20.4 FAUNA

The following Ft. Ternan faunal list has been drawn from Shipman et al (1981) and Andrews and Walker (1976).

TABLE 20.1

FORT TERNAN FAUNA

ORDER	GENUS/SPECIES	M.N.I.
LIPOTYPHLA	Amphechinus sp.	3
MACROSCELIDEA	Myohyrax sp.	1
	cf. Rhynchocyon sp.	1
	Macroscelididae	4
CHIROPTERA	Chiroptera indet	1
PRIMATES	Limnopithecus legetet	5
	Lorisine	1
	Proconsul africanus	2 or 1
	Proconsul nyanzae	3 or 1
	Ramapithecus wickeri	5
CREODONTA	Dissopsalis sp.	5
	Megistotherium osteothalastes	2
CARNIVORA	large Amphiocyonid	3
	small Amphiocyonid	1
TUBULIDENTATA	Orycteropus sp.	2
	Myorycteropus sp.	1
PROBOSCIDEA	Platybelodon (?)	6
	Deinotherium sp.	1
RODENTIA	Leakymus ternani	12
	Diamantomys sp.	5
	Paraphiomys pigotti	5
	Anomaluridae	3
	Bathyergidae	2
	Afrocricetodontine	1
	large Microcricetodontidae	1
	small Microcricetodontidae	1
	Megapedetes sp.	1
	Sciuridae	1
PERISSODACTYLA	Paradiceros mukirii	10
ARTIODACTYLA	Paleotragus primaevus	13
	Climacoceras africanus	9
	Samotherium africanus	3
	Listriodon sp.	2
	Propaleoryx sp.	1

	Bunolistriodon kidogosana	1
	Walangania africanus	2
	Dorcatherium chappuisi	4
	Dorcatherium parvun	1
bovidae	Oioceros tanyceras	94
	Protragoceras labidotus	69
	Gazella sp.	11
	Pseudotragus potwaricus	8
	Eotragus sp.	1

20.4.1 Habitat Indicator Species

There are few forest indicators from Ft. Ternan; they are: *Rhynchocyon sp.*, the anomalurid and possibly the loris and the tragulids (Nesbit Evans et al 1981). There are also a number of indicators of open or savanna conditions, specifically: *Megapedetes*, *Orycteropus*, *Myorycteropus* and the species of the family Bathyergidae. There are also clear indicators of a grassland environment, which is unique among the East African Miocene sites. There are 5 genera of bovids from Ft. Ternan and the two most common species , *Oioceros tanyceras* and *Protragoceras labidotus*, both bovids, constitute between them 50% of the total individuals from the site. From an analysis of the teeth of these forms, Shipman et al (1981) concluded that they were mixed feeders preferring grass.

In total, the habitat indicator species from Ft. Ternan are mixed, but the evidence of an open environment, possibly a woodland/savanna or even a grassland biome, is stronger.

20.4.2 Relative Abundances

The most common order is Artiodactyla at 30% followed by Rodentia 21%, Primates 10% and all carnivores at 8%. The dominance by ungulates may be indicative of secondary forest or more open conditions.

Nesbit Evans et al (1981) have calculated the browser/ grazer ratio from Fort Ternan to be 2:1 . This compares to a modern savanna biome 1:1 and modern forest environments 2:1 to 3:1. Thus, the Ft. Ternan ratio occupies an intermediate position between these two environmental types.

In total, there are no clear patterns apparent in the relative abundance statistics.

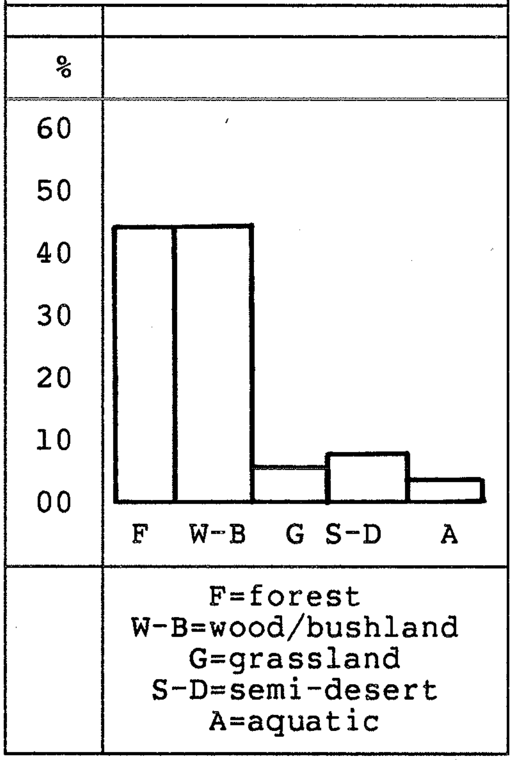
20.4.3 Taxonomic Habitat Index

The Ft. Ternan taxonomic habitat index has been calculated by Nesbit Evans et al (1981).

TABLE 20.2

HABITAT SPECTRUM

FORT TERNAN



The index shows equal dominance by forest and woodland-bushland forms while the other classes are very low. To obtain these figures Nesbit Evans et al must have considered the bovids as woodland-bushland dwellers rather than grassland forms. This would be contra Gentry (1970:310) whose analysis of the bovids from Ft. Ternan concluded that the species were more likely to have come from an open, or slightly wooded,biome. In the final analysis, however, moving the bovids into a different category would have a negligible impact on the index as a whole.

20.4.4 Ecological Diversity Analysis

The ecological diversity analysis was also calculated by Nesbit Evans et al (1981).

Taxonomic Order - The Fort Ternan spectrum is similar to those from extant floodplain environments, differing only in that the proportion of primates is higher than would normally be found today.

Size Spectrum - This spectrum resembles spectra from extant woodland-bushland biomes. One peculiarity in the analysis is the low number of forms falling into the 1.1-10 kg. class. Nesbit Evans et al (1981) believe that this is not due to sampling error but rather, accurately reflects the situation which existed. Because forms falling into the 0-1.1 kg. class are relatively common, and, since the smaller forms are more likely to have been lost in a fossil situation (Behrensmeyer et al 1980), Nesbit Evans et al are probably correct in their analysis. They go on to suggest that the absence of monkeys and small carnivores is responsible for the low numbers in the 1.1-10 kg. class as these types of animals form the bulk of species in this category today. Unfortunately, what this means ecologically is uncertain, but a lack of monkeys may suggest a dearth of trees in the area.

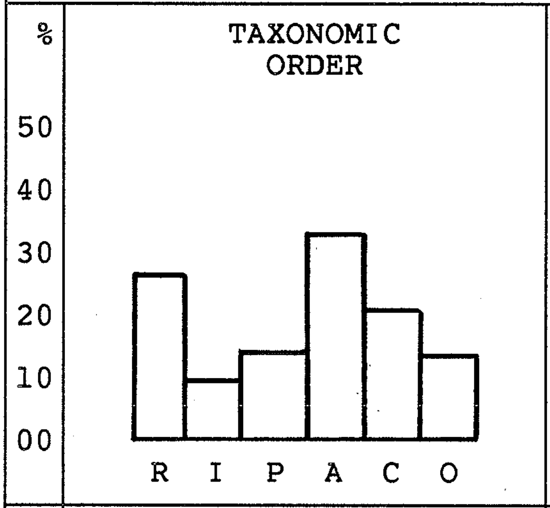
Locomotor Spectrum - The Miocene locomotor spectrum resembles extant floodplain and woodland-bushland biomes. Because, however, there are no aquatic vertebrates, with the exception of a single crocodile bone, from the site, a floodplain environment is not likely (Nesbit Evans et al 1981). So, an open environment, possibly a woodland is indicated here.

Feeding Adaptation - The Fort Ternan feeding adaptation spectrum does not closely resemble any extant pattern. Nesbit Evans et al (1981) believe the pattern falls between those from extant forest and savanna environments in Africa.

In total, the ecological diversity analysis demonstrates non-forest conditions at Fort Ternan. Because the nature of the fauna is not consistant with a floodplain environment, a woodland/bushland/savanna biome is more likely.

TABLE 20.3

ECOLOGICAL DIVERSITY ANALYSIS-FORT TERNAN



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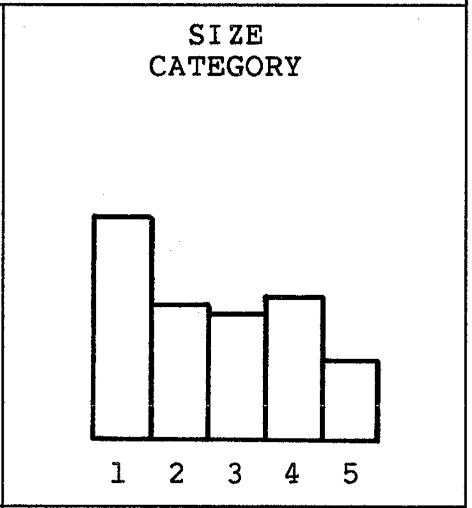

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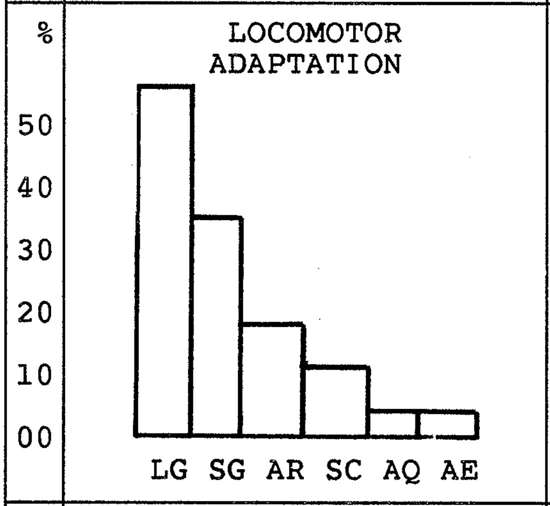

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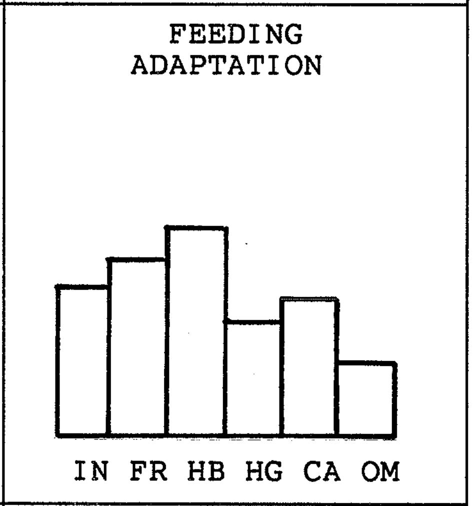

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20.4.5 Socioecology

Using Jarman's (1974) socioecological categories for antelopes, Nesbit Evans et al (1981) have analysed the bovids from Fort Ternan. Based on a number of characteristics of these forms (size, sexual dimorphism, limb length) they reached several conclusions regarding some of the social habits they might have had (ie. group size, home range size, territoriality and seasonality). They concluded that the socioecology is indicative of mammals living in closed to moderately closed habitats. It must be remembered, however, that this type of analysis is in its infancy and should not be relied upon too heavily.

20.4.6 Non-mammalian Fauna

Various non-mammalian fauna from Fort Ternan have been listed by Andrews and Walker (1976) and Shipman et al (1981).

1. MOLLUSCA
   - a) *Maizania* - evergreen forest.
   - b) *Cerastua* - wide distribution.
   - c) *Homorus* - wet evergreen forest.
   - d) *Burtoa nilotica* - woodland.
   - e) *Trochonanina* - forest and bushland.
   - f) *Gulella* - forest and thicket
2. ARTHROPODA
   - a) Potamidae
3. REPTILIA
   - a) Chamaelodontidae
   - b) *Crocodylus sp.* - M.N.I.=1
4. AVES
   - a) *Struthio cf. asiaticus* - M.N.I.=2
   - b) Falconidae
   - c) Acciptrid vulture - M.N.I.=1

d) Genetta sp. - M.N.I.=5

e) Percrocuta sp. - M.N.I.=3

The environmental implications of the gastropods are mixed but generally they point towards forest conditions (Andrews and Walker 1976). The crocodile, of course, indicates the presence of water nearby when the site was formed but since this form is represented by a single bone only, and since there are no other aquatic forms in the sample it must be considered that water was not a major factor at the site.

The ostrich Struthio on the other hand, may be seen as a good indicator of open conditions, perhaps even grassland (Nesbit Evans et al 1981).

20.5 FLORA

The only flora listed from Fort Ternan is a single leaf, probably from the Sterculiaceae family of woodland trees and shrubs (Andrews and Walker 1976).

20.6 PALEOGEOGRAPHY

It seems likely that the main fossiliferous area at Fort Ternan represents a period of soil and vegetative development between eruptions from the Tinderet volcano. Most of the stratigraphic sequence in the Fort Ternan levels is composed of pyroclastic materials, and while some levels have been influenced by water a rose diagram indicates that this was not the case in the fossiliferous beds themselves (Shipman et al 1981). Thus, the sedimentary environment here, as at most of the Tinderet sites was probably subaerial (Shipman et al 1981). There is general agreement that Fort Ternan was not a forest locale. Most researchers seem to feel that a woodland, savanna, wooded bushland or wooded grassland was the probable biome at this site (Nesbit Evans et al 1981, Andrews and Walker 1976, Gentry 1970). Most types of faunal analysis, and the species present themselves, seem to point towards this conclusisn.

Fort Ternan is significant because it shows one of the earliest appearances of Ramapithecus. It could be significant that this form occurrs at a site where the environment is quite clearly non-forest. Other forms, for example the bovids, which also were not common in the Early Miocene, first appear here in abundance. It has been postulated that the appearance of Ramapithecus and the other new forms may have been related to an ecological shift towards more open country (Shipman et al 1981). It is also possible, however, that there was an influx of mammals from another area (Eurasia) at about this time, which would explain the divergence in forms between the Early Miocene sites and Ft. Ternan (Andrews 1978).

An environmental shift in the Ft Ternan area could have readily been caused by volcanic activity from Tinderet, changing the prevailing biome from a forest (as at Songhor) to a more open environment (Shipman et al 1981). On the other hand, a number of new forms do appear at Fort Ternan and it must be assumed that they were invaders moving into a new territory. An environmental shift, however, would make it more likely that invading species would find niches available to them, and it is reasonable to believe that with a change in the environment came a change in the fauna.

Thus, *Ramapithecus* seems to have moved into an area that had little primate fauna, presumably because environmental conditions were not favorable for the primates common in the Early Miocene, *Limnopithecus*, *Dendropithecus* and *Proconsul*.

It is interesting to note, however, that the *Proconsul* species most common at the other Tinderet sites, *P. major* and *P. gordoni*, are absent from Fort Ternan entirely. These other Tinderet sites were almost certainly forest locations so it appears as if the above forms were unable to adjust to changing conditions. On the other hand, *Proconsul nyanzae*, unless intrusive, makes its only appearance in a Tinderet series site at Fort Ternan which may indicate that this form either preferred non-forest conditions or was more adaptable than the other *Proconsul* species.

21. SUMMARY OF THE EAST AFRICAN MIOCENE SITES

The dates listed in table 21.1 are based upon both K/ar and the stratigraphies of the various sites. The mean age of the sites is 18.64 m.y. and they are more or less normally distributed around this point.

TABLE 21.1

AGE OF THE EAST AFRICAN MIOCENE SITES

SITE	ESTIMATED AGE	PROBABLE ACCURACY
FORT TERNAN	14 m.y.	good
KIRIMON	13 m.y. +	uncertain
MABOKO	15-16 m.y.	fair
MOROTO I	16 m.y.	fair
MOROTO II	16 m.y.	fair
LOPEROT	17-19 m.y.	moderate
LOSIDOK	17-19 m.y.	moderate
MFWANGANO (HIWEGI)	17-19 M.Y.	moderate
NAPAK I (GROUP)	18 m.y.	good
RUSINGA (HIWEGI)	18-19 m.y.	good
NAPAK II (GROUP)	18.5-20 m.y.	moderate
KORU (KORU)	19.5 m.y.	good
KORU (LEGETET)	19.5 m.y.	good
SONGHOR	19.5 m.y.	good
KORU (CHAMTWARA)	19.6 m.y.	good
MFWANGANO (RUSINGA AGGLOM.)	19.6 m.y.	moderate
MFWANGANO (UPPER KIAHERA)	20.0 m.y.	moderate
RUSINGA (KIAHERA)	21.0 m.y.	moderate
BUKWA	22.0 m.y.	good
KARUNGU	23.0 m.y.	moderate
KORU (MESWA BRIDGE)	23.5 m.y.	good

TABLE 21.2

DEPOSITIONAL ENVIRONMENTS AND PROBABLE VEGETATION TYPES OF THE EAST AFRICAN MIOCENE SITES

DATE M.Y.	SITE	DEPOSITIONAL MODE	PROBABLE ENVIRONMENT
14	FORT TERNAN	SUBAERIAL	OPEN WOODLAND
	MABOKO	FLOODPLAIN	WOODLAND (?)
	MOROTO I	UNCERTAIN	UNKNOWN
	MOROTO II	RIVERINE/ FLUVATILE	UNKNOWN
	LOPEROT	RIVERINE (?)	FLOODPLAIN
18	LOSIDOK	LAKE MARGIN// FLUVATILE FLOODPLAIN	UNKNOWN
18.5	MFWANGANO (HIWEGI)	WATER BORNE SEDIMENTS/ FLOODPLAIN	FOREST (?)
	NAPAK I (GROUP)	LARGELY SUBAERIAL	FOREST
	RUSINGA (HIWEGI)	LAKE MARGIN/ RIVERINE/ FLOODPLAIN	FOREST AND SAVANNA (?)
	NAPAK II (GROUP)	LACUSTRINE	UNCERTAIN
	KORU (KORU)	SUBAERIAL	FOREST/WOODLAND
	KORU (LEGETET)	SUBAERIAL	FOREST
	SONGHOR	SUBAERIAL	FOREST
	KORU (CHAMTWARA)	SUBAERIAL	FOREST
	MFWANGANO (RUSINGA AGGLOMERATE)	WATER BORNE SEDIMENTS/ FLOODPLAIN	FOREST (?)
20	MFWANGANO (UPPER KIAHERA)	LARGELY SUBAERIAL	FOREST (?)

