

# A Reassessment of the Taxonomic and Phylogenetic Affinities of the Fossil Catarrhines from Fort Ternan, Kenya

TERRY HARRISON  
*New York University*

**ABSTRACT.** This paper presents a reassessment of the taxonomic and phylogenetic affinities of the fossil catarrhine primates from the important middle Miocene site of Fort Ternan in Kenya. Although the sample of specimens is rather small, the material can be attributed to at least five different species, identified here as *Kenyapithecus wickeri*, *Proconsul* sp., a large species of oreopithecoid, *Simiolus* sp., and a small species of catarrhine of indeterminate status. *Kenyapithecus wickeri* probably represents a conservative sister-taxon of the extant large hominoids. It is more derived than “*Sivapithecus*” *africanus* from Maboko Island, from which it can be distinguished at the generic level. A small species of catarrhine from Fort Ternan can be attributed to *Simiolus*. It is probably a different species from *Simiolus enjiessi* from the early Miocene of East Africa, but additional material is needed to confirm its taxonomic distinctiveness. The occurrence of at least five species of catarrhine primates at Fort Ternan confirms that species diversity levels were as high during the middle Miocene as they had been during the early Miocene. However, the overall taxonomic and ecological composition of the middle Miocene catarrhine community was quite different, evidently due to a significant change in the local ecological setting. Taxonomic differences between the catarrhine faunas at Fort Ternan and Maboko Island can probably be explained as a consequence of a chronological separation between the two sites, and, to a lesser degree, to paleoecological differences.

**Key Words:** Catarrhines; Hominoids; East Africa; Miocene; Fort Ternan; Taxonomy; Phylogenetic relationships; *Kenyapithecus*; *Simiolus*; *Proconsul*; Oreopithecoids.

## INTRODUCTION

The middle Miocene site of Fort Ternan in Kenya, the type locality of *Kenyapithecus wickeri*, has received a good deal of attention from palaeoanthropologists since it was first excavated by L.S.B. LEAKEY in 1961. During the 1960s and 1970s *Kenyapithecus wickeri* was considered to be closely related to, and possibly even synonymous with, the purported early hominid *Ramapithecus* from the Siwalik Hills of Indo-Pakistan. However, by the early 1980s, *Kenyapithecus* had suffered the same fate as its Asian counterpart, and was deplored as a potential candidate for human ancestry (see WOLPOFF, 1983). Nevertheless, the paucity of hominoid-bearing sites from the later part of the Miocene in Africa, especially those as well-dated as Fort Ternan, and with faunas as intensively studied, has meant that the site has remained one of the most important Neogene localities in sub-Saharan Africa. In recent years, with the cessation of active fieldwork at Fort Ternan, the focus of interest has shifted away from the study of the fossil primates themselves, to one encompassing more broad-based attempts to understand the paleoecology at Fort Ternan and its significance for interpreting changes in the catarrhine community structure in East Africa during the Miocene (e.g. ANDREWS & NESBIT EVANS, 1979; SHIPMAN et al., 1981; SHIPMAN, 1986; PICKFORD, 1983a, 1985a, 1986a, 1987; KAPPELMAN, 1991).

