

SEVEN DECADES OF EAST AFRICAN MIOCENE ANTHROPOID STUDIES

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1. INTRODUCTION

African Miocene anthropoid studies followed a full century after pioneer work in Europe and South Asia. Indeed, Eurasian fossil apes were collected decades before the Darwinian revolution. *Pliopithecus* is the first fossil primate known to Western science. Edouard Lartet discovered the type mandible near Sansan, France, in 1834; and, the Eppelsheim femur, which resembles Slovakian femora of *Pliopithecus*, was found in Germany in 1820 (Piveteau, 1957; Pohlig, 1895; McHenry and Corruccini, 1976). In 1856, Lartet introduced *Dryopithecus fontani* from southwestern France.

South Asian Miocene anthropoids came to the attention of the wider scientific community when Pilgrim published findings on them in the 1910s. Vertebrate faunas had been collected from the Siwaliks by Falconer and Cautley (1830–1850) for the British Museum and by Richard Lydekker (1876–1886) and Guy Pilgrim (1900–1930) for the Geological Survey of India Museum in Calcutta. Barnum Brown collected for the American Museum of Natural History in 1922–23 and G. Edward Lewis collected for the Yale Peabody Museum in 1931–33. In 1935, DeTerra collected specimens with the Yale–Cambridge India Expedition (Khatri, 1975).

The earliest studies of African Miocene anthropoid primates were focused on western Kenyan specimens. In 1933, A. Tindell Hopwood of the British Museum diagnosed a dozen dental and gnathic specimens that had been collected between 1926 and 1931 in the Koru area of Kenya. He named two “gibbon-like” mandibular fragments *Limnopithecus legetet* and dubbed a maxillary fragment and a deciduous molar *Xenopithecus koruensis*. Hopwood considered that both species represented extinct lineages. He named the remainder of the specimens *Proconsul africanus* and concluded that they were related to *Dryopithecus* and were ancestral to *Pan troglodytes*. Thus began the search-for-the-superalative period, in which researchers strove to link novel specimens directly to extant hominoid species.

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2. COLLECTION AND INTERPRETATION: 1931–1959

In 1931 and 1932, Louis Leakey, Donald MacInnes, and other members of the third East African Archaeological Expedition discovered Miocene anthropoid fossils on Rusinga Island, at the mouth of the Winam Gulf in Lake Victoria, and at Songhor, on the mainland, a few miles north of Koru. Leakey, MacInnes, and other scientists continued to revisit Rusinga Island and Songhor and opened new Miocene sites in western and northern Kenya during the 1930s and 1940s (L. Leakey, 1937; M. Leakey, 1984; MacInnes, 1943). In 1948, a University of California expedition recovered a few Miocene anthropoid fossils from the Lothidok Hills in northern Kenya (Madden, 1980; M.G. Leakey et al., 1995).

2.1 *Proconsul*, *Sivapithecus*, and *Limnopithecus*

In 1951, Wilfrid LeGros Clark and Louis Leakey published a detailed monograph on the 226 anthropoid specimens that had been collected before September 1948, from Rusinga Island, Maboko Island, Songhor, Koru and Lothidok. They consisted mostly of fragmentary lower and upper jaws and isolated teeth. Few of the upper and lower dentitions could be associated with confidence as belonging to the same individual. A notable exception is the skull of *Proconsul heseloni*, which was discovered in 1948 on Rusinga Island by Mary Leakey. Postcranial remains were quite rare and generally fragmentary.

Clark and Leakey (1951) diagnosed four species of dentally great ape-like forms: *Sivapithecus africanus* and small, medium and large species of *Proconsul*: *Proconsul africanus*, *Proconsul nyanzae*, and *Proconsul major*, respectively. They further diagnosed two species of dentally gibbon-like forms: *Limnopithecus legetet* and *Limnopithecus macinnesi*. With Hopwood's concurrence, they sank *Xenopithecus* into *Proconsul africanus*.

Clark and Leakey (1951) concluded that species of *Limnopithecus* belong to the Hylobatidae, and though somewhat inclined to create a new subfamily for *Proconsul* spp., ultimately they left them in the Dryopithecinae of the Pongidae.