	RUSINGA (KIAHERA)	FLOODPLAIN	WOODLAND-BUSH
	BUKWA	LACUSTRINE	WOODLAND (?)
	KARUNGU	RIVERINE/ LACUSTRINE/ FLOODPLAIN	WOODLAND-BUSHLAND
23.5	KORU (MESWA BRIDGE)	RIVER CHANNEL	UNKNOWN

A brief examination of table 21.2 shows that the sites older than approximately 20 m.y. do not seem to show well developed forest facies. The evidence from these sites tends to point towards a more open, probably woodland, biome. Similarly, sites younger than 18 m.y. also seem to have been predominantly non-forested. This is less conclusive, however, as many of the younger sites are poorly dated, poorly known stratigraphically, and have unknown or uncertain vegetation patterns.

The majority of the sites, and the bulk of the well documented ones, fall into a fairly narrow range chronologically: from approximately 18 to 20 million years. These sites generally have a well developed forest component. Even at the few sites where there are strong indications of non-closed forest conditions (as at Rusinga-Hiwegi) there is also good evidence to support the conclusion that there was forest as well.

Andrews (1981a) has recently re-iterated his position that forest conditions dominated during the East African Miocene period. There is strong evidence that this position, for the most part, accurately reflects conditions at those sites dated from @18-20 million years. Earlier and later sites may not, however, fit this pattern.

22. ASSOCIATIONS OF PROCONSUL FORMS WITH PARTICULAR ENVIRONMENTS

Based on the accumulated evidence presented above, the following sites can be considered to have been forested during (at least part of) the Miocene period: Mfwangano (Hiwegi and Rusinga Agglomerate horizons), Napak I (group), Rusinga (Hiwegi) (partim), Koru (Koru [probably], Legetet and Chamtwara), and Songhor. Table 22.1 shows the distribution of Proconsul forms in these sites (based on M.N.I. analysis).

TABLE 22.1

PROCONSUL ASSOCIATIONS WITH FOREST SITES

SITE	P. afr.	P. nya.	P. maj.	P. gor.	P. van.
MFWANGANO	5	3	-	1	1
NAPAK I	-	-	8	-	-
RUSINGA (HIWEGI)	35	41	-	-	3
KORU	1	-	1	-	-
LEGETET	1	-	3	-	-
CHAMTWARA	2	-	3	-	-
SONGHOR	5	-	15	17	3

The number of individuals from table 22.1, is expressed in table 22.2 as a percentage of the total number of individuals, by species, found in the East African Miocene.

Because, as has been discussed earlier, it is possible that forest was not the only environment present on Rusinga Island during the Miocene, the same analysis shown in table 22.2 has been re-calculated, (table 22.3) this time using the assumption that Rusinga-Hiwegi was largely non-forested.

An analysis of the above table reveals that two Proconsul forms, P. major and P. gordoni are consistently associated with sites that can quite clearly be classified as forest locations. It must be remembered, however, that P. gordoni is extremely limited in distribution, and that 17 of the 18 individuals known have come from a single site (Songhor). Thus, because of its limited distribution, it might be premature to suggest that P. gordoni was clearly a forest dwelling form. On the other hand, Songhor, perhaps more certainly than any other site, was forested. At Songhor P. gordoni is the most abundant Proconsuline and this is likely significant. In total, the association of P. gordoni with a forest biome may be considered a fairly well documented one.

TABLE 22.2

PERCENTAGE OF PROCONSUL INDIVIDUALS ASSOCIATED WITH FOREST SITES

SPECIES	M.N.I. FROM FOREST SITES	TOTAL M.N.I. ALL SITES	% TOTAL
P. africanus	49	53	92.5%
P. nyanzae	44	51	86.4%
p. major	30	34	88.5%
P. gordoni	18	18	100.0%
P. vancouveringi	7	8	87.5%

TABLE 22.3

PERCENTAGE OF PROCONSUL INDIVIDUALS ASSOCIATED WITH FOREST SITES - EXCLUDING RUSINGA-HIWEGI

SPECIES	M.N.I. FROM FOREST SITES	TOTAL M.N.I.- ALL SITES	% OF TOTAL
P. africanus	14	53	26.5%
P. nyanzae	3	51	6.0%
p. major	30	34	88.5%
P. gordoni	18	18	100.0%
P. vancouveringi	4	8	50.0%

Based on the analyses shown in tables 22.2 and 22.3, *P. major* may also be considered a forest dwelling species. Like *P. gordoni* it is strongly represented at Songhor, but unlike this latter form it is also well distributed elsewhere. P. major is known from a number of forest sites including: Koru, Legetet, Chamtwara and Napak I. The remaining individuals of P. major, those that do not come from the sites considered to have been forested, come from sites that are poorly known, such as Moroto and Kirimon. Thus, a relationship between P. major and forested locations can be substantiated.

P. vancouveringi must remain as somewhat of an enigma. Recently described (Andrews 1970, 1974) this form is poorly known, and, in fact, few specimens have been assigned to it (M.N.I.=8). While only 50% of these individuals (table 22.3) were found in sites that can be considered to have been forested, little significance can be attached to this because P. vancouveringi is so poorly distributed.

The final two Proconsul species, P. africanus and P. nyanzae, would seem to be less clearly associated with forested sites, based on the figures in table 22.3. P. africanus is known from sites such as Songhor, Legetet and Chamtwara that were probably forested but the evidence suggests that it was not common at these sites, certainly less so than other forms. Conversely, P. nyanzae has not been found at the above sites at all, and, based on table 22.3, can not really be considered as clearly associated with a forest biome.

When the specimens from Rusinga-Hiwegi are added to those described above, however, the picture changes dramatically (table 22.2). If Rusinga, during Hiwegi times, was largely forested then 92.5% of the P. africanus individuals and 86.4% of the P. nyanzae individuals would have been recovered from forest sites. Thus, the question of which type of habitat might have been preferred by these two forms largely revolves around the environment at a single site, Rusinga (Hiwegi levels). Unfortunately, as has already been discussed, the ecological picture from Rusinga, particularly in the Hiwegi levels, is unclear. Despite Andrews' (1981a) views it seems possible that there was open woodland or savanna on Rusinga along with the forested areas. On the basis of current evidence it is even possible that these more open areas might have constituted a greater area than the forest.

Where does this leave the question of the habitat preferences of P. africanus and P. nyanzae? If Rusinga is considered to have been largely forested then the data from table 22.2 would suggest that they were forest dwelling forms. If Rusinga is considered to have been largely non-forested then the data presented in table 22.3 would tend to suggest that neither was a forest oriented form. Thus, information must be included from other sites in order to make the most accurate assessment possible of the probable environmental preferences of these two forms.

P. africanus has been found at the best documented forest sites from the East African Miocene, Songhor, Legetet and Chamtwara, albeit not in great frequency. Its only association with sites that might be considered non-forested, other than Rusinga-Hiwegi, are its presence in Rusinga-Kiahera levels and the problematic specimens from Fort Ternan. Thus, based upon a fairly strong association with probable forest sites, and a weak association with sites that may have been non-forested, it is reasonable to speculate that *P. africanus* may have been found in forested areas on Rusinga.

P. nyanzae, however, is known from sites that were probably non-forested including Karungu, Rusinga-Kiahera and again Fort Ternan. Its only known appearance in a site that was probably forested, excluding Rusinga-Hiwegi, is at Mfwangano where it occurrs in low frequency in the Hiwegi levels. Significantly, there is an apparent negative relationship between *P. nyanzae* and the clear forest sites around Tinderet. *P. nyanzae* is the only African *Proconsul* species that does not appear at Songhor, and neither does it occur at any of the Koru sites.

It seems possible that Rusinga Island may have showed at least two distinct environmental types during the Miocene period; gallery forest along the river banks, lake margins and in moister areas; and more open parkland in drier areas breaking up the forest. It must be considered, then, that *P. nyanzae* may have been associated with the more open areas rather than the forested ones.

Finally, the inclusion of Rusinga-Hiwegi in the forest sites (table 22.2) alters the proportion of *P. vancouveringi* individuals that might be considered to have come from forest sites, from 50% to 87.5%. As in the case of *P. africanus*, *P. vancouveringi* is known from sites that may be considered to have been forested, notably Mfwangano and Songhor. Thus, this form might have been a forest dweller but because it is generally so poorly known, no firm conclusions can be drawn at this time.

23. FAUNAL CORRELATES

Because all of the *Proconsul* species occur at more than one site it is possible to analyse the fauna from every site at which a species has been found, in order to see if any other forms are consistently found with the *Proconsul* species in question. To this end faunal lists have been prepared charting all fossil forms from every site at which each individual *Proconsul* species has been found. Although the actual number of sites at which the various Proconsulines occur varies from species to species, the following charts have been prepared using co-occurrence between a *Proconsul* form and another species at 50% or more of the sites where the *Proconsul* form has been found as the criterion. For example, *Proconsul sfricanus* has been found at 8 East African Miocene sites. The chart for this form (table 23.1) lists all species found at four or more of these same sites. Based on the nature of species commonly associated with a *Proconsul* form, ecological preferences in the primate species may be revealed.

23.0.1 *Proconsul africanus*

P. africanus has been recovered from 8 sites, has been found with 148 species (out of a total East African Miocene listing of 200), and has been found commonly with 33 forms (table 23.1).

Only one species, a rodent, *Diamantomys leuderitzi*, has been found at all 8 sites that have yielded material assigned to *Proconsul africanus*. According to Pickford (1981) this form is characterised by extremely hipsodont teeth, which suggests an adaptation to grazing coarse ground vegetation. Although by no means certain, this would tend to suggest that *D. leuderitzi* was probably not a forest dweller, or, if it was, lived on the margins of the woods or by swamps, rivers,or anywhere that grasses would be abundant.

The two forms found at 7 of the 8 *P. africanus* sites, the primate, *Limnopithecus legetet* and the perissodactyl *Chalicotherium rusingense* are rather uncertain ecologically. *L. legetet*, however, may be considered an arboreally adapted form, and, indeed, on the basis of its dentition, has been linked to the Hylobatinae (LeGros Clark and Leakey 1951).

The species found at 6 sites with *P. africanus* are somewhat more revealing. The insectivore *Rhynchocyon clarki*, the rodents *Paraphiomys stromeri* and *P. pigotti* and the tragulid artiodactyl *Walangania africanus* can all be considered, to varying degrees, as being indicators of forest conditions. *Rhynchocyon clarki* in particular is considered by Pickford (1981) to be an excellent habitat indicator species.

TABLE 23.1

SPECIES FOUND IN ASSOCIATION WITH P. AFRICANUS

FOUND AT:	AGREE WITH Proconsul africanus	GENUS/SPECIES
8 SITES	100%	Diamantomys leuderitzi
7 SITES	87.5%	Limnopithecus legetet Chalicotherium rusingense
6 SITES	75%	Rhynchocyon clarki Paraphiomys stromeri Paraphiomys pigotti Walangania africanus
5 SITES	62.5%	Amphechinus rusingensis Galerix africanus Rhynchocyon sp. Prodeinotherium hobleyi Afrocricetodon songhori Masritherium aequitorialis
4 SITES	50%	Prochrysochloris miocaenicus Protenrec tricuspis Gymnurechinus leakeyi Dendropithecus macinnesi Proconsul major Progalago dorae Progalago minor Progalago robustus Teratodon speki Hyaenodon andrewsi Kichechia zamane Epiphiomys coryndoni Phiomys andrewsi Simonomys genovefae Paranomalurus soniae Paranomalurus bishopi Bathyergoides sp. Dorcatherium pigotti Dorcatherium parvun Dorcatherium songhorensis

Of the remaining forms that have commonly been found with

P. africanus several may be indicators of forest conditions. They are: *Prochrysochloris miocaenicus*, *Rhynchocyon sp.*, *Progalago* (3 sp.) *Paranomalurus* (2 sp.), and *Dorcatherium* (3 sp.).

Conversely, a few forms can be taken as indicators of more open conditions. *Hyaenodon andrewsi*, *Bathyergoides sp.* and several of the hedgehogs would fall into this category. In total, however, the number of species, and the degree of agreement, seem to suggest that *P. africanus* would have been found in an environment favoured by forest adapted forms.

In terms of negative correlations, *P. africanus* has not been found with a total of 52 species. With the exception of two forms, however, these are all species which have appeared very infrequently in the fossil record. No conclusions, therefore, can be drawn from the fact that they have not been found in association with *P. africanus*. Two forms, however, occur at three sites, but never, as yet, with *P. africanus*. They are: a proboscidean, *Trilophodon angustidiens* and a perissodactyl *Dicerorhinus sp.*. Unfortunately, once again, the environmental affinities of these species are unknown.

23.0.2 *Proconsul nyanzae*

P. nyanzae has been found at 4 sites (excluding sites that are questionable), in association with 122 forms (out of 200), and has been found commonly with 41 species.

There are 7 forms found at all four sites at which *P. nyanzae* occurs. Of these, several can be considered as possible forest indicators. These are: *Paraphiomys pigotti* and the two species of *Dorcatherium*. *Dendropithecus macinnesi* is also considered to be an arboreal form by Andrews (1981a) and this is supported by an analysis of postcranial and dental remains of this species recently carried out by Aiello (1981).

Of those forms that occur at three of the *P. nyanzae* sites, none are strong habitat indicators. The tragulids and *Paraphiomys* may indicate forest conditions while *Pachyhyrax championi* is more likely to have lived in relatively open areas.

Species found with *P. nyanzae* at two of the four sites generally seem to be forms adapted to more open environments. *Hyaenodon*, *Orycteropus africanus*, *Kenyalagomys*, *Megapedetes* (2 sp.) and the hyraxes fall into this category. Of this group, only *Limnopithecus legetet* might be considered as a forest form.

TABLE 23.2

SPECIES FOUND IN ASSOCIATION WITH P. NYANZAE

FOUND AT:	AGREE WITH Proconsul nyanzae	GENUS/SPECIES
4 SITES	100%	Dendropithecus macinnesi Prodeinotherium hobleyi Paraphiomys pigotti Aceratherium acutirostratrum Masritherium aequitorialis Dorcatherium pigotti Dorcatherium parvun
3 SITES	75%	Myohyrax oswaldi Anasinopa leakeyi Platybelodon kisumuensis Paraphiomys stromeri Diamantomys leuderitzi Pachyhyrax championi Chalicotherium rusingense Dicerorhinus leakeyi Brachypotherium heinzelini Hyotherium dartevillei Xenochoerus africanus Dorcatherium crassum Walangania africanus Bunolistriodon jeanelli Propaleoryx nyanzea
2 SITES	50%	Proconsul africanus Limnopithecus legetet Metapterodon kaiseri Pterodon africanus Hyaenodon andrewsi Metapterodon zadoki Kichechia zamane Orycteropus africanus Kenyalagomys rusingae Simonomys genovefae Megapedetes sp. Megapedetes pentadactylus Pachyhyrax pygmaeus Megalohyrax championi Chalidotheruim pattersoni Brachyodus africanus Canthumeryx sirtensis Hyotherium sp. Ampullaria ovata

Perhaps more revealing, however, than the individual species usually found with *P. nyanzae* is the overall types of forms. Of the 22 species which occur at 3 (75%) or 4 (100%) of the *P. nyanzae* sites 9 or 41% are artiodactyls. If the perissodactyls are added to this sample then 13 or 59% of the species commonly associated with *P. nyanzae* are ungulates. This emphasis on ungulates, if anything, probably indicates that *P. nyanzae* may have been commonly found with species that preferred open areas as opposed to closed forest.

In total, the forms commonly associated with *P. nyanzae* do not form as concise a picture as those found with *P. africanus* did. There are habitat indicators present which seem to point towards a number of different environments, rather than singling out any particular one.

It seems possible that the forms that are not associated with *P. nyanzae* may be significant. The forest indicators that this species is found with are, to a certain degree, open to debate. The most clear forest indicators, such as those commonly found with *P. africanus* :i.e. *Rhynchocyon* and *Paranomalurus* are not commonly found with *P. nyanzae*. Also, few of the known small primates from the East African Miocene that are considered to be forest indicators are found with *P. nyanzae*, and of those forms, none are commonly found with it. Such primates as both species of *Komba*, *Micropithecus clarki*, *Victoriapithecus sp*. and some forms of *Progalago* have not yet been found with *P. nyanzae*.