---

**Table 1.** A catalogue of fossil catarrhines from Fort Ternan<sup>a)</sup>.

Accession No.	Specimen	Taxon	Previous references <sup>b)</sup>
KNM-FT 7	Right mandibular fragment with P <sub>4</sub> -M <sub>1</sub> . Dentition damaged and worn.	<i>K. wickeri</i>	<i>R. wickeri</i> (5,6) <i>K. wickeri</i> (8)
KNM-FT 8	Left C <sup>1</sup> germ preserved in a maxillary fragment. ♀	<i>K. wickeri</i>	<i>R. wickeri</i> (6) <i>K. wickeri</i> (8)
KNM-FT 11	Left I <sup>1</sup> . Unworn; slightly abraded.	Indet. sp.	cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 12	Edentulous mandibular symphysis.	Indet. sp.	cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 13	Edentulous mandibular symphysis of an immature individual.	<i>Simiolus</i> sp.	
KNM-FT 14	Left mandibular fragment of an immature individual with M <sub>1</sub> exposed in its crypt.	<i>Simiolus</i> sp.	cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 15	Left C <sup>1</sup> . Worn. ♀	Indet. sp.	cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 16	Left M <sup>1</sup> . Slightly worn.	<i>Proconsul</i> sp.	<i>Dryopithecus</i> cf. <i>africanus</i> (6) <i>P. africanus</i> (7) <i>?P. africanus?</i> (8)
KNM-FT 17	Left M <sub>1</sub> . Unworn.	Indet. sp.	cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 18	Right P <sub>4</sub> .	Indet. sp.	cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 19	Left M <sup>3</sup> . Moderately worn.	<i>Simiolus</i> sp.	cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 20 <sup>c)</sup>	Left mandibular fragment with C <sub>1</sub> -M <sub>3</sub> . Dentition moderately worn. ♀	<i>Simiolus</i> sp.	cf. <i>Limnopithecus</i> (3) cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 21 <sup>c)</sup>	Right M <sub>2</sub> . Moderately worn.	<i>Simiolus</i> sp.	cf. <i>Limnopithecus</i> (3) cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 23 <sup>c)</sup>	Right M <sub>3</sub> . Moderately worn.	<i>Simiolus</i> sp.	cf. <i>Limnopithecus</i> (3) cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 24 <sup>c)</sup>	Right P <sub>4</sub> . Moderately worn.	<i>Simiolus</i> sp.	cf. <i>Limnopithecus</i> (3) cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 25 <sup>c)</sup>	Right I <sub>2</sub> . Slightly worn.	<i>Simiolus</i> sp.	cf. <i>L. legetet</i> (6) <i>L. legetet</i> (7)
KNM-FT 28	Right C <sub>1</sub> . Unerupted. ♂	<i>K. wickeri</i>	<i>Dryopithecus</i> cf. <i>nyanzae</i> (6) <i>P. nyanzae</i> (7) <i>K. wickeri</i> (8)
KNM-FT 29	Left P <sup>3</sup> . Slightly worn.	<i>Proconsul</i> sp.	<i>Dryopithecus</i> cf. <i>africanus</i> (6) <i>P. africanus</i> (7) <i>?P. africanus?</i> (8)
KNM-FT 34	Left M <sub>3</sub> . Heavily worn.	<i>K. wickeri</i>	<i>Dryopithecus</i> cf. <i>nyanzae</i> (6) <i>P. nyanzae</i> (7) <i>K. wickeri</i> (8)
KNM-FT 35	Right P <sub>3</sub> . Slightly worn; damaged.	<i>K. wickeri</i>	<i>Dryopithecus</i> cf. <i>nyanzae</i> (6) <i>P. nyanzae</i> (7) <i>K. wickeri</i> (8)
KNM-FT 36	Right M <sup>1</sup> . Badly weathered.	Oreopithecid	cf. <i>Oreopithecus</i> (3) Suidae (6) <i>Oreopithecus</i> sp. (9)

(continued)

Table 1. (continued)