Clark and Leakey (1951) suggested that *Propithecus* gave rise to more advanced hylobatine apes like *Limnopithecus*, and that *Proconsul* was derived from them. *Limnopithecus legetet* and *Limnopithecus macinnesi* represented not greatly modified survivals of the ancestral stock from which *Proconsul* emerged. They considered *Proconsul* to be a probable ancestor of modern African apes, but they did not designate which species of *Proconsul* may have given rise to *Pan* and *Gorilla*. *Limnopithecus legetet* may have been ancestral to *Pliopithecus* and ultimately, through *Pliopithecus*, to modern lesser apes. They considered *Sivapithecus africanus* to be the most likely ancestor of the Eurasian dryopithecine apes.

Clark and Leakey (1951) were not specific about possible ancestry of the Hominidae. They proposed that specialization for brachiation occurred independently in the ancestral Asian and African apes. In their scheme, hominid evolution did not include a brachiating phase. Instead, there was a direct transformation of limbs like those of *Proconsul* because of selection for bipedalism.

In 1948, Louis Leakey discovered associated jaws and limb bones of at least four *Limnopithecus macinnesi* in a block of limestone on Rusinga Island. They were monographed by Clark and Thomas in 1951 and were restudied by Denise Ferembach (1958). Clark and Thomas (1951, p. 12) concluded that the posture and gait of

Limnopithecus probably “resembled the quadrupedal monkeys rather than the brachiating gibbons.”

With the addition of two rib fragments, a badly damaged fragment of humeral shaft, and a fragment of scapula, Ferembach (1958) concluded that *Limnopithecus* possessed no special affinity with hylobatid apes. Instead, she inferred that *Limnopithecus* had closer affinities with African pongid apes, especially chimpanzees. Further, she stated that filiation among *Limnopithecus legetet*, *Pliopithecus antiquus*, and *Pan paniscus* was supported by available fossil evidence.

Ferembach (1958) concluded that *Limnopithecus* was basically arboreal since nearly all of its postcranial characteristics resemble those of chimpanzees or colobine monkeys. She inferred that *Limnopithecus macinnesi* progressed by arm-swinging, though not of a modern hylobatid sort, and quadrupedism in trees; but they walked bipedally on the ground. She provided no direct morphological evidence that *Limnopithecus macinnesi* were bipedal. She simply surmised that they might have been bipedal because they lacked features related to terrestrial quadrupedism and had a predisposition for brachiation.

In 1951, on Rusinga Island, T. Whitworth collected postcranial bones of a subadult *Proconsul*, which were closely associated with upper and lower dentitions attributable to *Proconsul africanus*. The specimens were monographed by Napier and Davis (1959), who concluded that *Proconsul africanus* possessed many features that indicate arboreal habits, including both quadrupedism and some brachiation, but there was no direct evidence for terrestrial habits.

Three decades later, Alan Walker (1992) extracted several additional postcranial bones from a block of limestone that had been returned by the British Museum to the National Museums of Kenya. They belonged to the same individual [KNM-RU 2036] that Whitworth had discovered in 1951. Further search on Rusinga Island also produced an informative leg and foot, lacking phalanges, which were reasonably assigned to *Proconsul nyanzae* (Walker and Pickford 1983; Walker and Teaford 1988, 1989).

3. TAXONOMIC SHUFFLES, ANCESTORS, AND FUNCTIONAL INTERPRETATIONS: 1960–1999

The period of initial description and taxonomy of the African Miocene anthropoids (1926–1959) was followed by taxonomic reassignments, somewhat more fine-grained functional and phylogenetic interpretations, and discoveries of additional specimens.

3.1 *Limnopithecus*, *Pliopithecus*, *Dendropithecus*, and *Proconsul*

In 1963, Elwyn Simons sank *Limnopithecus* into *Pliopithecus*, arguing that geographic separation should not outweigh morphological similarity when considering possible congeneric status for primate species. Ten years later, Simons and Fleagle (1973, 140) withdrew this view, stating that “although the dentitions of the two forms are indeed very similar, particularly in the lower molars, the skeletal evidence suggests that generic distinction is indeed justified. Although difficult to evaluate quantitatively, the postcranial differences are certainly greater than those separating modern ape genera.” They concluded that *Limnopithecus macinnesi* was an arboreal arm-swinging form based on simi-

larities of its forelimb with that of *Ateles*.