Overall, the speculation that *P. nyanzae* may have been found in more open habitats is neither clearly supported nor denied by this analysis. This ambiguity itself, however, may be significant considering the clear pattern this analysis disclosed for *P. africanus*.

23.0.3 *Proconsul major*

P. major has been found at 8 sites, in conjunction with 116 forms (out of 200), and has commonly been found with 26 species.

The species found in association with *P. major* (table 23.3) are remarkably similar to those found with *P. africanus*. In fact, only 4 of the forms (11%) commonly found with *P. major* were not found generally with *P. africanus*. That these two forms are commonly associated with the same spec-

TABLE 23.3

SPECIES FOUND IN ASSOCIATION WITH P. MAJOR

FOUND AT:	AGREE WITH Proconsul major	GENUS/SPECIES
8 SITES	100%	
7 SITES	87.5%	Paraphiomys stromeri Paraphiomys pigotti
6 SITES	75%	Diamantomys leuderitzi Walangania africanus
5 SITES	62.5%	Limnopithecus legetet Kichechia zamane Bathyergoides sp. Chalicotherium rusingense Dorcatherium songhorensis
4 SITES	50%	Erythrozootes chamerpes Prochrysochloris miocaenicus Protenrec tricuspis Amphechinus rusingensis Galerix africanus Rhynchocyon clarki Rhynchocyon sp. Dendropithecus macinnesi Proconsul africanus Progalago dorae Micropithecus clarki Teratodon speki Hyaenodon andrewsi Paranomalurus soniae Paranomalurus bishopi Paranomalurus walkeri Afrocricetodon songhori

ies may be an indication that they preferred similar environments.

In terms of habitat indicator species, there are a number of good forest indicators commonly found with P. major. These are: Rhynchocyon, Paranomalurus, Prochrysochloris and a number of species of small primates, notably Progalago and Micropithecus.

There are also a few non-forest indicators associated with P. major. Bathyergoides and Hyaenodon andrewsi fall into this category. In total, however, there appears to be a clear relationship between P. major and a group of species that were almost certainly forest dwellers. The conclusion, therefore, that this form was also a forest dweller appears to follow naturally.

23.0.4 Rangwapithecus species

This analysis has not been fully carried out on the Rangwapithecus species, gordoni and vancouveringi. In the case of P. gordoni, this is simply because this form does not have a wide enough distribution. Its only documented appearance outside of Songhor where it is common, is at Mfwangano, in the Hiwegi levels. This, though, is an extremely isolated appearance, and could possibly even be a mis-identification as P. gordoni is not found at any other Western Kavirondo site. Thus, the total distribution of this form may be limited to a single site.

P. vancouveringi is known from three sites: Maboko, Rusinga (Hiwegi), and Songhor, but its total M.N.I. equals only 8. With such a limited frequency, conclusions drawn regarding this form must also be limited.

Only three species occur at all three P. vancouveringi sites: Amphechinus rusingensis, Limnopithecus legetet, and, somewhat surprisingly, the gastropod Limicolaria. Of the above, only L. legetet may be considered a fairly good habitat indicator species, possibly indicating forest conditions. Limicolaria today has a wide distribution ranging from bushland through full forest conditions (Andrews and VanCouvering 1975).

A total of 52 forms occur at two of the three P. vancouveringi sites. There are habitat indicator species from a number of environments included in this group. Possible forest species present are: Rhynchocyon, Dendropithecus, Paraphiomys and Paranomalurus. Indicators of non-forest conditions include: Hyaenodon, Kenyalagomys, Megapedetes and Pachyhyrax.

Unlike the other Proconsulines, P. vancouveringi, perhaps because of its limited distribution, is commonly associated with a variety of non-mammalian fauna. Non-mammalian forms found at two P. vancouveringi sites are: Ligatella, Homorus, Tayloria, Maizania and Trochonanina (all gastropods), cichlid fish, chelonians and pythons.

Of the above, *Homorus*, *Tayloria* and *Maizania* are all considered to be forest forms by Andrews and VanCouvering (1975). *Ligatella* today is found in bushland. The fish and reptiles indicate that *P. vancouveringi* may have preferred habitats near water. Because, however, of the limited distribution of this form such conclusions are, of course, very speculative. Furthermore, only one individual of *P. vancouveringi* is known from Maboko, and this might always be an aberrant occurrence, or even a mis-identification.

In summation, an analysis of the fauna commonly found (at greater than 50% of the sites) with each species of *Proconsul* revealed that two forms, *P. africanus* and *P. major* are typically associated with a variety of species that for the most part were probably forest oriented. *P. nyanzae*, on the other hand, was associated with a suite of forms which could not be readily characterised as having come from any particular environment.

The two *Rangwapithecus* species were analysed only briefly as their distribution was too limited to draw any firm conclusions.

24. POST-CRANIAL ADAPTATIONS

The morphology of any fossil form, in particular the post-cranial morphology, must be expected, at least to a certain degree, to reflect the habitat and behavioral patterns of that form. In the same manner that an Anomalure (flying squirrel) is considered to be a forest form because its skeleton is adapted to dwelling in, and moving between, trees; the post-cranial skeleton of Miocene primates should show adaptations which enhanced the survival capabilities of each form in its environment. Thus, Proconsul skeletal remains may yield important information concerning possible environmental adaptations made by several species in this genus.

Unfortunately, in terms of the whole suite of African Miocene Proconsul species, little information can be gleaned from this source. The biggest problem, of course, is the lack of post-cranial material which has been recovered, and can be assigned with confidence to any of the forms described on the basis of dental morphology. There are few post-cranial elements which have been recovered for even two Proconsul forms, and so non-dental morphological comparisons between species are rare.

Nevertheless, the existing skeletal material will be discussed as it may help to point out possible environmental differences between Proconsul forms. Conclusions can be drawn from the form of the post-cranial elements regarding possible environmental adaptations of the individual species that have had remains of this nature assigned to them. Such conclusions will either tend to support, or tend to deny, inferences concerning the environmental preferences of the Proconsul species based upon the preceeding paleoecological analyses.

The best known, and most intensively studied, Proconsul post-cranial remains, are the fragmentary humerus, ulna and radius first described by Napier and Davis (1959) and assigned to Proconsul africanus. There have been many contradictory statements made about this material, but in the final analysis it must be accepted that the forelimb of P. africanus exhibits similarities to many groups of primates.

Napier and Davis (1959) initially concluded that the P. africanus forelimb most clearly resembled Presbytis, an arboreal quadrupedal, semi-brachiating form. After re-examining the material, Pilbeam (1969) listed at least 14 characters of the forelimb in which the morphology of the P. africanus remains was comparable to the extant genus Pan. A later study supported the conclusion that the P. africanus forelimb was essentially pongid-like (Zwell and Conroy 1973).

More recent studies, however, have emphasized the basic "monkey-ness" (Andrews 1981b) of the African Miocene pongids. Several researchers apparently now consider *P. africanus* to have been a slow, deliberate climber (Fleagle 1976), an arboreal quadruped (Morbeck 1975, Schon and Ziemer 1973). With this viewpoint accepted several authors have gone on to discuss whether *P. africanus* was a below or above branch feeder (Andrews 1981b, Aiello 1981).

In total, then, the evidence pointing to a locomotor pattern for *P. africanus* is contradictory. Speculations, however, have been presented, based upon the forelimb evidence, suggesting that this form might have been a "knuckle-walker" (Conroy and Fleagle 1972); or, at the opposite end of the spectrum, evidence to suggest that this form was a brachiator (Lewis 1971, 1972). In between, this species may be considered to have been an arboreal quadruped, much in the manner of many monkeys.

In terms of the paleoecology of *P. africanus*, however, in view of the fact that there is no comparable material from another *Proconsul* form, the distinctions discussed above are of little significance. Almost all of the adaptations and possible modes of locomotion discussed above are essentially geared to an arboreal lifestyle. There is little significant divergence from the viewpoint that the forelimb of *P. africanus* was adapted for an arboreal mode of living. Thus, the implied notion is always that *P. africanus* was a forest dwelling form.

Even if the viewpoint that the *P. africanus* forelimb shows more terrestrial (ie. knuckle walking) affinities is followed, the basic pattern is not altered. The only extant knuckle walkers, *Pan* and *Gorilla*, while they may spend up to 90% of their time on the ground, are primarily, although not exclusively, forest dwellers (Lasker 1973). In the final analysis, it is possible that much of the research done on the forelimb of *P. africanus* has been coloured by the belief that "since this form is a primate, it must have been living in the trees". Nevertheless, on morphological grounds there apparently is no evidence to suggest that this form was adapted for anything except an arboreal lifestyle, or at the outside, limited terrestriality in an arboreal setting.

The conclusion drawn from the paleoecological analysis, that *Proconsul africanus* was likely a forest form, seems, then, to be supported by the morphology of the forelimb.

Recently, finds of leg and foot bones of both *P. africanus* and *P. nyanzae* have revealed further information concerning the post-cranial skeletons of these forms (Walker 1983, Pickford 1982). Morphologically these remains, and hence the forms they represent, appear to have been very similar, differing primarily in size. Walker (1983) believes that these remains are more like extant apes than monkeys and concludes that both P. africanus and P. nyanzae were probably slow moving arboreal forms. Furthermore, he believes that these fossils show few adaptations for terrestrial dwelling in the Cercopithecoid pattern. Thus, according to this opinion, at least two species of Proconsul can firmly be placed in an arboreal setting.

There have also been two fossil tali, and one calcaneous assigned to the genus Proconsul, these from Rusinga and Songhor (LeGros Clark and Leakey 1951). Unfortunately, these have not yet been assigned to any particular form although LeGros Clark and Leakey stated that they would more likely have come from either, or both, the larger Proconsul species.

In form, they concluded, these foot bones were most similar to those from quadrupedal cercopitheciids (LeGros Clark and Leakey 1951). They go on to suggest that Proconsul sp. was likely adapted to quadrupedal locomotion, either terrestrially or arboreally, although the size of the form(s?) would preclude much activity in the trees (LeGros Clark and Leakey 1951).

It is interesting to note, then, that one or more of the larger Proconsul forms may have been adapted to a more terrestrial lifestyle, although this does not preclude, of course, that it may have still been a forest dweller.

25. DENTAL ADAPTATIONS

As was the case with the post-cranial morphology, it may be possible to draw ecological conclusions from the dentitions of fossil forms. Unlike the post-cranial remains, when dealing with the *Proconsul* forms, the dentitions are quite well known. Of the five *Proconsul* species discussed here only the dentition of *P. vancouveringi* is not reasonably complete: this form's anterior dentition being unknown (Andrews 1978).

Recently, Kay (1977) analysed the dentitions of the Early Miocene African Hominoids to determine their probable diet. He compared the Miocene primates to extant forms whose diets are reasonably well documented in order to determine whether the fossil forms were most likely frugivorous or folivorous.

Briefly, Kay's method used measurements of selected dental traits such as cusp height and the summed surface areas of the trigonid and talonid basins, to determine trends in the dental structure. Primarily he was looking for:

1. Cusp Height - reflecting capacity for resistance to dental wear.
2. Shearing Blade Lengths - reflecting the importance of shearing in the diet.
3. Total Basin Areas - reflecting the importance of crushing and grinding in mastication.

Using principal components on the above variables Kay demonstrated that he was able to separate correctly extant frugivorous primates from ones with a primarily folivorous diet. His method not only separated fruit from leaf eating monkeys, but also proved efficient in separating the primarily folivorous *Gorilla* and *Symphalangus* from fruit eating apes, thus demonstrating that his methodology can be applied to the higher primates as well as monkeys.

Kay then went on to calculate the above variables as they occur in Proconsuline teeth from Rusinga and Songhor. He measured specimens described as all species of *Proconsul* except *P. vancouveringi*, as well as two species of *Limnopithecus*. The calculated values for *P. africanus*, *P. nyanzae* and *P. major* fell within the confidence limits of modern frugivorous species. In addition, the values for *P. major* and *L. legetet* were very close to those from *Pan troglodytes*, a frugivore. Kay concluded, on this basis, that the evidence strongly suggested that the above Miocene forms probably had diets consisting largely of fruit.

The final Miocene form studied, P. gordoni, had values that fell between those of extant frugivores and folivores. Since the scores for this form were fairly similar to those from Gorilla and several species of Hylobates, Kay concluded that P.gordoni may not have been primarily frugivorous but he did not go as far as to say that it was folivorous.

It must be assumed that a forest environment, with year-round fruit production, is the only environment that a frugivorous species can live in. Savanna and woodland biomes, typically with a dry season in which fruit would be unavailable (Strahler 1970), probably would not support a frugivorous form. On the other hand, a primarily folivorous species could exist anywhere where there are leaves, but primates in this class today are forest dwellers who eat the leaves from trees. Thus, in terms of the ecologies of the Proconsul forms, Kay's work is somewhat predetermined. As either frugivores or folivores these forms must have been forest oriented.

There are, however, two facets of Kay's work, that deserve further consideration. First, the study shows that the dietary limits of the Proconsul forms might well be within the parameters of extant primate forms. Secondly, Kay's work suggests that all of the Miocene apes, with the possible exception of P. gordoni, apparently had the same diet - largely fruit.

Recent work by Andrews (1981b) has carried Kay's conclusions a step further. Andrews believes that the Miocene apes must have been able to eat ripe fruit only, as they lacked the dental adaptations to a folivorous diet seen today in Colobines, and, as they probably lacked the ability to detoxify unripe fruit , an ability today held only by monkeys.

The sum total of Kay's and Andrews' work leads to the conclusion that at least three species of Proconsul: P. africanus, P. nyanzae and P. major were arboreal frugivores. Additionally, they may have been able to eat only ripe fruit.

In reference to P. africanus and P. major these conclusions follow with the body of information presented earlier which suggested that these forms were primarily forest dwellers. Their conclusions, however, lend no support to the notion, based on previously presented information, that P. nyanzae may not have been a forest oriented form.

It must be noted, however, that there are some problems with Kay's work. First, dividing primates into two very broad categories, folivorous and frugivorous, tends to obscure the finer points of dietary adaptations unique to any given species. As Andrews (1981b) points out, primary food adaptations do not necessarily preclude the eating of other types of food. For example, colobines, primarily folivorous, also eat fruit when available, and this may, in certain instances, constitute much of their diet (Andrews 1981b). Also, those cercopithecines that are considered primarily frugivorous eat leaves, and indeed, need them for survival (Andrews 1981b).

As a specific example that a broad characterization of diet may be essentially, but not entirely, correct, the chimpanzee may be used. This form is considered a frugivore (Lasker 1973, Kay 1977), and Kay's dental calculations placed it in this class. Goodall has, however, pointed out that while fruit is the primary food of chimpanzees, they also eat leaves and seeds among other vegetable matter (Lasker 1973). In addition to this chimpanzees relish termites and other insects, and even eat meat when they can get it. So, characterizing this form as a frugivore, while essentially correct, is somewhat misleading.

Thus, if broad characterizations cannot be applied with complete accuracy to extant, well studied, forms, they can be assumed to be even less accurate when dealing with fossil forms. Kay's analysis, on its simplest level, really only shows that the Miocene apes, except perhaps _P_. _gordoni_ did not have the specific dental adaptations necessary to effectively consume leaves. While these forms may have been primarily fruit eaters, their specific diets may have shown considerable disparity.

Furthermore, it has been pointed out that chimpanzees have several dental adaptations which allow them to more readily consume fruit. For example, they exhibit greatly broadened incisors which allows them to scale fruit easily (Tattersall 1970). Additionally, their fairly well developed canines have a role in fruit eating (Jolly and Plog 1976). These can be considered to be specific adaptations which enhance this form's ability to obtain its necessary dietary resources. The _Proconsul_ forms, with only slightly enlarged incisors (Tattersall 1970, Andrews 1978) and and not particularly robust canines (Andrews 1978), while they might be tending towards the chimpanzee pattern, may also be seen as having no specific, unique, adaptations to a frugivorous diet. It has, however, simply been assumed that the primitive primate dietary pattern was frugivorous, and that Proconsulines, lacking specific dental adaptations to another form of diet, must have been frugivorous (Andrews 1981b). This, of course, cannot be specifically proven, and the fact must remain that the Proconsulines do not show specific adaptations to a frugivorous diet.

Finally, a basic assumption, implicit in the works of both Kay and Andrews, is that the African Miocene pongids were arboreal forms. This is reinforced, as was mentioned earlier, by the belief that a frugivorous form must necessarily be a forest species. Chimpanzees, however, classed as frugivores, while they are generally forest dwellers, are not uncommon in savanna/woodlands (Jolly and Plog 1976). They are adaptable, and spend a considerable portion of their time on the ground (Jolly and Plog 1976, Lasker 1973), and may be considered well suited to more open terrain. So, the chimpanzee is a good example of a frugivore which is neither totally frugivorous nor necessarily a forest dweller. Thus, any conclusion that all Miocene apes were forest dwellers, based on dental/dietary evidence, may not be acceptable.

If Kay's and Andrews' works are taken at face value, however, then the dental/dietary tends to support the other data presented which suggested that most of the Miocene pongids were forest dwellers. On the other hand, the dental evidence suggests that *P. nyanzae* was also a forest oriented form, a conclusion which is not necessarily in agreement with other data. It is not beyond the realm of possiblity, however, that *P. nyanzae*, may have inhabited a more open biome yet was still primarily frugivorous, as is the case with some chimpanzees today.