Accession No.	Specimen	Taxon	Previous references <sup>b)</sup>
KNM-FT 37	Right P <sup>4</sup> . Moderately-heavily worn.	Oreopithecid	cf. <i>Oreopithecus</i> (3) Suidae (6) <i>Oreopithecus</i> sp. (9)
KNM-FT 38	Right M <sub>3</sub> . Badly weathered.	Oreopithecid	cf. <i>Oreopithecus</i> (3) Suidae (6) <i>Oreopithecus</i> sp. (9)
KNM-FT 39	Right C <sup>1</sup> . Moderately-heavily worn. ♂	<i>K. wickeri</i>	<i>Dryopithecus</i> cf. <i>nyanzae</i> (6) <i>P. nyanzae</i> (7) <i>K. wickeri</i> (8)
KNM-FT 40	Right M <sub>3</sub> in mandibular fragment. M <sub>3</sub> heavily worn and damaged.	<i>K. wickeri</i>	<i>Dryopithecus</i> cf. <i>nyanzae</i> (6) <i>P. nyanzae</i> (7) <i>K. wickeri</i> (8)
KNM-FT 41	Left C <sup>1</sup> . Slightly worn; tip of crown missing. ♂	Indet. sp.	<i>Dryopithecus</i> cf. <i>africanus</i> (6) cf. <i>Rangwapithecus</i> <i>gordoni</i> (8)
KNM-FT 45	Left mandibular fragment with P <sub>3</sub> -P <sub>4</sub> . Dentition slightly to moderately worn.	<i>K. wickeri</i>	cf. <i>Dryopithecus</i> (3) <i>R. wickeri</i> (4,6) <i>K. wickeri</i> (8)
KNM-FT 46a <sup>d)</sup>	Left maxilla with P <sup>4</sup> -M <sup>2</sup> . Dentition slightly worn.	<i>K. wickeri</i>	<i>K. wickeri</i> (1,8) <i>R. wickeri</i> (6)
KNM-FT 46b <sup>d)</sup>	Left C <sup>1</sup> . Moderately worn. ♀	<i>K. wickeri</i>	<i>K. wickeri</i> (1) <i>R. wickeri</i> (6) ? <i>K. wickeri</i> (8)
KNM-FT 47 <sup>d)</sup>	Right maxilla with M <sup>1</sup> -M <sup>2</sup> . Dentition slightly worn; M <sup>1</sup> damaged.	<i>K. wickeri</i>	<i>K. wickeri</i> (1,8) <i>R. wickeri</i> (6)
KNM-FT 48 <sup>d)</sup>	Right M <sub>1</sub> . Slightly worn.	<i>K. wickeri</i>	<i>K. wickeri</i> (1,8) <i>R. wickeri</i> (6)
KNM-FT 49	Left I <sup>1</sup> . Unerupted.	<i>K. wickeri</i>	<i>K. wickeri</i> (2,8) <i>Dryopithecus</i> cf. <i>nyanzae</i> (6) <i>P. nyanzae</i> (7)
KNM-FT 2751	Right distal humerus.	Indet. sp.	<i>Dryopithecus</i> cf. <i>nyanzae</i> (6) <i>P. nyanzae</i> (7) <i>Kenyapithecus?</i> (10)
KNM-FT 3381	Right proximal ulna.	Indet. sp.	hominoid? (10)
KNM-FT 3636	Left C <sub>1</sub> . Heavily worn. ♀	<i>K. wickeri</i>	<i>K. wickeri</i> (8)
KNM-FT 3637	Right I <sup>2</sup> . Slightly worn.	<i>K. wickeri</i>	<i>K. wickeri</i> (8)
KNM-MB 124 <sup>e)</sup>	Left I <sub>2</sub> in a mandibular fragment. Crown slightly worn.	<i>Simiolus</i> sp.	
KNM-SO 1102 <sup>e)</sup>	Right C <sub>1</sub> . Slightly worn. ♀	<i>Simiolus</i> sp.	<i>L. legetet</i> (7)