In 1977, Peter Andrews and Simons created a new genus for *Limnopithecus macinnesi*, largely because its limb bones evinced greater development of suspensory behavior than those of other Miocene anthropoids. They renamed it *Dendropithecus macinnesi*. The only postcranial features that they specifically mentioned in the diagnosis of *Dendropithecus* are hind limb bones similar in size range to *Hylobates*; length and slenderness of the long bones, which sets it apart from *Pliopithecus* and *Dryopithecus*, including *Proconsul*; lack of conspicuous muscular markings; straightness of the humeral shaft; and the lack of the entepicondylar foramen and broad distal humeral condyles of *Pliopithecus*.

In 1983, Fleagle proffered that, like *Ateles*, *Dendropithecus macinnesi* was a very suspensory arboreal quadruped. Further, he concurred that *Proconsul africanus* was an arboreal quadruped and less suspensory than *Dendropithecus macinnesi* or *Pliopithecus*.

On the other hand, on the basis of an allometric study of modern and Miocene anthropoids and their limb proportions, Aiello (1981) concluded that while *Proconsul africanus* were below-branch feeders, *Dendropithecus* and *Pliopithecus* were above-branch feeders. She further stated that *Proconsul africanus* was a more likely ancestral type for the extant Pongidae and *Homo* than the other Miocene anthropoid species for which there was postcranial evidence.

Jungers (1984) conducted an extensive allometric analysis of the locomotor skeletons of anthropoid primates, leading him to conclude that *Dendropithecus* and *Pliopithecus* had long limbs and were basically arboreal, suspensory, monkey-like creatures rather like *Ateles*, but without a prehensile tail. Also in contrast to Aiello (1981), Jungers (1984) concluded that *Proconsul africanus* had relatively short limbs and was a relatively slow-moving arboreal quadruped. Here he echoed Walker and Pickford's (1983) conclusions based on more complete remains of KNM-RU 2036.

3.2 *Proconsul*, *Dryopithecus*, and *Sivapithecus*

In 1962 and 1963, Louis Leakey proposed the erection of a new family, the Proconsulidae, which would include the genus *Proconsul* and some specimens of *Dryopithecus* and *Sivapithecus*. He did not specify which individual fossils he would include in the new family. He commented that erection of the Proconsulidae was justified by the distinctive structure of the canine teeth, the face, and, where known, the skull. In particular, he cited the shape of the mandibular arch, the nature of the mandibular fossa, the absence of a simian shelf, and the special nature of the canine teeth (L. Leakey, 1963).

On the basis of a comprehensive review of available fossil materials, in 1965 Simons and Pilbeam sustained Gregory and Hellman's pongid subfamily, the Dryopithecinae, which Leakey had termed a dust bin, and rejected Leakey's proposal for the Proconsulidae. Indeed, they pursued a course that was diametrically opposite to that of Leakey and sank *Proconsul* into *Dryopithecus*.

Simons and Pilbeam (1965) retained the nomen *Proconsul* as a subgenus of *Dryopithecus* and sank *Proconsul africanus*, *Proconsul nyanzae*, and *Proconsul major* into it. They arrived at this decision after systematically comparing *Proconsul africanus* with the type specimens of *Dryopithecus fontani*. LeGros Clark, senior author of the original expanded diagnosis of genus *Proconsul*, concurred with their revision.

Simons and Pilbeam (1965) confirmed the essential identity between the type maxillary fragment of *Sivapithecus africanus* and some maxillae attributed to Indian *Sivapithecus*,

especially *Sivapithecus sivalensis*. Further, they concluded that there was no justification for generic distinction between *Sivapithecus* and *Dryopithecus*. Thus, they sank *Sivapithecus africanus* into their newly created taxon, *Dryopithecus (Sivapithecus) sivalensis*.

Simons and Pilbeam (1965) suggested that *Dryopithecus nyanzae* might be close to the ancestry of *Ramapithecus punjabicus* and thus remotely related to later Hominidae. They proposed that *Dryopithecus major* were almost certainly ancestors to modern gorillas. They inferred that either *Dryopithecus fontani* or *Dryopithecus nyanzae* were probably ancestors to modern chimpanzees.