If Kay's and Andrews' conclusions are followed than one particularly interesting question is raised: If all the *Proconsul* forms were forest dwellers, if all, or at least the vast majority, were frugivorous, if all these frugivorous species required ripe fruit, if many, as will be shown shortly, were sympatric, then what was the relationship between them?

26. GEOGRAPHICAL DISTRIBUTION OF THE PROCONSUL SPECIES

TABLE 26.1

DISTRIBUTION OF PROCONSUL FORMS BY SITE

SPECIES	Ko	Le	Ch	So	FT	Mf	RK	RH	Ka	Ma	Lo	Na	Mo
P. africanus	X	X	X	X	X	X	X	X					
P. nyanzae					X	X	X	X	X		X		
P. major	X	X	X	X							X	X	X
P. gordoni				X		X							
P. vancouveringi				X		X		X		X			

Ko=Koru, Le=Legetet, Ch=Chamtwara, So=Songhor, FT=Fort Ternan, Mf=Mfwangano, RK=Rusinga Kiahera, RH=Rusinga Hiwegi, Ka=Karungu, Ma=Maboko, Lo=Losidok, Na=napak, Mo=Moroto.

The distribution of Miocene Proconsulines by site can be seen in table 26.1. On the basis of this information, possible home ranges for these forms have been mapped out. These may be seen in the appendix.

Although occurrences of single individuals of a species have been included in table 26.1, this has been done with reservations. One specimen of any particular form, because of the actions of natural forces and the possibility of misidentification, may not accurately indicate that that species actually lived at a site. It is necessary, however, to use most of these single individual occurrences, in order to maximize the amount of information available.

In several cases severe stratigraphic or identification problems exist, coupled with an extremely low frequency of appearance of a particular form. In these cases, data have not been included as it is simply too problematic to do so.

The first case is the one individual of *P. major* from Kirimon. There is a strong possibility that this specimen might be a misidentification (Pickford 1981). The single individuals of each *P. major* and *P. gordoni* from Rusinga constitute the second case. These are the only known representations of these species at a site dominated by *P. nyanzae* and *P. africanus*. Thus, it must be considered possible that they may be misidentifications. Furthermore, their specific site designations are unknown (Andrews 1978) and this presents a considerable problem when dealing with the complicated lithology of Rusinga Island. Since they could, in fact, have come from any horizon on Rusinga, it is probably advisable to simply exclude these specimens from further analysis. Finally, in the case of *P. major*, there is no other evidence to suggest that this form's range included any of the 5 Kisingiri sites. Thus, if it has been found at Rusinga, this would be an extremely isolated occurrence.

TABLE 26.2

MINIMUM NUMBERS OF PROCONSUL FORMS BY SITE

SPECIES	Ko	Le	Ch	So	FT	Mf	RK	RH	Ka	Ma	Lo	Na	Mo	TOT
P. africanus	1	1	2	5	2	5	4	35						55
P. nyanzae					3	3	4	41	2		1			54
P. major	1	3	3	15							1	8	2	33
P. gordoni				17		1								18
P. vancouveringi				3		1		3		1				8
TOTAL M.N.I.	2	4	5	40	5	10	8	79	2	1	2	8	2	

26.1 PROCONSUL AFRICANUS

P. africanus is limited in distribution to the Kavirondo Rift Valley sites as it has not, as yet, been discovered in any of the Northern (Uganda) locations. Based on minimum numbers *P. africanus* is the most common Proconsuline from Mfwangano and shares the highest frequency with *P. nyanzae* in the Kiahera horizon on Rusinga. In addition, *P. africanus* has been found in considerable numbers in the Hiwegi levels on Rusinga although *P. nyanzae* is more frequent there. Thus, the major finds of this form seem to centre on the Kisingiri volcano at the Western end of the Kavirondo Rift. At these Kisingiri sites, 44 of the 55 individuals of P. africanus (80%) have been found.

P. africanus is also present at the Tinderet sites, at the Eastern end of the Kavirondo Rift, but it occurs in lower frequencies here than at the Kisingiri locations. Only a total M.N.I. of 9 (excluding Fort Ternan) individuals have been recovered from the Tinderet locations. P. africanus is never the most common Proconsuline at these sites, although it shares the highest frequency with P. major at Koru (M.N.I.=1 apiece).

Based on current information it is possible to postulate that P. africanus had a home range centered on the Kisingiri area, where it occurred in great frequency. Further from this area, at Tinderet, it may have been less common. While this distribution may be an artifact of excavation, or even chance, it may also be possible that ecological differences, or competition with other forms kept this species from becoming too numerous at the Tinderet sites.

26.2 PROCONSUL NYANZAE

Apart from one, or maybe two individuals from Losidok, and the problematic remains from Fort Ternan, all the P. nyanzae fossils to date have come from the Kisingiri area. Near Kisingiri it is known from: Karungu, Mfwangano, Rusinga-Kiahera and Rusinga-Hiwegi, and at all of these sites it is either the most abundant Proconsul form or very nearly so. Thus, as was the case with P. africanus, a home range for P. nyanzae, centered on the Kisingiri volcano, may be indicated.

This notion, however, is somewhat more supportable for P. nyanzae than for P. africanus. To date this form has not been found at the Early Miocene Tinderet locations, as have all the other Proconsulines. It is reasonable to assume that had P. nyanzae been at any of the Koru locations or Songhor, some individuals likely would have been recovered. Since a M.N.I. of 51 Proconsul individuals have been recovered from these sites, the non-occurrence of P. nyanzae can probably not be attributed to excavation or identification techniques, nor to chance.

P. nyanzae is rarely found with either P. major or P. gordoni. In the latter case this is due to the fact that the only appearance of P. gordoni in an appreciable frequency is at Songhor. P. major, on the other hand, is known from 7 sites and yet is found at only one location where P.

nyanzae is also present. Furthermore, there have been problems with the primate identifications from this site, Losidok, and it is still distinctly possible that only one species, P. major is present (following Andrews 1978). Thus, it seems possible that these forms may have been sympatric only to a very limited degree. at least to a certain degree. If such a separation in ranges existed it may have been a result of competition between these two forms, an issue that will be discussed more fully in the following chapter.

Of the other Proconsulines, P. nyanzae is strongly sympatric with P. africanus. Not only do these forms co-occur at a number of sites, but they also are common at the same locations. Finally, P. nyanzae is sometimes found with P. vancouveringi, but the number of individuals and range of occurrence of this latter form is small enough to make any conclusions regarding the spatial relationship between the two species questionable.

26.3 PROCONSUL MAJOR

P. major is common at the Early Miocene Tinderet sites,and, unlike any other Proconsul form, is also common at the Northern (Ugandan) sites. It has not, as yet, been clearly identified from the Kisingiri area.

P. major has been found with all the other Proconsulines, in varying degrees. As has already been mentioned, it has almost never (or perhaps never) been found with P. nyanzae. It has been found at 4 sites with P. africanus, although only at the sites where this form is not highly frequent. P. major was clearly sympatric with P. gordoni, however, as both forms were frequent at Songhor. Finally, it has been found with P. vancouveringi, but, once again, no conclusions should be drawn from this because of the nature of the P. vancouveringi remains.

26.4 PROCONSUL GORDONI

P. gordoni has an unusual distribution. While it is the most frequent Proconsuline at Songhor (M.N.I.=17) it has been found at only one other site, Mfwangano, and even here it is extremely rare (M.N.I.=1). It must be assumed that this limited distribution is the result of chance occurrence, although it might be an indication that this form was not widespread spatially.

Since, however, *P. gordoni* is currently known from only two sites, discussion regarding its distribution, and spatial relationships with other *Proconsul* forms, must be curtailed. As was mentioned, there is a good chance that this form was strongly sympatric with *P. major*.

26.5 PROCONSUL VANCOUVERINGI

In total M.N.I., *P. vancouveringi* is less frequent than even *P. gordoni*, and, although it is fairly widely distributed, it is extremely rare in all of its occurrences. At two of the four sites at which it appears it is represented by a single individual, while at the other two sites its frequency is only slightly greater (M.N.I.=3). *P. vancouveringi* has occurred with *P. africanus* at three sites but shows no pattern of co-occurrence with any of the other *Proconsul* forms.

It is impossible to judge, at this time, if this smallest of Proconsulines was in fact less common than the other species of this genera, if it has not been found due to chance factors, or if it had a behavioral pattern that tended to preclude it from becoming fossilized.

At the present time, all that can be said is that, for whatever reason, *P. vancouveringi* occurrs only rarely in the fossil record. Because of this no firm conclusions can be reached regarding this species.

27. RELATIONSHIPS BETWEEN THE PROCONSUL SPECIES

Table 27.1 lists the total M.N.I. for each Proconsul species, as recorded in chapter 29. Table 27.2 gives the breakdowns of individuals from each species as they are found together with those from all other species, at all sites. This is expressed in terms of percentages of co-occurrence in table 27.3.

TABLE 27.1

PROCONSUL M.N.I.

SPECIES	TOTAL M.N.I.
P. africanus	55
P. nyanzae	54
P. major	33
P. gordoni	18
P. vancouveringi	8

TABLE 27.2

CO-OCCURRENCE OF PROCONSUL FORMS (MNI)

SPECIES	P. afr	P. nya	P. maj	P. gor	P. van
P. africanus n=55	-	51	22	18	7
P. nyanzae n=54	46	-	1	1	4
P. major n=33	9	1	-	17	3
P. gordoni n=18	10	3	15	-	4
P. vancouveringi n=8	45	44	15	18	-

TABLE 27.3

% CO-OCCURRENCE OF PROCONSUL FORMS (MNI)

SPECIES	P. afr	P. nya	P. maj	P. gor	P. van
P. africanus n=55	-	94.5	66.8	100	85.7
P. nyanzae n=54	84	-	3	5.5	50
P. major n=33	16.5	2	-	94.5	37.5
P. gordoni n=18	18	5.5	45.5	-	50
P. vancouveringi n=8	82	81.5	45.5	100	-

27.1 PROCONSUL AFRICANUS/PROCONSUL NYANZAE

P. africanus individuals occur with 94.5% of the P. nyanzae individuals (tables 27.2 and 27.3) while those of P. nyanzae have been found with 84% of the P. africanus individuals. The difference is due to the fact that a greater number of P. africanus individuals come from sites where P. nyanzae is not present. Thus, P. africanus/P. nyanzae does not equal P. nyanzae/P. africanus. This, of course, holds true in the analyses of each pair of Proconsul species.

The averaged percentage of co-occurrence between individuals of these two forms is 89.25%. This tends to indicate that there was a strong relationship between these two forms, based on geographical distribution and frequency of occurrence. The bulk of their agreement is due to the fact that they are both very common in the Hiwegi levels on Rusinga Island.

Since, as this analysis indicates, these forms are generally found together, they must be considered fairly strongly sympatric. On the surface, this in turn would tend to indicate that they might have had similar habitat preferences, and does not lend much support to the notion that *P. nyanzae* may have preferred more open habitats while *P. africanus* was primarily a forest dweller. It must be remembered, however, that the individuals from Rusinga Island, constituting the vast majority of the individuals of each of these forms, have been gleaned from dozens of specific sites which likely would have differed ecologically from one another, perhaps even to a considerable degree. Thus, once again, the environmental interpretation of Rusinga Island is of paramount importance.

It has been suggested here that two biomes, forest and savanna/woodland, may have existed side by side on Rusinga Island during the Early Miocene (@ 18-20 m.y.). Furthermore, it is possible that *P. nyanzae* may have preferred the more open of these two environments while *P. africanus* primarily exploited the other. Because, however, the Rusinga location, to date, has been treated as a whole, rather than as a group of sites, these two forms naturally appear, when analysed, to have been exploiting a single environment, or even habitat. With specific site locations for all of the fossils, if possible, and a good understanding of the environmental indicators from each individual site, it may be seen that these forms, while sympatric to a considerable degree, were actually utilizing quite different habitats within a limited geographic area.

27.2 PROCONSUL AFRICANUS/PROCONSUL MAJOR

The agreement between *P. africanus/P. major* is 66.8%, while between *P. major/P. africanus* it is only 16.5%: the average is 41.65%.

Both of these forms have been found at the Tinderet sites and this accounts for the agreement between them. *P. major* has not been found in the Kisingiri area where *P. africanus* is most common, and this sharply brings down the percentage of *P. africanus* individuals that have been found together with *P. major* specimens. Furthermore, just as *P. africanus* has been found frequently at the Kisingiri sites, *P. major* apparently was abundant at the Tinderet sites. Thus, in total, it may be considered that these two forms were sympatric only in a limited way.

There are two possible explanations for this limited sympatry. First, the ecological analyses of the Kisingiri and Tinderet sites indicates that there probably was a considerable amount of, at least, micro-ecological differences between them . Thus, *P. major*, the most clearly forest oriented form among the *Proconsul* species, might not have been found at the Kisingiri sites if there was a considerable amount of savanna/woodland there. Second, as will be discussed later, competition with *P. nyanzae* may have prevented *P. major* from expanding into environments West of Tinderet.

27.3 PROCONSUL AFRICANUS/PROCONSUL GORDONI

Ther agreement between *P. africanus/P. gordoni* is 100%, while between *P. gordoni/P. africanus* it is only 18%, for an average of 57%.

The pattern of co-occurrence between these two forms is almost identical to that between *P. africanus* and *P. major*. *P. gordoni*, however, is known in high frequency from only Songhor so no firm conclusions can be reached concerning the relationship between these two forms based on geographic range. On current evidence, it seems possible that these species were not strongly sympatric, although there was a certain overlap in range, as at Songhor.

27.4 PROCONSUL AFRICANUS/PROCONSUL VANCOUVERINGI

The agreement between *P. africanus/P. vancouveringi* is 85.7% while between *P. vancouveringi/P. africanus* it is 82%, for an average of 83.5%.

On the basis of this information it may be postulated that these two forms were largely sympatric. This is highly conjectural, however, as the nature of the *P. vancouveringi* remains does not allow for any firm conclusions to be drawn.

27.5 PROCONSUL NYANZAE/PROCONSUL MAJOR

The agreement between *P. nyanzae/P. major* is only 3% while between *P. major/P. nyanzae* it is but 2%, for an average of 2.5%.

This seems to be a clear indication that these two forms must be considered, on the basis of available information, to have been almost totally non-sympatric. The distribution of the *P. major* individuals centre on Tinderet, while those of *P. nyanzae* are found abundantly at the Kisingiri sites. Furthermore, *P. nyanzae* has not been found at the Early Miocene Tinderet sites where *P. major* fossils are frequent: and

P. major has not been found at the Early Miocene Kisingiri sites where P. nyanzae was common.

It is interesting to note that these are the two largest African Proconsul forms, and the fact that they have never been (conclusively) found together may indicate that they were competitors. This could in fact be an example of compatative exclusion, which is one result of competition between species. Competitive exclusion occurs when the ecological requirements of closely related species are sufficiently similar that their co-existence is unstable and their populations are forced to occupy mutually exclusive domains (Terborgh 1971).

Since, however, P. major was almost certainly a forest dweller while there are some indications that P. nyanzae may have inhabited a more open biome, their distribution might have come about as a result of ecological divergence. In this concept, if two species are competitors, eventually one, or both, will be forced to move into different ecological niches because of the competition (Mayr 1963). Such a relationship is, of course, impossible to prove in a fossil situation. Nevertheless, the separation in range between these two forms is such that it is not likely to have come about as a chance occurrence.

Admittedly, it is not entirely necessary that these two forms had to have been competitors to achieve their bi-polar distribution. Certainly, if they were simply adapted to, or preferred, different environments, they might never have been found together. That such a situation may have existed, is borne out, to a certain degree, by the ecologies of the sites where they have been found. Still, once again, that they preferred different environments might simply be an indication of competition between them, rather than a situation that arose in the absence of competitive pressure.

27.6 PROCONSUL NYANZAE/PROCONSUL GORDONI

The agreement between P. nyanzae/P. gordoni is 5.5% while between P. gordoni/P. nyanzae it is also 5.5%.

The percentage of co-occurrence between these two forms is only marginally greater that the average between P. nyanzae and P. major. The low figures are due to the fact that P. nyanzae does not occur at Songhor where 17 out of the 18 individuals of P. gordoni have been found. Once again, it may be possible that the ecologies of these two forms differed considerably from one-another, but such a conclusion must be very tentatively made in light of P. gordoni's peculiar distribution.

27.7 PROCONSUL NYANZAE/PROCONSUL VANCOUVERINGI

The agreement between *P. nyanzae/P. vancouveringi* is 50% while between *P. vancouveringi/P. nyanzae* it is 81.5% for an average of 65.75%.

While there is a fairly high rate of agreement between these two forms, this is due only to the fact that have both been found in the Hiwegi levels on Rusinga where *P. nyanzae* is very frequent. Because of the nature of the Rusinga location and the scant number of *P. vancouveringi* remains, no conclusions regarding the nature of the relationship between these two forms can be drawn at this time.

27.8 PROCONSUL MAJOR/PROCONSUL GORDONI

The agreement between *P. major/P. gordoni* is 94.5% while between *P. gordoni/P. major* it is 45.5% for an average of 69.5%.