a) Several specimens previously identified as fossil catarrhines from Fort Ternan are excluded from this list: KNM-FT 22 is now missing from the collections of the National Museums of Kenya; KNM-FT 3318, a right dC<sub>1</sub>, is almost certainly from the early Miocene locality of Songhor, rather than Fort Ternan, and can be attributed to *Proconsul major* (see also PICKFORD, 1985a); KNM-FT 3376, an isolated incisor, does not belong to a primate; b) the numbers in parentheses refer to the following primary references: (1) LEAKEY, 1962; (2) LEAKEY, 1967; (3) LEAKEY, 1968; (4) ANDREWS, 1971; (5) WALKER & ANDREWS, 1973; (6) ANDREWS & WALKER, 1976; (7) ANDREWS, 1978; (8) PICKFORD, 1985a; (9) HARRISON, 1986; (10) SENUT, 1989; c) KNM-FT 20, 21, 23, 24, 25, KNM-MB 124, and KNM-SO 1102 are almost certainly attributable to a single individual; d) KNM-FT 46a and KNM-FT 47 are clearly attributable to a single individual. However, the isolated canine, KNM-FT 46b, which is usually associated with KNM-FT 46a, is more likely to represent a different individual based on its differential preservation and its more pronounced degree of wear (see also PICKFORD, 1985a). KNM-FT 48 was considered by LEAKEY (1962) to belong to the same individual, but there is insufficient evidence to support such a claim (see also PICKFORD, 1985a); e) KNM-MB 124 and KNM-SO 1102 have been wrongly accessioned as having been recovered from Maboko and Songhor respectively. They are quite evidently associated with KNM-FT 20-25.

The intention of this paper is to provide an updated assessment of the taxonomic and phylogenetic status of the fossil catarrhine primates from Fort Ternan. In addition to *Kenyapithecus wickeri*, several other species of catarrhines have been identified from the small sample of fossil primates available. Although no new specimens have been recovered from Fort Ternan since the last expedition to the site in 1974, new discoveries from other Miocene localities in East Africa, as well as changes in our appreciation of the evolutionary history of Miocene catarrhines in general over the past few years, have necessitated a reinterpretation of the fossil primates from the site. In addition to simply providing an updated taxonomy of the Fort Ternan primates, the results of this study have wider implications for understanding the phylogenetic, biogeographical, and ecological relationships of the catarrhine primates in East Africa during the middle Miocene.

#### THE FOSSIL CATARRHINES FROM FORT TERNAN

During the course of excavations at Fort Ternan, between 1961 and 1974, a total of 38 catarrhine primates was recovered from the site (Table 1)<sup>1)</sup>. These can be attributed to at least five different species, identified here as *Kenyapithecus wickeri*, *Proconsul* sp., a large species of oreopithecoid, *Simiolus* sp., and a species of small catarrhine primate of uncertain affinity. Most of the individual specimens discussed here have been described in previous publications (LEAKEY, 1962, 1967, 1968; ANDREWS, 1971, 1978; WALKER & ANDREWS, 1973; ANDREWS & WALKER, 1976; PICKFORD, 1985a; HARRISON, 1986; see Table 1), so no further detailed descriptions are required.

#### *Kenyapithecus wickeri*

The hypodigm of *Kenyapithecus wickeri* LEAKEY, 1962 currently comprises 15 craniodental specimens, all derived from Fort Ternan, of which the majority are isolated teeth (Table 1). Detailed descriptions and good illustrations of the most important specimens have been presented previously by ANDREWS and WALKER (1976) and by PICKFORD (1985a). The convoluted taxonomic history of *Kenyapithecus* (LEAKEY, 1962, 1967, 1968; SIMONS, 1963, 1969, 1972; SIMONS & PILBEAM, 1965; PILBEAM, 1969; ANDREWS, 1971, 1973, 1978; AGUIRRE, 1975; CONROY & PILBEAM, 1975; FRAYER, 1976; ANDREWS & WALKER, 1976; GREENFIELD, 1979; SZALAY & DELSON, 1979; MADDEN, 1980) has been succinctly summarized elsewhere (ANDREWS & MOLLESON, 1979; PICKFORD, 1985a).

The purported sister-species to *K. wickeri*, "*Sivapithecus*" *africanus* LE GROS CLARK and LEAKEY, 1950 (commonly included in the genus *Kenyapithecus*), from the middle Miocene localities of Maboko Island, Majiwa and Kaloma<sup>2)</sup>, is now much better known than the type species (PICKFORD, 1982, 1985a, b, 1986b, c; BENEFIT & MCCROSSIN, 1989). Further recent discoveries of *Kenyapithecus* have been reported from other middle Miocene sites

1) Abbreviations used in the text and Tables are as follows: FT: Fort Ternan; KNM: National Museums of Kenya; KR: Kapsibor; M: British Museum Natural History, London; MB: Maboko Island; MJ: Majiwa and Kaloma; SO: Songhor; WK: Kalodiri.