3.3 *Limnopithecus*, *Micropithecus*, and *Dendropithecus*

In 1958, Walter Bishop recovered fragmentary mandibular and isolated dental specimens, which Louis Leakey identified preliminarily as *Limnopithecus legetet* and *Proconsul nyanzae*, respectively, on the flank of the Napak volcano in the Karamoja District of Uganda. Further, in 1961, Bishop and Whyte (1962) collected additional large hominoid specimens from Napak and from the vicinity of Moroto Mountain in the Karamoja District. Later in 1961, David Allbrook collected more remains of a large hominoid at Moroto II (Allbrook and Bishop, 1963). During a 6-week period in 1963 and 1964, Bishop (1964) and company systematically collected many mammalian remains from Napak and Moroto, including a well-preserved palate and snout with face present to the lower left orbit of a small species provisionally referred to *Limnopithecus*. Fleagle's (1975) preliminary comments on the palate from Napak IV were that the proportions of the maxillae, zygomatic bones and teeth are much more similar to those of a living gibbon than those of *Pliopithecus* are, and Simons and Fleagle (1973, p. 138) stated, "In morphology and facial proportions the specimen is virtually identical to living gibbons. . . although it is considerably smaller in absolute size."

In 1969, Walker provisionally reported that specimens of *Limnopithecus legetet* were among the fossils collected by Makerere University College expeditions, beginning in 1965, from the Bukwa II site, on Mount Elgon in the Sebei District of Uganda.

In 1978, Fleagle and Simons diagnosed a new species, *Micropithecus clarki*, on the basis of dental and cranial bits from the Miocene deposits at Napak. They concluded that it had greatest affinity with *Dendropithecus macinnesi* and that it had no clear link with specific Oligocene anthropoids or with *Pliopithecus* of Europe.

Pickford (1982) noted that if *Micropithecus* or *Dendropithecus* incorporated bilophodonty into their molars, they would be viable ancestors for *Victoriapithecus*, a Middle Miocene monkey that is especially abundant on Maboko Island. If this scenario were correct, the Cercopithecoidea evolved in Africa from small-bodied dental apes during the Early Miocene. Six years later, Pickford and Senut (1988, p. 51) rejected the possibility that a species of East African Early Miocene anthropoid could have evolved into *Victoriapithecus* because of "the morphological distance between *Victoriapithecus* and all lower Miocene primates from West Kenya."

3.4 *Proconsul*, *Dryopithecus*, and *Morotopithecus*

At Moroto II, the 1963–64 expedition collected 56 additional pieces, which Bishop (1964) ascribed to the same individuals of *Proconsul major* as the 1961 palatal and mandibular

fragments. Allbrook and Bishop (1963) gave preliminary descriptions of the cranial remains. In 1968, Walker and Rose described remarkably African ape-like vertebral remains, presumably of one individual, from Moroto II.

The Ugandan remains of *Proconsul* constituted the primary empirical base for Pilbeam's (1969) doctoral thesis at Yale University. He was inclined to associate the palate, two mandibular fragments and vertebral fragments from Moroto II as a single male of *Dryopithecus (Proconsul) major*. He concluded that all of the large hominoid specimens from the three Napak sites belong to *Dryopithecus major*. He described the face as a scaled-down long-snouted male gorilla with a gracile upper face. From the relatively low-crowned teeth, shallow palate, and other features, Pilbeam (1969) inferred that the Ugandan pongids were less well adapted than modern gorillas are to chewing tough vegetable matter.

Pilbeam's (1969) reassessment of Kenyan specimens of *Proconsul* and *Sivapithecus* indicated close morphological affinities and conspecific status among *Dryopithecus major* from Koru and Songhor and the large Ugandan hominoids. He concluded that *Dryopithecus nyanzae* probably represents remnant populations of the ancestral stock that gave rise to *Dryopithecus major*. Progressive adaptation to a tough vegetal diet on the heavily forested slopes of active volcanoes like Moroto and Napak transformed *Dryopithecus major* into *Gorilla gorilla*. Pilbeam's (1969) *Dryopithecus major* might well have been a knuckle-walker, though probably it was more active and less terrestrial than extant gorillas are.

Pilbeam (1969) concluded that *Dryopithecus africanus*, though probably lacking knuckle-walking adaptations, was a likely ancestor to *Pan troglodytes*. This would mean that the lineages leading to modern chimpanzees and gorillas were specifically separated ≥ 20 Ma.

Pilbeam (1969) retreated from the assignment of certain medium-sized African specimens to *Dryopithecus sivalensis* (Simons and Pilbeam 1965) on the grounds that they were probably earlier than the Indian forms, though he thought they might represent ancestors of Eurasian *Dryopithecus*, especially *Dryopithecus (Sivapithecus) sivalensis*.