There is a fairly high rate of agreement between these two forms but, once again, it is largely due to the fact that almost all of the *P. gordoni* individuals come from a single site, Songhor. These two species are, however, the two most abundant Proconsulines at Songhor, with M.N.I.'s of 17 (*P. gordoni*) and 15 (*P. major*) respectively. Since all of the ecological evidence thus far gained, suggests that Songhor was likely a closed forest site, it may be possible that not only were these two forms sympatric but they may also have consistently exploited similar environments.

27.9 PROCONSUL MAJOR/PROCONSUL VANCOUVERINGI

The agreement between *P. major/P. vancouveringi* is 37.5% while between *P. vancouveringi/P. major* it is 45.5% for an average of 41.5%.

The above figures indicate neither a positive nor an inverse relationship existed between these two forms, based upon their distributions and frequencies. Because of the nature of the *P. vancouveringi* sample, no further conclusions are warranted here.

27.10 PROCONSUL GORDONI/PROCONSUL VANCOUVERINGI

The agreement between P. gordoni/P. vancouveringi is 50% while between P. vancouveringi/P. gordoni it is 100% for an average of 75%.

This would tend to indicate a high degree of sympatry between them but, again, this result is largely a result of P. gordoni's distribution. These two forms appear, at least to a certain degree, to have been sympatric, but at this time it is impossible to estimate how strong the agreement between them might have been.

28. SUMMARY AND CONCLUSIONS

In this paper an attempt has been made to draw together all of the ecologically pertinant material that is available in published form concerning the East African Miocene genera Proconsul. To this end, each site at which a, or several, Proconsul species have been found, has been examined in detail in order to assess the probable environment that existed there during the Miocene.

In general terms, it was determined that sites older than 20 m.y., and younger than 18 m.y., were not clearly definable ecologically, but seemed to reflect rather open environments. Those that fell into the 18-20 m.y. bracket generally appear to have been forested. Rusinga-Hiwegi was a special case in which both facies, forest and savanna/woodland, were clearly represented in the fauna, and it was proposed that both biomes existed together, perhaps separated by a moisture gradient.

Using the assembled ecological information from these sites, the likelihood of each Proconsul species inhabiting any particular environment was examined. It was determined that P. major and P. gordoni were almost certainly forest adapted forms, P. africanus and P. vancouveringi were probably forest dwellers, and P. nyanzae may have preferred a savanna/woodland biome. These conclusions were based, not only on the determined ecologies of the sites where they were found, but also on the basis of other faunal forms that each species was typically associated with.

Further information was gained from an analysis of the few post-cranial remains that have been assigned to this genus. The forelimb of P. africanus revealed that there may have been adaptations present in this form to an arboreal lifestyle, a suggestion which tended to confirm the conclusion drawn earlier that this species was probably a forest dweller. Leg and foot bones of both P. africanus and P. nyanzae also indicated that these forms may have lived in an arboreal setting. On the other hand, an analysis of the tali and a calcaneous assigned to P. nyanzae and/or P. major revealed possible adaptations to terrestrial living, whether in an arboreal or non-forest setting. Thus, this could neither help confirm nor deny the hypothesis that P. major was a forest dweller while P. nyanzae preferred more open terrain.

Analyses of the Proconsul dentition carried out by Kay (1977) and Andrews (1982) suggested that all of the species under discussion here were forest dwellers, frugivorous (except perhaps P. gordoni), and adapted for a diet of ripe fruit only. This conclusion was found to be, for the most part, consistent with those from the other forms of analysis carried out. Several problems with the results, and especially the underlying assumptions , of both Andrews' and Kay's papers were discussed: and it was concluded that there is a possibility that their three generalized conclusions listed above may not accurately apply to all of the specific *Proconsul* species.

Finally, the distribution of all the *Proconsul* species was charted, and geographical ranges for *all* of the forms proposed. In addition to this, co-occurrence between the individuals of each species was calculated in order to determine to what extent these forms were sympatric. It was concluded that with some exceptions the forms were largely sympatric with one another, at least to some degree.

In the light of information presented in this paper several questions should be asked concerning the relationships between the various *Proconsul* species. As far as can be determined, in many ways *all* of these forms were similar: dental morphology, probable frugivorous diet, probable concentration on ripe fruit as the dietary staple, probable forest habitat for most forms and possible adaptations to a certain amount of terrestrial locomotion. Additionally, all were sympatric with at least two other *Proconsul* forms.

If all of these factors have been correctly assessed, it would be small wonder if there was competition between some of these species. One example of such a relationship might have existed between *P. nyanzae* and *P. major*. It has never been satisfactorily *been demonstrated* that these two forms were sympatric and it is within the range of possibility that they were allopatric.

Of all of the Miocene Proconsulines *P. major* is the clearest in terms of ecological preference. *It is* widely distributed at the majority of the sites that can be labelled as forest. On the other hand, there seems to be evidence to suggest that *P. nyanzae* may have preferred an open savanna/woodland biome. *The evidence* for this is:

1. Many of the forms with which it is commonly associated are non-forest species.

2. It is not commonly found, as are most of the other *Proconsul* species, with many forms that are good indicators of a forest biome.

3. It is not found, as are all of the other *Proconsul* species, at the sites that were very likely *forested*: Legetet, Chamtwara, Songhor and Napak.

4. It has been recovered from several sites, such as Karungu, which were probably non-forested.

5. It is common at Rusinga where a woodland/savanna biome probably existed side-by-side with an evergreen forest biome.

6. It has an apparently negative association with P. major, a congeneric species that probably preferred a forest habitat.

Thus, on the basis of present evidence, these two forms P. nyanzae and P. major may have been separated, not only geographically, but also ecologically.

In ecological theory, there are a number of ways in which such a distribution may have been achieved, and several of them involve competition between closely related species. First, competitive exclusion would force them to occupy mutually exclusive domains if they were competitors with extremely similar requirements. Thus, they would have had separate ranges, which they apparently may have had: but also they would each have lived in basically the same habitat that they had shared, which does not seem to have been the case here.

The theory of ecological divergence would account for both the separate ranges, and for the fact that both forms seem to have inhabited different environments as well. If two forms with similar requirements are competitors, one may be out-competed and forced into a different habitat (Mayr 1963), and thus diverge ecologically from its competitor. So it may be possible that P. nyanzae was out-competed in a forest situation and gradually began to inhabit more savanna/woodland type areas.

There is no doubt that competition for food must have been intense. Following Andrews (1981b), not only were all of the Miocene pongids frugivores, but they would also have been able to eat only ripe fruit. This means that in some cases, such as at Songhor, there would have been four Proconsul species vying for the same resource. Added to this, the other Miocene primates common in this area such as Dendropithecus and Limnopithecus were also probably frugivores (Kay 1977). Furthermore, there are a considerable number of smaller primates from the East African Miocene, and if the primitive primate diet was fruit, as has been suggested by Andrews (1981b), they would also have been in competition for this resource. Finally, there are many non-primate frugivores, primarily rodents, present in the fossil record: not to mention a number of frugivorous forms that are generally not present in the fossil record, such as bats. As Andrews (1981b) points out, in any one year fruit is a non-renewable resource, and with this many forms relying upon the same food, competition between them may be postulated.

It must be assumed that to maximize their resource utilization each species must have had a particular foraging strategy. It is probable that the most easily reached fruit would have been the first taken. As fruit in the more inaccessable areas of the trees became the primary food source, the larger _Proconsul_ forms, such as _P. major_ and perhaps _P. nyanzae_ would probably have been unable to reach it. A possible foraging strategy for the larger forms might have been to eat ripened fruit that had fallen to the ground.

It is quite certain that _P. major_, approximately the size of a female gorilla (@ 200 lbs.) was not highly mobile in the trees. Thus, it probably did much of its food gathering on the ground. This form is considerably larger than _P. nyanzae_, however, and to suggest that it competed for fruit with this latter form is highly conjectural. However, if they were competitors for a particular resource, using a particular foraging strategy, it may have resulted in one form being forced out.

In any event, On the basis of current evidence it appears as if their ranges were geographically separated, and even if food was not the critical factor, it is possible that these two forms were in competition for some limiting resource.

If _P. nyanzae_ and _P. major_ had a common ancestor, as seems likely based upon their similar morphologies, then their distribution, rather than being a result of competition, may have come about as a product of allopatric speciation. Allopatric species arise when a deme (in this case a breeding unit which could become either form) becomes separated from the parent population by a geographic barrier, and further inter-breeding between the two populations becomes impossible (Mayr 1963). Then, due to selective pressures and genetic drift, two separate species arise which are effectively unable to breed with one another.

While this would account for the apparent separation in range between these two forms, their morphological similarities, and for the fact that they may have utilized different environments, it is problematic to postulate allopatric speciation in this case. Many of the species found at the _P. nyanzae_ sites are the same forms found at the _P. major_ sites. These forms include species similar to the ones in question, for example _P. africanus_ , other primates, and a number of other forms. If a geographic barrier gave rise to two species in separate areas it would, in all likelihood, have changed the characters of the entire faunas substantially in the two regions. It is possible, however, that the removal of the geographic barriers that caused the speciation would have allowed the two separate faunas to re-integrate to a certain degree, resulting in some of the same forms being found with both nyanzae and major. In such a case, that the two species themselves did not overlap substantially in range would probably be due, once again, to competitive factors.

The fact that P. nyanzae and P. major may have been competitors has been anticipated, if several lines of evolutionary theory are followed. According to Pianka (1978), work by Elton (1948) has shown that: "fewer pairs of congeneric species will occur within any given natural community than would be found in a completely random sample from the various species and genera occurring over a broader geographic area". To Pianka this suggests that competitive exclusion would be more frequent between congeneric species than between distantly related ones. It should be remembered also that competitive exclusion (to extinction) may be considered the most final, and most unlikely result of interspecific competition (Winterhalder 1980). It would be much more likely to see competition between forms resulting in: character displacement (Brown and Wilson 1956), ecological divergence (Mayr 1963), or a repulsion interaction (Terborgh 1971).

On the basis of the distributions of the five species of Proconsul taken as a whole, there is some evidence which might suggest that some form of barrier to the E/W movement of animals existed during, at least part, of the Miocene. There is a bi-polar distribution with two Proconsul species (P. nyanzae, P. africanus) being common at the Kisingiri sites while a different pair (P. major, P. gordoni) are common at Tinderet. There does not seem to have been much interchange of Proconsul individuals between these two regions. Once again, however, this distribution may also be seen as a result of competition between some of the species involved rather than being due to geographic isolation.

There was apparently little sympatry between P. nyanzae/ P. gordoni while between P. africanus/P. gordoni there was moderately strong correspondance. As discussed earlier, however, because of the distribution of the P. gordoni individuals, this lack of sympatry is doubtful and should not be stressed as being significant. It is interesting to note, though, that all of these three forms are quite similar in size, and it is possible that either P. africanus or P. nyanzae, or both, was in competition with P. gordoni for some scarce resource.

Based on the range and frequency of appearance at the various sites, two pairs of species may be seen as both congeneric and strongly sympatric. These are: P. africanus/P. nyanzae and P. major/P. gordoni.

According to the evidence already presented, not only were the former pair similar in both size and morphology, but they may have even had a similar diet. Following Pianka (1978) it could well be expected that there would be strong competition between congeneric forms that share many characteristics, and these two species fall into this category. If they were competitors, their competition apparently did not end in the most obvious results i.e. competitive exclusion (geographic) or repulsion interaction. If they were competitors, however, their struggle may have resulted in ecological separations that were primarily non-geographical in nature. Detailed investigation of closely related congeneric forms living today have often shown that there are subtle but important ecological differences between such species. These differences usually fall into one of three types:

1. The species exploit different habitats or microhabitats (in the same area).

2. They eat different foods.

3. They are active at different times.

Thus, for P. africanus and P. nyanzae to have co-existed successfully they may have been exploiting different environments, as was suggested earlier.

In regards to P. gordoni and P. major , these forms seem to be in roughly the same situation as the preceeding pair, but because of the great size difference between them, micro-habitat and behavioral differences are much more easily postulated. While such differences will not show up in the fossil record, it is almost certain that they would have existed, and have been substantial.

Finally, it is possible that the African Proconsul species represent an adaptive radiation. If these forms, as now appears likely, had a common ancestor from which they expanded to fill unoccupied ecological niches, it would be expected that there would be a degree of distinctness in the habitats of the various species (Mayr 1963). Just because the forms are largely found together, there is no reason to believe that they had "ecologically significant overlap of niche or habitat" (Winterhalder 1980). Thus, although found together, their ecologies may have varied considerably as perhaps with P. africanus and P. nyanzae.

The models of how new species may be formed during an adaptive radiation are many and varied. The most prevalent idea, and the simplest concept, is allopatric speciation. Unfortunately, this does not necessarily satisfactorily account for how all of the Proconsul species are found with at least two congeneric forms apiece. Sympatric speciation, on the other hand, despite the fact that dozens of mechanisms have been proposed, has never really been reliably demonstrated (Mayr 1963). It is, in fact, difficult to find any mechanism whereby one form can be divided, or give rise to, five morphologically similar but distinct species, when all would inhabit a fairly restricted geographic area. Thus, one is forced to return to geographic barriers and allopatric speciation to find a model which can accurately account for the appearance of the Proconsul forms. While not apparent in the fossil record, the Proconsul forms probably arose due to geographic isolation. Later, the geographic barriers must have been removed in some manner, allowing the diverse populations to inter-mingle. By this time, however, a degree of morphological and habitat distinctness must have been achieved by each species, and inter-breeding have become impossible.

Finally, Proconsul can be seen as being a successful genus in two senses. First, it expanded to occupy new niches in the Early Miocene of Africa, and was a presence there for at least several million years. Secondly, and more importantly, it was a genus which may be seen as being a base stock for many later primates, including Homo.

29. MIOCENE HOMINOIDEA

29.1 EARLY MIOCENE AFRICAN HOMINOIDS

These forms do not exhibit heavy buttressing of the gnathic region nor do they have thick molar enamel.

1. *Proconsul* (*Proconsul*) *africanus* (Hopwood 1933)
2. *Proconsul* (*Proconsul*) *nyanzae* (Clark and Leakey 1950)
3. *Proconsul* (*Proconsul*) *major* (Clark and Leakey 1950)
4. *Proconsul* (*Rangwapithecus*) *gordoni* (Andrews 1974)
5. *Proconsul* (*Rangwapithecus*) *vancouveringi* (Andrews 1974)

29.2 MIDDLE MIOCENE EUROPEAN HOMINOIDS

The following forms exhibit neither heavy buttressing of the gnathic region nor thickening of the molar enamel.

1. *Dryopithecus fontani* (Lartet 1856)
2. *Dryopithecus laietanus* (Simons and Pilbeam 1965)

29.3 MIDDLE TO LATE MIOCENE 'RAMAPITHECINE' HOMINOIDS

These forms exhibit both heavy buttressing of the gnathic region and thickening of the molar enamel.

1. *Sivapithecus sivalensis* (1) (Lydekker 1879)
2. *Sivapithecus indicus* (Pilgrim 1910)
3. *Sivapithecus darwini* (2) (Andrews 1976)
4. *Sivapithecus meteai* (3) (Andrews and Tekkaya 1980)
5. *Bodvapithecus altipalatus* (4) (Kretzoi 1974)
6. *Rudapithecus hungaricus* (5) (Kretzoi 1974)
7. *Ouranopithecus macedoniensis* (6) (deBonis and Melentis 1977)

8. *Ankarapithecus meteai* (7) (Ozansoy 1957)
9. *Ramapithecus punjabicus* (Pilgrim 1910)
10. *Gigantopithecus blacki* (Von Koenigswald 1935)
11. *Gigantopithecus bilaspurensis* (Simons and Chopra 1969))
12. *Sivapithecus africanus* (8) (Clark and Leakey 1950)
13. *Kenyapithecus wickeri* (9) (Leakey 1962)
14. *Dryopithecus darwini* (10) (Abel 1902)
15. *Sivapithecus chinjiensis* (11) (Pilgrim 1915)
16. *Sivapithecus simonsi* (12) (Kay 1982)
17. *Australopithecus afarensis* (Johanson, White and Coppens 1978)
18. *Kenyapithecus africanus* (13) (Pickford 1982)
19. *Kenyapithecus* sp. nov. (Pickford 1982)

29.3.1 notes

(1) May be synonymous with *Ramapithecus punjabicus* (Andrews and Tekkaya 1980).

(2) May include material first designated *Dryopithecus darwini* (Abel 1902) and then assigned to *D. fontani* (Simons and Pilbeam 1965) (Andrews 1976).

(3) New species proposed for the synonymized material originally designated as *Ankarapithecus meteai* and *Ouranopithecus macedoniensis* (Andrews 1976, Andrews and Tekkaya 1980)

(4) May be synonymous with *Sivapithecus indicus* (Andrews 1976).

(5) May be synonymous with *Ramapithecus punjabicus* (Andrews 1976).

(6) See note 3.

(7) See note 3.

(8) May be synonymous with *Sivapithecus sivalensis* (Simons and Pilbeam 1965), or *Kenyapithecus wickeri* (Leakey 1967), or no known Miocene form (Andrews and Molleson 1979); or may be synonymized with *Kenyapithecus wickeri* to form *Kenyapithecus africanus* (Pickford 1982), or may be synonymous with *Kenyapithecus africanus* but distinct from *Kenyapithecus wickeri* (Pickford 1982).