2) The type specimen of *Sivapithecus africanus* (M 16649) was identified by LE GROS CLARK and LEAKEY (1950, 1951) to have been recovered from Rusinga Island, although, in the initial description of the specimen, MACINNES (1943) made no reference to a specific locality. However, there is good circumstantial evidence to support the contention that M 16649 was, in fact, recovered from Maboko Island, rather than Rusinga Island (ANDREWS & MOLLESON, 1979).

in Kenya, including Emuruilem in the Samburu Hills (PICKFORD, 1983b, 1986c; ISHIDA et al., 1984), Kaimogool North and Chepetet West, Nyakach (PICKFORD, 1986d) and Muruyur in the Baringo Basin (PICKFORD, 1988; BROWN et al., 1991), but no detailed information on this material is yet available. Preliminary reports suggest, however, that the material is morphologically most similar to "*Sivapithecus*" *africanus* from Maboko Island. Clearly, a reassessment of the taxonomic and phylogenetic status of *Kenyapithecus* must await the detailed comparison of these extensive new collections. In the meantime, however, it is worthwhile here to report briefly on my own analysis of the *K. wickeri* material.

The most recent review of the status of *Kenyapithecus* has been presented by PICKFORD (1982, 1985a, b, 1986b, c), and a number of important conclusions reached by him have been confirmed by the present study. These are as follows: (1) *Kenyapithecus* is best regarded as a valid genus, morphologically distinct from the more conservative *Proconsul*, as well as from the Eurasian genera, *Dryopithecus* and *Sivapithecus* (= *Ramapithecus*), with which it has been commonly synonymized; (2) all of the specimens from Fort Ternan previously attributed to *Proconsul nyanzae* (ANDREWS & WALKER, 1976; ANDREWS, 1978) can more appropriately be assigned to *K. wickeri*; (3) *K. wickeri* is strongly sexually dimorphic, at least in canine size and morphology; (4) *K. wickeri* is specifically distinct from "*S.*" *africanus*, and may even require separation at the generic level; and (5) *K. wickeri* appears to be more specialized cranio-dentally than "*S.*" *africanus*, with the former possibly sharing significant synapomorphies with modern large hominoids.

The last two of these conclusions imply that a major rethinking of the taxonomic and phylogenetic position of *Kenyapithecus* is called for. However, the implications of these findings have been largely overlooked by subsequent workers, who have preferred to recognize *K. wickeri* and "*S.*" *africanus* as congeneric (or even conspecific), and to regard *Kenyapithecus* as a conservative thick-enamelled large hominoid of uncertain affinities (KELLEY & PILBEAM, 1986; MARTIN, 1986; ANDREWS & MARTIN, 1987; DELSON, 1988; ANDREWS, 1988). Although I agree with PICKFORD that the inadequacy of the material dictates an element of caution in making phylogenetic statements about *Kenyapithecus*, I feel that there is sufficient evidence to confirm the conclusions outlined above, and even to develop them one step further.

The major differences in the dentition and lower facial morphology between the material from Fort Ternan and Maboko certainly provide justifiable grounds for a taxonomic separation between them (see Table 2 for details). The nature and distribution of the differences effectively rules out the possibility that they can be explained as the result of individual variation or sexual dimorphism (*contra* GREENFIELD, 1979; KAY & SIMONS, 1983). In my view, the differences, especially in the lower facial morphology, are profound enough to merit a generic separation between *Kenyapithecus wickeri* and "*Sivapithecus*" *africanus*. A more precise statement of their taxonomic status and affinities will have to await detailed comparisons with other Miocene hominoids, especially the thick-enamelled hominoids from Turkey and Central Europe (ABEL, 1902; STEININGER, 1967; ANDREWS & TOBIEN, 1977; ALPAGUT et al., 1990). Nevertheless, some preliminary conclusions can be presented here that may help in resolving the relationships of *Kenyapithecus wickeri*.