(9) Is synonymous with *Ramapithecus wickeri* (Andrews 1976). May be synonymous with *Ramapithecus punjabicus* (*Simons and Pilbeam 1965*).

(10) See note 2.

(11) May be synonymous with *Sivapithecus sivalensis* (Simons and Pilbeam 1965) but Prasad (1969) maintains that it is a distinct form.

(12) sp. nov.

(13) See note 8.

30. MIOCENE HOMINOID EVOLUTION

From 1856 to the present, hundreds of primate fossils of Miocene and Pliocene age have been found on all continents of the old world. Over the years dozens of species and genera, usually considered to be members of *Dryopithecus*, were erected to represent these forms. Consequently, by 1965 the plethora of named forms was so confusing that it became necessary to take steps to alleviate the situation. This was done by Simons and Pilbeam who undertook a synthetic review of these fossils and devised a new taxonomic schema to include all of the hominoid material.

Simons and Pilbeam proposed, based upon the morphology of the fossils, that the hominoid material could adequately be contained within three genera: *Dryopithecus*, *Ramapithecus* and *Gigantopithecus*. *Dryopithecus*, they believed, could be further divided into three subgenera (*Dryopithecus*, *Proconsul*, *Sivapithecus*) containing 7 species. The latter two genera were represented by a single species apiece. All of the dryopithecine species were similar morphologically and, indeed, some were seen as being so alike that their division was primarily on geographic and temporal bases, rather than on morphological factors (as between *D.* (*P.*) *africanus* and *D.* (*D.*) *laietanus*, *D.* (*D.*) *fontani* and *D.* (*P.*) *nyanzae*, *D.* (*P.*) *major* and *D.* (*S.*) *indicus*).

Simons and Pilbeam went on to tentatively suggest that from one or more of these dryopithecine species had arisen *Pan* and *Gorilla* on one hand, and *Ramapithecus* and perhaps even later Hominids on the other. The exact phylogenetic relationships between the species defined, however, were generally left unexplored.

This view of the evolution of the Hominoidea, expressed diagramatically in Fig 30.1, held precedence for about 10 years. The period from the mid-seventies to the present, however, has been one of increased activity both in terms of new Miocene Hominoid material uncovered, and in the hypotheses presented to fit them into an adequate evolutionary framework.

By 1976 the only changes to this view of Miocene Hominoid evolution were relatively minor: new species were added to *Proconsul* (Andrews 1974), and it was proposed that *Proconsul* and *Sivapithecus* be changed from subgeneric to full generic status (Andrews 1976). Subsequently, new finds and newly proposed species have necessitated a re-evaluation of Miocene Hominoid evolution. These new forms, *Ouranopithecus macedoniensis* (de Bonis and Melentis 1977), *Sivapithecus meteai* (Andrews and Tekkaya 1980), *Sivapithecus darwini* (Andrews 1976), *Bodvapithecus altipalatus* (Kretzoi 1974) and *Rudapithecus hungaricus* (Kretzoi 1974), were of particular

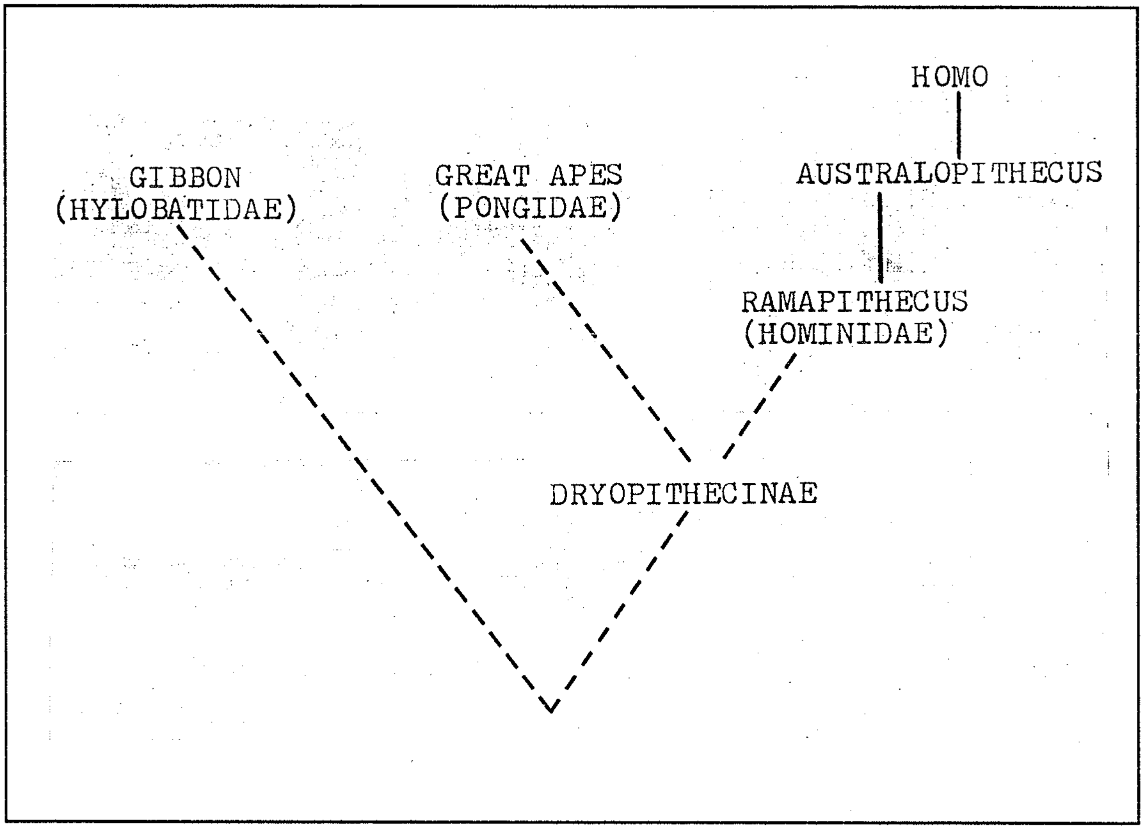

Figure 30.1: HOMINOID EVOLUTION

interest because they shared with many of the other Mid-Miocene Eurasian Hominoids (Sivapithecus, Ramapithecus, Gigantopithecus) several distinct features: a highly buttressed gnathic region and greatly thickened enamel on the molar teeth (Andrews 1976).

Using these features primarily as an index of relationship Andrews (1976) proposed that the Miocene Hominoids could be divided into 2 groups:

1. Proconsul - including Proconsul, Limnopithecus and Rangwapithecus, the early African forms, and
2. Sivapithecus - including the Mid-Miocene Asian forms Sivapithecus, Ramapithecus and Gigantopithecus. His associated diagram, fig 30.2, showed this close alignment between the above forms.

In 1977, Pilbeam et al argued for the retention of two distinct Mid-Miocene Eurasian Hominoid groups,

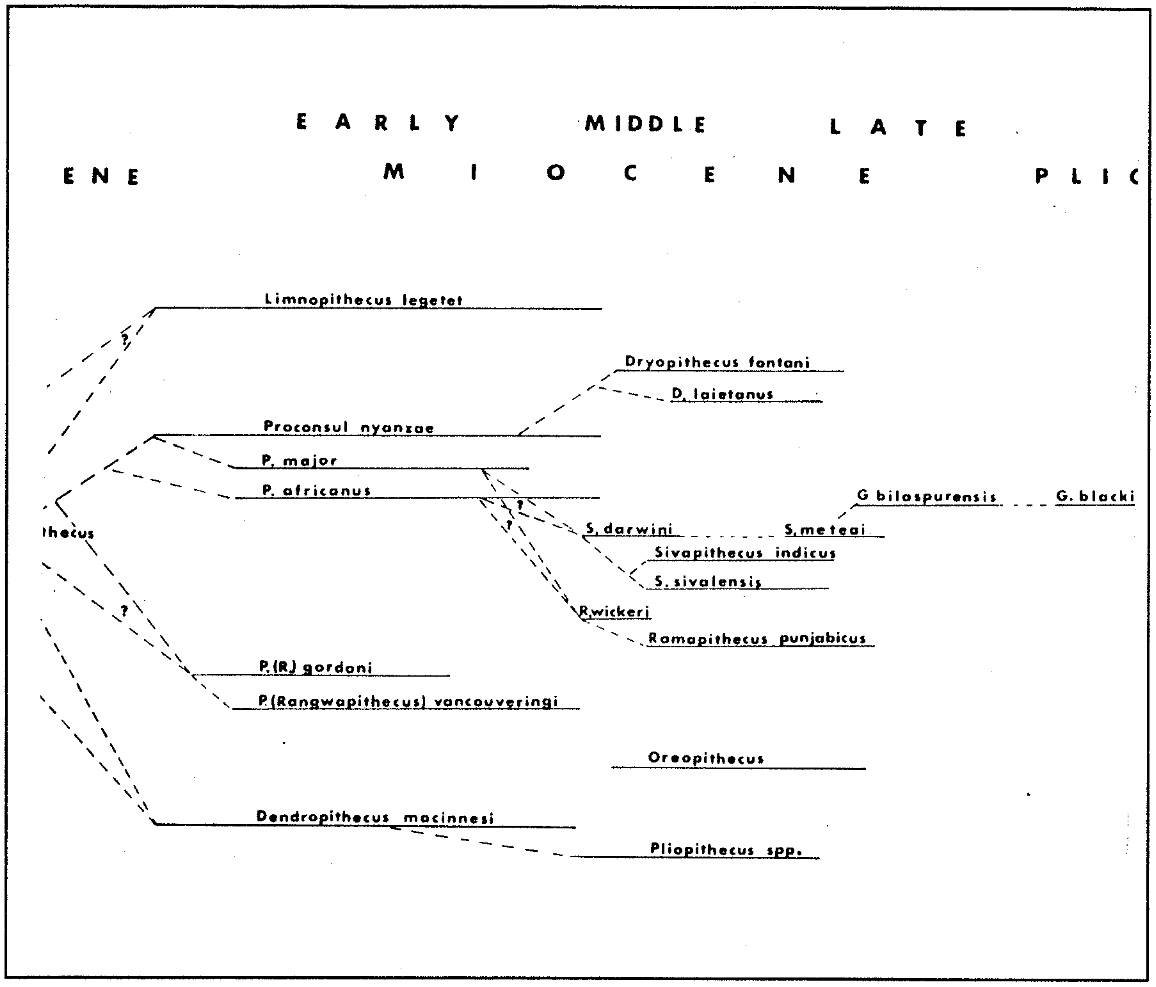

Figure 30.2: Miocene Hominoid Evolution (Andrews 1976)

the Sivapithecini and the Ramapithecini (see fig. 30.3 for their evolutionary positions), but by 1979 Pilbeam had altered his position to one similar to Andrews' (1976) (see fig. 30.4).

At the present time it seems to have been generally conceded that far from Sivapithecus and Ramapithecus being from distinct families, they probably constituted between them only a single genus (Pilbeam 1979, Greenfield 1979, 1980, Andrews 1982, Lipson and Pilbeam 1982, Kay 1981, Wolpoff 1982).

Kenyapithecus, Ankarapithecus and perhaps even Australopithecus afarensis (Wolpoff 1982) are includ-

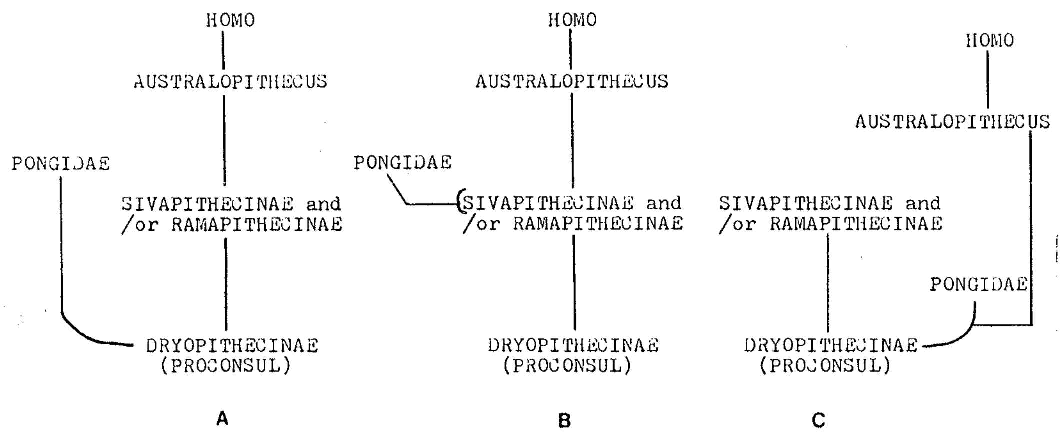

Figure 30.3: Hominoid Evolution (Pilbeam et al 1977)

ed in this group which has variously been called Ramapithecinae, Sivapithecinae, Ramapithecini, Sivapithecini, Ramapithecines and ramamorphs.

If it is accepted for the moment that all of the forms listed above do, indeed, constitute a single group, then several important questions should be raised:

1. What is the origin of this group?
2. What is its evolutionary position?
3. What is the significance of the features that join these forms together (ie. heavy molar enamel, robust gnathic regions)?

The first question raised above is basically the easiest to answer although the answer itself raises a further question. All of the recently proposed sys-

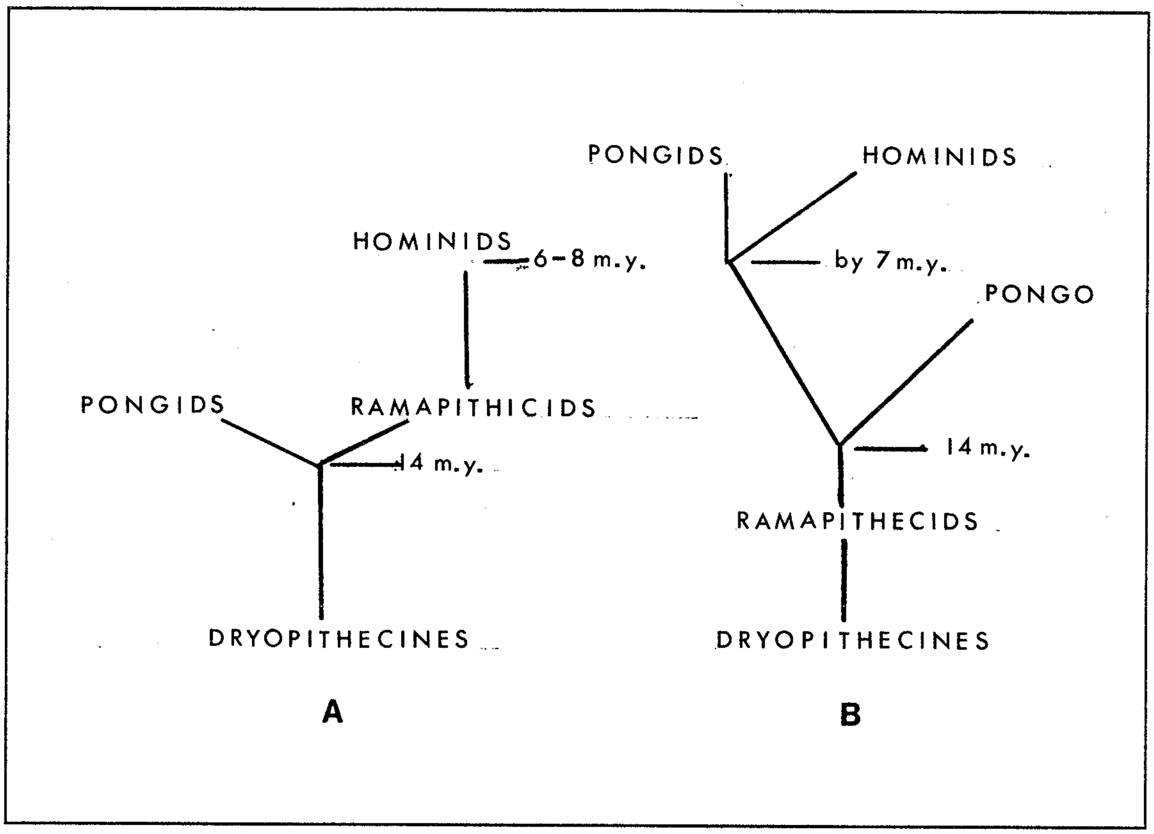

Figure 30.4: Hominoid Evolution (Pilbeam 1979)

tems of Miocene Hominoid evolution place the origin of the 'ramapithecines' somewhere within the Dryopithecinae, or more precisely, within Proconsul (Pilbeam et al 1977, Pilbeam 1979, Andrews 1976, 1978, 1982, Greenfield 1979, 1980, Pickford 1982, Lipson and Pilbeam 1982, Wolpoff 1982).

Since the first 'ramapithecines' in Africa appeared 14-12 m.y. ago, they occupy a logical temporal/geographical position to have been derived from Proconsul. Furthermore, Pickford (1982) states that it would take few changes in dental morphology, aside from those already mentioned, to derive Kenyapithecus (as represented at Majiwa and Kaloma) from Proconsul.

It is possible that a number of smaller African 'ramapithecines' (the actual number of forms represented by fossils that have been designated Kenyapithecus, Ramapithecus, and Sivapithecus in Africa is questionable) appear at about the same time (14-12 m.y.). One of these could have given rise to later Eurasian forms and thus could have been the first 'ramapithecine'. Conversely, these forms may all have been derived from an as yet unknown form, itself derived from Proconsul, which would have existed between 17-14 m.y. and would have had, presumably, some changes in dental/gnathic morphology from the Proconsul pattern.

In 1976, however, Andrews proposed a lineage of larger Hominoid forms, running from Proconsul major through Sivapithecus darwini to Sivapithecus indicus. If true this would have required a second, and independant, acquisition of the 'ramapithecine' dental/ gnathic complex by Sivapithecus darwini.

At first glance this would seem to be a doubtful proposition. In an evolutionary sense it seems more reasonable to believe that a single form developed any particular trait, or traits, and then gave rise to subsequent forms which displayed the same feature. On the basis of current evidence, however, it appears as if Sivapithecus darwini, a large form, arose in Asia at about the same time (15 m.y.) that smaller 'ramapithecines' were appearing in Africa (Andrews and Tobien 1977, Pickford 1982, Pickford and Andrews 1981). Thus, it is possible that there were two lineages present. Either of these could have given rise to the main body of 'ramapithecine' forms which subsequently appeared in Eurasia. Regardless of the 'ramapithecine' lineage, however, in either event, a (or several) Proconsul form would have been ancestral to the 'ramapithecine' group.

The second question raised above is a considerably more perplexing one. If the 'ramapithecines' do constitute a single, albeit dispersed, group; how does it fit into the larger pattern on Hominoid evolution? If it is accepted that the origin of the 'ramapithecines' lay within Proconsul then the first link of the lineage has been drawn a link that would be accepted by most researchers (i.e. Pilbeam 1979, Greenfield 1980). From this point, however, views concerning Hominoid evolution diverge considerably. The major question, of course, is: where do the lineages that eventually lead to Pongo, Pan and Gorilla, and Homo lie?

It is generally believed that the line leading to Pongo diverged at quite an early date from the line which led to Pan, Gorilla and Homo (Andrews 1982). Recent finds, especially from Pakistan and China (Pilbeam 1982) indicate that at least some of the 'ramapithecines' were morphologically (in dental, gnathic and facial regions) very similar to Pongo. This has led to the conclusion, widely held, that one of (at least) the 'ramapithecines' lies on the Pongo lineage (Greenfield 1980, Lipson and Pilbeam 1982, Andrews 1982, Wolpoff 1982, Pilbeam 1982).

For many paleoanthropologists, the origins of the Hominids and the African pongids also lies somewhere in the 'ramapithecines'. Thus, both Greenfield (1980) and Wolpoff (1982) envision a Hominid/African Pongid common ancestor arising from the 'ramapithecus' complex. The advantage of their approach is that it coincides with the belief of the molecular anthropologists whose work with serum proteins and other genetic markers has indicated that the split between these two groups may have been much more recent than most workers in the field believe, perhaps as little as 5 m.y. ago. Not only would such a "late divergence hypothesis" be consistent with the molecular evidence but it would also help to explain existing morphological similarities between Australopithecus and Pan.

The major fault with this schema, in my opinion, is that it requires forms that apparently exhibit the primitive condition in a set of dental/gnathic characters (Pan, Gorilla), to be derived from a form (a 'ramapithecine') which displayed a derived condition in regard to the same features. Not only this, but Pan's closest relatives, Australopithecus, Homo and the 'ramapithecines' would all share the derived condition (thick molar enamel, heavily buttressed jaw) while it displays the primitive (or secondarily derived) pattern. While this scenario is possible, in an evolutionary sense, it does not seem to be the most likely solution.

A second approach would be that posed by Lipson and Pilbeam (1982) (see fig 30.5). In this approach Pan and Gorilla may be derived directly from Proconsul and their lineage need not pass through a thickly enamelled dentition stage. Unfortunately, Lipson and Pilbeam's model requires the independant acquisition, from that of the 'ramapithecines', of specific dental/gnathic characteristics by Australopithecus or its direct ancestor. Thus, the dental/gnathic features in common between Australopithecus and the 'ramapithecines' would not be shared derived characters, but rather, would be convergences. While this also seems unlikely, it may be postulated that the last common ancestor of the African pongids and the Hominids, between 15 and 10 m.y. ago, was some sort of intermediate form which could have given rise to the thickly enamelled Hominids (thus resulting in convergence with the 'ramapithecines') and to the thinly enamelled Pongids. While this model does not agree completely with the molecular evidence and the late divergence theory (as explicated by Greenfield 1980) in regard to the exact timing of the Hominid/Pongid split, the difference is comparatively slight, only 3-5 million years.

The third approach is basically the model proposed by Simons and Pilbeam in 1965, which may be termed an early divergence hypothesis (see fig 30.1). This model has the lines leading to Pongo, Pan and Gorilla, and Homo essentially separate in, or shortly after, Proconsul times. Proconsul is considered ancestral to the Mid-Miocene genus Dryopithecus and later pongids on one hand, and to the 'ramapithecines' and later Hominids on the other. The thickly enamelled, gnathically robust Australopithecus and Pongo can be derived from the 'ramapithecines'. The less robust extant Pongids lie on a line which begins with Proconsul and contains Dryopithecus as an offshoot.

The major advantage of this model is that it relies upon neither convergences nor secondarily derived primitive-appearing characters to explain the morphologies of the fossils and extant forms involved. Its major fault is that it places the ape/human split at a much earlier date than the molecular evidence indicates.

A critical factor in this hypothesis is: to what degree does the available evidence link the extant Pongids to a Proconsul precursor? In the past links have been proposed between Proconsul species and Pan and Gorilla (Simons and Pilbeam 1965, Napier and Davis 1959, Pilbeam 1969). In recent times, however, this concept was challenged (see Andrews 1978) and even one of its major proponents (Pilbeam 1977) refuted it. New evidence has, once again, however, changed the picture substantially.

In the last two years or so nearly complete lower leg and foot bones attributed to both P. africanus and P. nyanzae have been discovered, the latter set in the collections of the National Museum of Kenya (Walker 1983, Pickford 1982). These bones are very ape-like in their morphology (Walker 1983) which is consistent with much of the information presented by Napier and Davis (1959) concerning the forelimb of P. africanus. Furthermore, a new reconstruction of the P. africanus cranium found by Mary Leakey in 1948 has allowed for a revised estimation of the brain size/

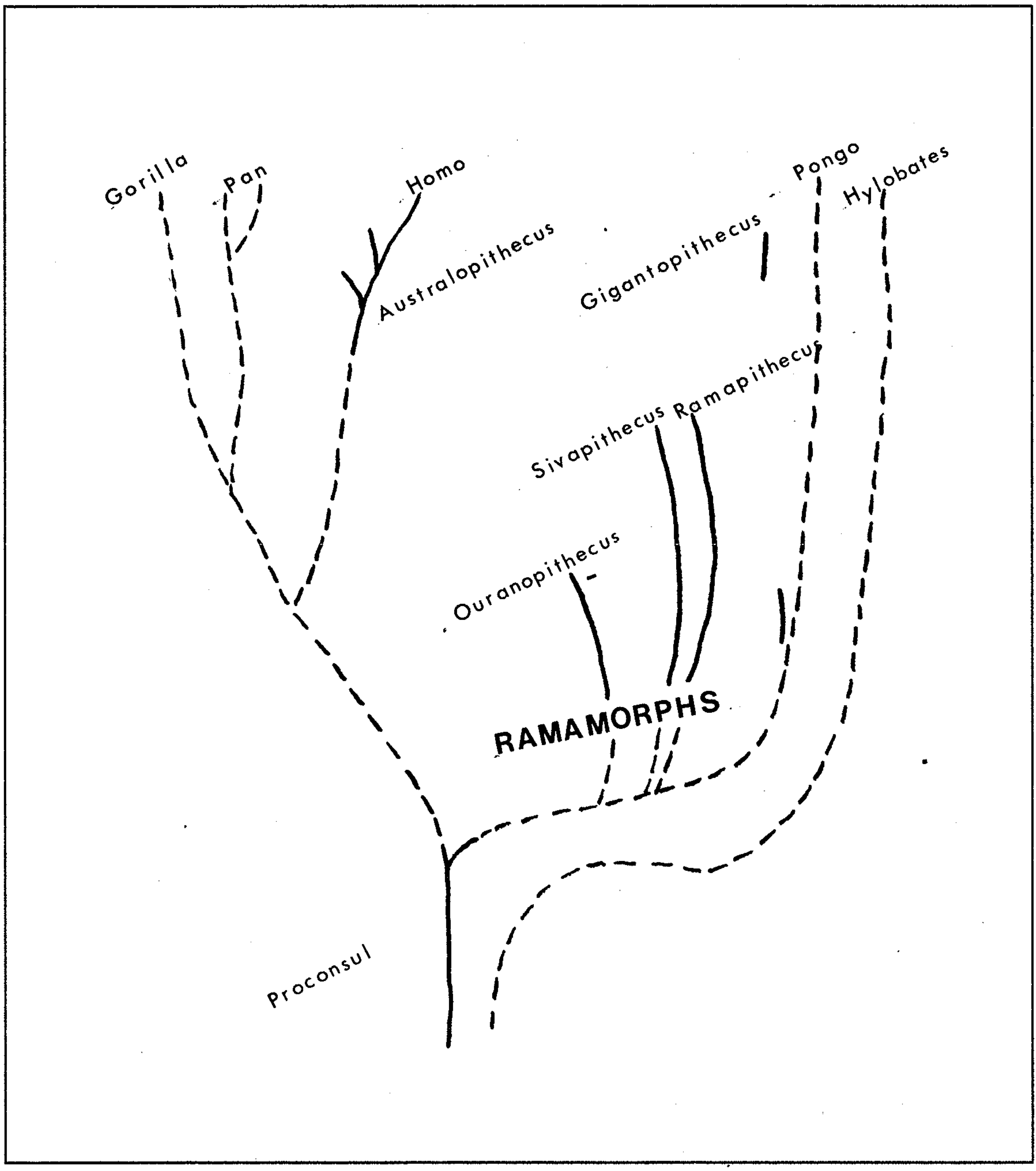

Figure 30.5: Miocene Hominoid Evolution (Lipson and Pilbeam 1982)

body weight ratio for this form, and it was found that in this regard P. africanus was essentially ape-like rather than monkey-like (Walker 1983). Thus, despite a number of similarities to Cercopithecoids in the structure of the hand, wrist and hip, it seems probable that Proconsul was at least as much like modern apes as it was like modern monkeys. For this reason a lineage leading from Proconsul to Pan can now, again, be proposed.

On the basis of the above evidence, it is my opinion that the early divergence hypothesis constitutes the most logical and rational picture of Hominoid evolution throughout the Miocene to the present. Although perhaps not for exactly the same reasons, the model proposed by Simons and Pilbeam in 1965, and recently reiterated by Pilbeam (1979) (see fig 30.4A) and Kay (1983) is again supportable.

The most logical ancestor of Australopithecus must surely have been one of the 'ramapithecines' as there are strong dental/gnathic similarities between the two groups (Greenfield 1980, Wolpoff 1982), and Pongo, in all likelihood, arose out of this group as well (Pilbeam 1982, Andrews 1982). On the other hand, the most logical ancestor of the great apes of Africa is Proconsul, or at least a Proconsul derived dryopithecine. This view can be seen in fig. 30.6.

The two major drawbacks to this schema lie in accounting for: a) the molecular evidence for a late Hominid/Pongid divergence date, and, b) the considerable number of similarities that exist between Pan and Homo. In regard to the first question raised, this monograph will follow the lead of Wolpoff (1982) and Pilbeam (1983) who state that they can accept the branching sequence (Pongo first, followed at a later date by the major Pongid/Hominid divergence) provided by the molecular method, but not the dates it provides. The molecular evidence places the Pongid/Hominid split in the 5-7 m.y. ago range, but this date is not supported by the fossil remains (Wolpoff 1982). On the basis of these remains, it may be postulated that the Pongid/Hominid split occurred between 17-14 m.y. ago (Fig. 30.6).

In regard to the second question, there is no doubt that there are considerable similarities between Pan and Homo, which must indicate some degree of affinity between these species. It must be realized, however, that both forms are known in minute detail, not only dentally, but also in terms of facial, cranial and skeletal structure. Furthermore, there is a full range of behavioral and developmental data available for both species. Thus, with this kind of information to work with, it would be very surprising to not find a number of similarities between these forms.

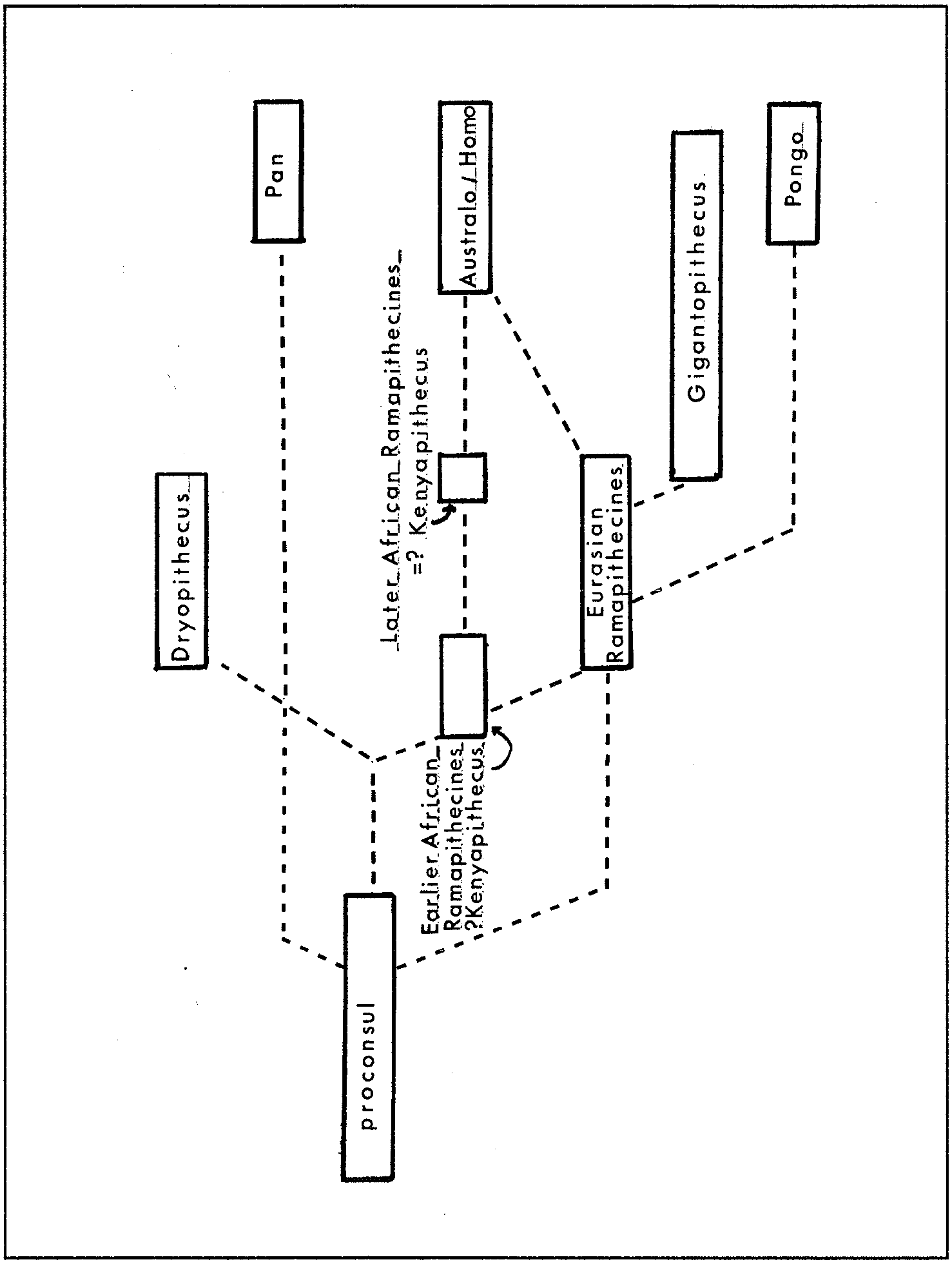

Figure 30.6: Miocene Hominoid Evolution

Furthermore, it should also be pointed out that, despite the differences between fossils that have been the focal points of most morphologically based arguments, there are a great number of similarities in the morphologies (primarily dental) of all the

Miocene Hominoids. When reading about the 'ramapithecines' one can be left with the impression that these dentally and gnathically robust forms bear almost no relationship, morphologically, to the more gracile forms such as Proconsul and Dryopithecus. In actuality, the dental morphology of all of these groups is quite similar, which is why Simons and Pilbeam grouped most of them together in 1965. For example, at this time Simons and Pilbeam were forced to assign a fossil found in 1902 by Abel (called at the time Dryopithecus darwini) to one of the dryopithecine species they were discussing. The choice actually lay between the thickly enamelled, gnathically robust large sivapithecine, Sivapithecus indicus, and the thinly enamelled, gnathically gracile medium sized European dryopithecine, Dryopithecus fontani. They placed the fossil in Dryopithecus. This fossil is now seen as being clearly 'ramapithecine' and has been used in the designation of a new, heavily buttressed, thickly enamelled large form, Sivapithecus darwini (Andrews 1976). Thus, it is plain that the dental morphologies of Dryopithecus and Sivapithecus are not wildly divergent. In point of fact, there are many dental similarities between Proconsul, Dryopithecus and many of the 'ramapithecines', and these have been discussed by Simons and Pilbeam (1965), Andrews (1978) and others.