*Kenyapithecus wickeri* and "*Sivapithecus*" *africanus* share a number of derived characters that serve to distinguish them from the more conservative pattern seen in *Proconsul*. These include a relatively thick mandibular corpus, a mandibular symphysis with a well-developed inferior transverse torus, large and quite narrow upper premolars with the

---

**Table 2.** Morphological characters distinguishing *Kenyapithecus wickeri* from "*Sivapithecus africanus*".

Element	Specimens	Distinguishing features of <i>K. wickeri</i>
I <sup>1</sup>	FT 49	Relatively broader and lower-crowned; more pronounced lingual cingulum; lack of a distinct lingual pillar; more deeply furrowed lingual face.
I <sup>2</sup>	FT 3637	Relatively broader; more coarsely wrinkled lingual surface.
C <sup>1</sup>	FT 8, 39, 46b	Larger in females (the basal area of FT 46b is 25% larger than the largest female canine from Maboko); crown less bilaterally compressed.
P <sup>4</sup>	FT 46a	Relatively slightly broader; better-defined transverse crests linking the paracone and protocone; no lingual cingulum; less-complex wrinkling of the enamel surface.
Upper molars	FT 46a, 47	Taper slightly distally, giving the crown a more trapezoidal (rather than rectangular) shape; relatively narrower (the length-breadth proportions for M <sup>1</sup> and M <sup>2</sup> are 95.5 and 99.2 respectively, while those from Maboko range from 87.6–94.7 and 90.7–92.6 respectively); lack of secondary wrinkling; almost complete suppression of the lingual cingulum; slightly larger average size.
C <sub>1</sub>	FT 28, 3636	Female canines slightly larger in size.
Lower molars	FT 7, 34, 48	Slightly larger in size; relatively narrower (at least in M <sub>1</sub> ); M <sub>3</sub> hypoconulid arranged more in line with other buccal cusps.
Maxilla	FT 46a, 47	Root of the zygomatic process originates higher on the face, and is more strongly laterally flaring and upwardly sweeping; canine fossa more distinct; maxilla much less pneumatized in the region above the premolars; maxillary sinus more elevated, with its floor situated well-above the apices of the molar roots; palate relatively deeper.

\*For a more detailed discussion of many of these features, see ANDREWS and WALKER (1976), WARD and PILBEAM (1983), KAY and SIMONS (1983), and PICKFORD (1985a, 1986c).

paracone only slightly more elevated than the protocone, molars with thick enamel, low occlusal relief and reduced development of the cingula. However, this combination of shared derived features is also seen in other later Miocene hominoids, such as *Sivapithecus*, *Gigantopithecus*, *Lufengpithecus*, and *Ouranopithecus*, as well as in early hominids, and may possibly represent a suite of features primitively retained from the ancestral large hominoid morphotype (MARTIN, 1983, 1986; ANDREWS & MARTIN, 1987).

While "*Sivapithecus africanus*" retains some conservative traits in its molar morphology and facial pattern that more closely approximates the more generalized catarrhine morphology exemplified by *Proconsul*, *K. wickeri* has developed some distinctive specializations which it shares with later large hominoids. As noted by a number of authors, the dentition of *K. wickeri* is very similar to that of *Sivapithecus* from the Siwalik Hills (PILBEAM, 1969; SIMONS, 1981; KAY & SIMONS, 1983; KELLEY & PILBEAM, 1986), and it is difficult to identify consistent characters that would serve to distinguish them. Moreover, *K. wickeri* shares the distinctive derived upper canine morphology of *Sivapithecus*, in which the root is more medially inclined, externally rotated and quadrangular in cross-section (ANDREWS & WALKER, 1976; WARD & PILBEAM, 1983; PICKFORD, 1985a). In the placement and orientation of the zygomatic process of the maxilla, the presence of a well-developed canine fossa, the lack of pneumatization of the anterior alveolar region of the maxilla, the configuration of the maxillary sinus and the depth of the palate, *K. wickeri* conforms closely to the derived pattern typical of *Sivapithecus* and *Pongo*. It seems likely that these specializations in facial morphology in *K. wickeri* relate to increasing the robusticity of the maxilla in the region of the cheekteeth and to improving the mechanical effectiveness of the masticatory musculature, both associated functionally with powerful chewing. Although the derived hominoid features shared by *K. wickeri* and *Sivapithecus*

may possibly be interpreted as functional convergence, it seems most parsimonious at present to assume that the detailed similarities in the dentition and facial morphology are homologous. These shared characteristics could be used to support the claim that *Kenyapithecus* represents a conservative member of the *Pongo-Sivapithecus* clade. However, it would appear more likely, based on comparisons with other extant hominoids, that the features shared by *Kenyapithecus* and *Sivapithecus* are, in fact, primitive retentions from the ancestral large hominoid morphotype (see also BROWN & WARD, 1988). Clearly, more detailed comparisons between *Kenyapithecus* and other later Miocene large hominoids, such as *Ouranopithecus*, *Dryopithecus*, and *Lufengpithecus* are needed in order to resolve this issue. At present, I would favor retaining *Kenyapithecus* as a distinct genus that represents the conservative sister-taxon of the extant large hominoids. "*Sivapithecus*" *africanus*, which appears to share only primitive traits with the latter clade, should therefore be included in a separate genus. However, the decision over the correct taxonomic status of "*S.*" *africanus* must await careful comparative studies of the Maboko material with the samples from Pasalar in Turkey and the conservative thick-enamelled hominoids from the Vienna Basin (ABEL, 1902; STEININGER, 1967; ALPAGUT et al., 1990).

#### *Proconsul* sp.

A number of workers have noted that several isolated teeth from Fort Ternan are similar in their morphology to the corresponding teeth of *Proconsul africanus*, and that they may be attributed provisionally to this species (LEAKEY, 1968; ANDREWS & WALKER, 1976; ANDREWS, 1978; PICKFORD, 1985a, 1986b). My comparisons confirm that at least two isolated teeth, a left M<sup>1</sup> (FT 16) and a left P<sup>3</sup> (FT 29) are morphologically and metrically consistent with *Proconsul africanus* from the early Miocene of East Africa. The upper molar can be distinguished from those of *K. wickeri* in retaining a well-developed lingual cingulum and what appears to be relatively thin enamel, while the premolar exhibits such conservative traits as a relatively broad crown and a marked difference in height between the protocone and paracone. Clearly, these teeth belong to a medium-sized proconsulid rather than *Kenyapithecus*, but beyond this there is insufficient evidence to provide a reasonable basis for the assessment of their specific affinities. They are certainly most like the early Miocene species *Proconsul africanus*, but as the hypodigm of this latter taxon is currently in a state of flux (KELLEY, 1986; KELLEY & PILBEAM, 1986; PICKFORD, 1986; TEAFORD et al., 1988; WALKER & TEAFORD, 1988, 1989; RUFF et al., 1989; CAMERON, 1991), it may be preferable to consider the Fort Ternan specimens as belonging to an indeterminate species of *Proconsul*.