It is my opinion that this degree of similarity amongst Miocene Hominoids, regardless of whether they likely fall on the Hominid or Pongid lineage, is simply the result of the common heritage they all share from their Proconsul ancestry. A proposition that the extant descendants (the African Pongids and man) of these forms themselves still show similarities based upon their common ancestry (common until 17-14 m.y. ago), more distant though it may be, is not unreasonable.

The third, and final, question raised above, regarding the significance of the important 'ramapithecine' dental/gnathic adaptations, may best be seen in an ecological sense since it has been proposed (Kay 1981, Wolpoff 1983) that this feature was related to a change in habitat and/or diet in a (or several) Miocene Hominoid form.

In 1981, Kay proposed a new model to explain 'ramapithecine' dental/gnathic adaptations based upon, but differing from, Jolly's "seed eaters" hypothesis (Jolly 1970). In his hypothesis Jolly argued that certain dental/gnathic (and many other) traits, such as thickened dental enamel, appeared as a consequence of a shift to a diet which required heavy grinding and chewing of food particles. He proposed that the diet of the form which developed thick dental enamel (a Hominid), was largely composed of small tough seeds which were nutritious, but hard to masticate. Unfortunately, Jolly's theory was too broadly oriented and made many assumptions concerning the relationship between morphological and behavioral traits. For example, his form, in order to acquire enough food to survive, would have had to demonstrate thumb opposability, an upright stance and bipedalism (Wolpoff 1982). A further assumption was that this form must have been terrestrial and a savanna/grassland dweller in order to collect seeds.

Kay's (1981) position is that, to arrive at the 'ramapithecine' dental/gnathic pattern it is only necessary that a dietary shift be made to foods that are hard to crack or chew. This shift need not have been to seed-eating, with its implications of terrestriality and bipedalism, but could have been to nut eating. Eating nuts would require a robust dental/ gnathic complex but would also yield a rich, nutritious and easily assimiliated food source. Such a diet would not necessarily require any assumptions as to the habitat or locomotor pattern of a nut eater, as such foods can be found in both forest and savanna habitats (Kay 1981). In this regard, however, it is Kay's belief that the 'ramapithecines' were forest oriented forms. As evidence for his "nut-eaters" theory, Kay presents Pongo and Cebus apella, both of whom eat hard nuts, have very thick dental enamel, and are forest dwellers.

While they do not agree on a 'ramapithecine' habitat affiliation, or precise diet, Jolly, Kay and Wolpoff (1982) would all agree that the 'ramapithecine' dental/gnathic adaptations resulted from a shift to a diet consisting of hard, difficult to chew objects. What these hard foods were would depend, to a large part, upon what environment the 'ramapithecines' inhabited.

The earliest 'ramapithecine' appearances occur at sites where paleoecological analysis indicates that a woodland or more open biome prevailed. The environment at Ft. Ternan was probably a woodland, and two other African sites of corresponding age, Majiwa and Kaloma (Kenya), both of which also contain 'ramapithecine' remains, had vegetation types that ranged from open to closed woodland (Pickford 1982). Thus, it is possible to support an association between the African 'ramapithecines' and a non-forest, probably woodland/savanna biome.

It is also possible, at least to a certain degree, to support a similar contention in regard to the more numerous, and more widely dispersed, Eurasian 'ramapithecines'.

The Siwalik Hills of Northern Pakistan and India have, for the last one hundred or so years, proved to be the most prolific collection area for fossils of 'ramapithecines'. Lithologically, the Siwaliks are divided into horizons, three of which contain Hominoid fossils. These are: a) Chinji @14-11 m.y. ago, b) Nagri @11-7.5 m.y. ago and c) Dhok pathan @7.5-6.0 m.y. ago (Krynine 1937, Vasishat et al 1978a, Vasishat et al 1978b, Pilbeam et al 1977a).

Chinji times, represented primarily by the important sites of Ramnagar and Chinji (Pilbeam et al 1977a), and containing fossils of Sivapithecus indicus and Sivapithecus punjabicus (S. sivalensis + Ramapithecus punjabicus) (Andrews and Tekkaya 1980, Andrews 1982), were probably dominated by rainforests and large watercourses (Krynine 1937, Vasishat et al 1978b). It has recently been speculated, however, that in the Chinji period more savanna-like conditions may have been common (Pilbeam 1979, Johnson 1977). The Chinji fauna from the site of Ramnagar is itself ambiguous and not particularly indicative of any environmental type (Vasishat et al 1978a). It is interesting to note, however, that some forms, notably Hipparion and numerous bovids, are often used in the Siwaliks as marker species differentiating Chinji (where they are not found) sites from succeeding Nagri (where they are common) locations (Pilbeam et al 1977a). Since these forms may be seen as being indicative of rather open conditions (de Bonis and Melentis 1980), it seems likely that this type of environment was not prevalent in Chinji times.

On the other hand, Nagri sites, such as Haritalyangar (India), Sethi Nagri, and those from the Khaur area seem to have been clearly woodland/savanna in nature. Pongids, equids and giraffids, including Hipparion, dominate the faunas (Badgley and Behrensmeyer 1980), which include S. indicus, s. punjabicus and Gigantopithecus bilaspurensis (Vasishat et al 1978a, Pilbeam et al 1977a, Prasad 1964). Whatever the dominant vegetative pattern was in the Chinji period, by Nagri times it seems likely that the primates present were associated with a woodland/savanna biome.

There is general agreement that the prevailing environment during Dhok pathan times was grassland

(Vasishat et al 1978a, Badgley and Behrensmeyer 1980, Tattersall 1969, Krynine 1937). Such conditions were apparently unsuitable for most 'ramapithecines' as they, with the exception of Gigantopithecus, disappear from the fauna.

Further west, the site of Rudabanya has yielded remains of 'ramapithecines' which have been named Bodvapithecus and Rudapithecus by Kretzoi (1975). The floral and faunal remains from this site are consistent with those from Nagri sites in the Siwaliks, up to and including the aquatic zonation often found in those locations (Kretzoi 1975, Badgley and Behrensmeyer 1980, Vasishat et al 1978a).

In the extreme east, remains of S. indicus have been turning up frequently (Wolpoff 1982) in recent times. The flora at the site of Lufeng (China) has both deciduous and evergreen elements, with a strong aquatic facies represented (Andrews 1981). The paleoecology is considered by Andrews (1981) to be a temperate woodland, a conclusion that is consistent with the Siwalik and European sites which have yielded S. indicus remains.

'Ramapithecine' fossils from the Sinap series in Turkey (=? Sivapithecus meteai) have been found in association with giraffids, rhinocerotids, proboscideans and Hipparion. The paleoenvironment here was likely a woodland/bushland biome (McHenry et al 1980).

From Greece, specimens of Ouranopithecus (=? S. meteai) are generally found with perissodactyls, proboscideans and artiodactyls (giraffids and bovids) (de Bonis et al 1974, de Bonis and Melentis 1980). At the site of Pikermi, Hipparion is common while the fauna at the important "Ravin de la Pluie" location is dominated by bovids (de Bonis and Melentis 1980). In short, the paleoecology of Pontian Greece was probably an open woodland possibly even verging on grassland.

Remains of a 'ramapithecine (S. darwini) from Pasalar (Turkey) are significant because of their early date (@15 m.y. ago) (Andrews and Tobien 1977). Since these may be the oldest 'ramapithecine' remains known, their paleoecological setting is crucial. Information available, however, concerning this site, is extremely provisional, and does not allow for any paleoecological reconstruction. Andrews (1981) apparently believes, though, that a woodland biome prevailed at Pasalar. If so, this would mean that virtually all of the 'ramapithecine' remains have been found in association with woodland/savanna/bushland biomes.

Returning, then, to the question of 'ramapithecine' diet; it seems likely that many of Kay's conclusions, but not his interpretation of the 'ramapithecine' habitat, can be supported by paleoecological evidence. Very little of this evidence indicates that the 'ramapithecines' were forest dwellers, but even in a woodland/savanna habitat nuts should be readily available, at least for most of the year. For the 'ramapithecines' to have specialized in other hard foods, such as grain, they probably would have inhabited more open, grassland areas. A grassland association can be supported for Gigantopithecus but not for other 'ramapithecines'.

In conclusion, it is possible to speculate, as Wolpoff (1982) has, that one, or several, Proconsul forms moved into new niches , and thus became associated with a different, non-forest habitat. One (or more) of these forms subsequently gave rise to a later, successful, adaptive radiation of associated forms (the 'ramapithecines').

It is possible that this dietary/ecological shift happened more than once as the small African 'ramapithecines' may have appeared almost contemporaneously with a large Asian form. Andrews (1976) has proposed that this earliest Asian form, Sivapithecus darwini was descended from Proconsul major. It is unlikely that the small African 'ramapithecines' would have been derived from this large proconsuline, so the smaller species of Proconsul must be considered better potential ancestors for them. Wolpoff (1982) speculates that the form ancestral to the African 'ramapithecines' was probably about the size of P. nyanzae. It is possible, based upon the paleoecological evidence presented in this paper, that Proconsul nyanzae, unlike the other proconsulines, may have been associated with non-forested, woodland/savanna/ bushland, biomes. If so, this form would be a more likely ancestor to the woodland dwelling 'ramapithecines' on two counts, size and habitat.

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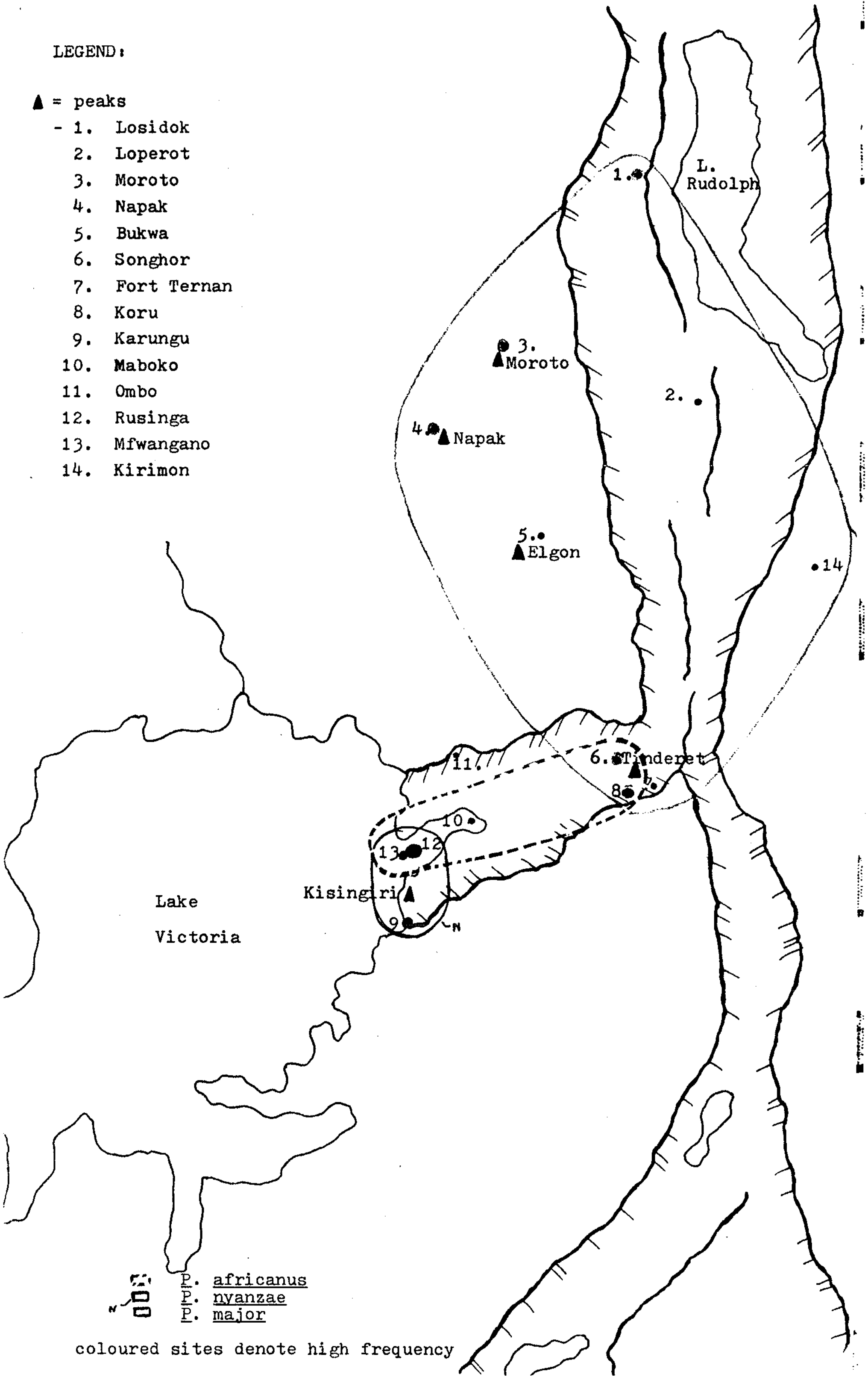
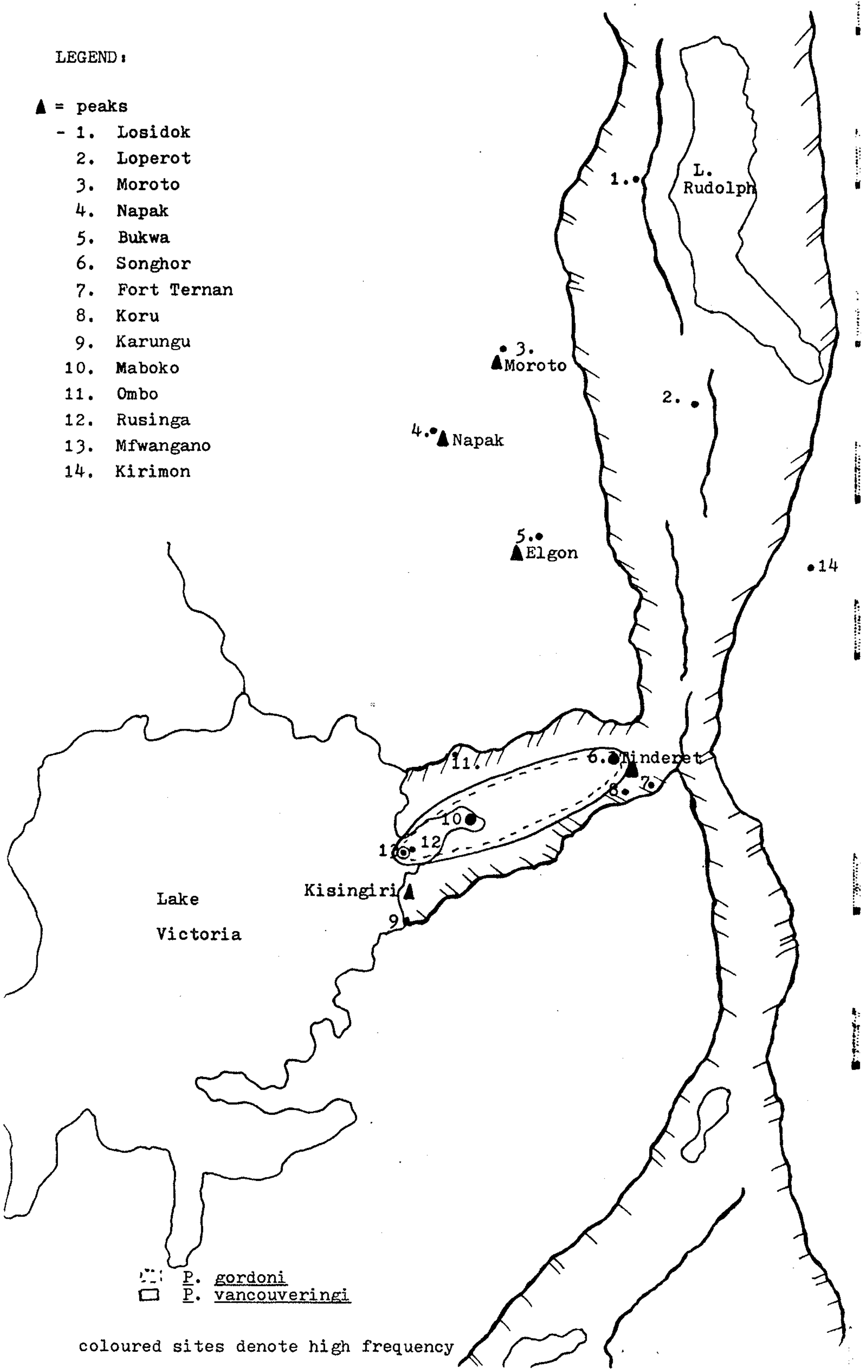
APPENDIX



coloured sites denote high frequency


LEGEND:
▲ = peaks
1. Losidok
2. Loperot
3. Moroto
4. Napak
5. Bukwa
6. Songhor
7. Fort Ternan
8. Koru
9. Karungu
10. Maboko
11. Ombo
12. Rusinga
13. Mfwangano
14. Kirimon
L. Rudolph
Moroto
Napak
Elgon
Tinderet
Kisingiri
Lake Victoria
P. gordoni
P. vancouveringi
coloured sites denote high frequency