#### Oreopithecids

LEAKEY (1967, 1968, 1969) noted the presence of a large species of oreopithecid at Fort Ternan, based on three isolated teeth, a right M<sup>1</sup> (FT 36), a right P<sup>4</sup> (FT 37), and a right M<sub>3</sub> (FT 38). LEAKEY suggested that the specimens closely resembled *Oreopithecus bambolii* from the late Miocene of Italy, and tentatively referred the material to the same genus. Additional comparisons by SIMONS (1969, 1972) led him to conclude that the Fort Ternan material may even be attributable to the same species as the European taxon. However, the occurrence of oreopithecids at Fort Ternan was contested by later workers, who concluded that the specimens probably belonged to a suid (ANDREWS & WALKER, 1976). A re-examination of the material by the author has confirmed earlier assessments that these specimens do in fact represent isolated teeth of an oreopithecid primate

---

(HARRISON, 1986). In addition, a single isolated upper molar (KR 9755) recovered by PICKFORD at the neighboring and contemporaneous locality of Kapsibor (HARRISON, 1986; PICKFORD, 1986d) provides additional evidence that a large oreopithecoid occurred in the Fort Ternan sediments. The concordance in size and morphology of these isolated teeth indicates that they can all be referred to a single species. The Fort Ternan specimens are larger and more derived than the middle Miocene oreopithecoid, *Nyanzapithecus pickfordi* from Maboko Island (HARRISON, 1986), and are much more similar to the corresponding teeth of *O. bambolii* from Italy. HARRISON (1986) has argued that the degree of resemblance to *O. bambolii* is sufficient to place the Fort Ternan material in the same genus, at least provisionally, until more complete material is obtained from the middle Miocene of East Africa.

#### *Simiolus* sp.

In 1968, LEAKEY announced the discovery of two mandibular fragments and some isolated teeth belonging to a small catarrhine primate from Fort Ternan (LEAKEY, 1968). Although he was uncertain of its true affinities, suggesting a possible relationship to *Pliopithecus* from Europe, LEAKEY tentatively assigned the material to an unknown species of *Limnopithecus*. SIMONS (1969), who provided a brief review of the Fort Ternan primates, regarded LEAKEY's cautious approach as unnecessary, owing to SIMONS' earlier synonymy of *Limnopithecus* with *Pliopithecus* (SIMONS, 1963; SIMONS & PILBEAM, 1965). SIMONS (1969) concluded that the differences between the Fort Ternan small catarrhine and *Pliopithecus antiquus* were likely to be at a level no greater than that between species of a single genus, and consequently referred the material to *Pliopithecus* sp.

ANDREWS and WALKER (1976) presented a more detailed discussion of the small catarrhine primate specimens from Fort Ternan. They suggested that the dentition was less specialized than that of *Dendropithecus macinnesi* and *Pliopithecus antiquus*, and that, on the basis of its size and more generalized morphology, it should tentatively be referred to *Limnopithecus legetet*. This assessment was further supported by ANDREWS (1978) in his revision of the East African Miocene hominoids, and followed by a number of subsequent authors (e.g. SZALAY & DELSON, 1979; SHIPMAN et al., 1981). More recently, however, ANDREWS (1980) has concluded that the affinities of the material may be with *Dendropithecus* rather than *Limnopithecus*.

A detailed study of the small catarrhines from Fort Ternan by the author suggests that more than one species is represented in the collections. Unfortunately, the material is much too fragmentary to be certain just how many taxa are actually represented, but there are clear indications that at least two species are present. One species is quite well-represented, including several partial mandibles (FT 13 and FT 14), an almost complete mandibular tooththrow (FT 20-25, MB 124, and SO 1102), and a single isolated tooth (FT 19) (see Table 1 for details).

As discussed above, several authors have made reference to this material (LEAKEY, 1968; ANDREWS & WALKER, 1976; ANDREWS, 1978), but no details have yet been published. A brief description of each specimen is therefore provided.

FT 20-25 is the most complete specimen, consisting of a crushed and fragmentary mandible with C-M<sub>3</sub> on the left side and some associated lower teeth from the right side (I<sub>2</sub>, P<sub>4</sub>, M<sub>2</sub>, and M<sub>3</sub>). In addition, an isolated left I<sub>2</sub>, MB 124, and a right lower canine, SO 1102, incorrectly accessioned as having been recovered from Maboko Island and Songhor respectively, are identical in morphology and preservation to the antimeres in the associated