In 1994 and 1995, Gebo and coworkers (1997) collected additional postcranial specimens from Moroto I and II. Although dated at 20.6 Ma, they evidence more ape-like features than any other Early or Middle Miocene anthropoid. Gebo et al. (1997) created a new species, *Morotopithecus bishopi*, for the entire collection of large anthropoid specimens from Moroto. Unfortunately, they may have included a nonprimate scapular fragment (MUZM 60) in the hypodigm (Benefit, 1999; Pickford et al., 1999; Senut, 1999). Further, Gommery (2003) noted that there are two large hominoids represented at Moroto: *Ugandapithecus major* (formerly *Proconsul major*) and *Afropithecus turkanensis*, of which *Morotopithecus* is a synonym.

3.5 Fort Ternan

In 1961, Louis and Mary Leakey directed the collection of > 1200 fossils at Fort Ternan, which is a few miles south of Koru. In 1962, Louis Leakey announced the discovery of primates there but concentrated on specimens that he diagnosed as *Kenyapithecus wickeri*. He mentioned discovery of "a very large upper canine, scarcely [*sic*] distinguishable from those of *Proconsul nyanzae*. . ." (L. Leakey, 1962, p. 690).

In 1968, Leakey gave a brief report in *Nature* on the primates that were associated with *Kenyapithecus wickeri*. He also mentioned isolated teeth and parts of two mandibles

of Hylobatidae that were too different to be assigned to *Limnopithecus legetet* or *Limnopithecus macinnesi*. He noted that there were > 300 specimens of Miocene Hylobatidae at the Nairobi Museum.

In a commentary in *Nature*, Simons (1969) accepted the hylobatid status of the Fort Ternan specimens but referred them to *Pliopithecus* because at the time he considered *Limnopithecus* to be a junior synonym of *Pliopithecus*.

One mandibular specimen of a nonhylobatid primate from Fort Ternan evidenced a simian shelf and bicuspid P³, features that Leakey (1968) had never observed in specimens of *Proconsul*, but which occur in European and Asian *Dryopithecus*. Therefore, he provisionally referred this new Fort Ternan specimen to *Dryopithecus*. Leakey (1968) also noted that there were two canine teeth typical of *Proconsul* in the collection.

Simons (1969) concurred that the new mandible from Fort Ternan was that of *Dryopithecus* and referred it to *Dryopithecus* cf. *sivalensis*. But he suggested that the canines should also be referred to *Dryopithecus sivalensis* because canines of Indian *Dryopithecus sivalensis* closely resemble those of *Dryopithecus nyanzae*, and it is unlikely that *Dryopithecus nyanzae* survived as lately into the Miocene.

Andrews and Walker (1976) concluded that, apart from *Ramapithecus*, there are 3 hominoid species from the Fort Ternan deposits. *Limnopithecus legetet* was the most common primate at the site. Fourteen specimens and probably many fewer individuals represented it. They concluded that *Dryopithecus* cf. *nyanzae* was represented at Fort Ternan by 7 specimens. They provisionally recognized *Proconsul* cf. *africanus* on the basis of ≥ 2 isolated teeth.

In 1986, Pickford listed *Micropithecus* sp., *Rangwapithecus gordonii*, *Kenyapithecus wickeri*, perhaps *Proconsul* sp., and an oreopithecoid at Fort Ternan. In 1992, Harrison confirmed the presence of *Kenyapithecus wickeri* and *Proconsul* sp. and identified specimens of *Simiolus* sp., probably *Oreopithecus* sp., and perhaps *Kalepithecus* sp. in the Fort Ternan anthropoid sample.

3.6 Taxonomic trials of the 1970s

During the 1950s, 1960s, and sporadically thereafter, collecting continued at established eastern African Miocene localities and further primate remains were recovered from Rusinga Island, Songhor, Koru, and Maboko Island. Anthropoid fossils also were found on Mfangano Island in the Winam Gulf of Lake Victoria. Andrews (1978) noted that the size of the fossil primate collection at the Centre for Prehistory and Palaeontology in Nairobi had more than doubled between 1951 and 1970.

In 1978, Andrews listed the following numbers of specimens:

Species	<i>n</i>	Pickford (1986)
<i>Dendropithecus macinnesi</i>	160	152
<i>Proconsul</i> (<i>Rangwapithecus</i>) <i>gordonii</i>	79	78
<i>Proconsul</i> (<i>Rangwapithecus</i>) <i>vancouveringi</i>	10	5
<i>Limnopithecus legetet</i>	136	159
<i>Proconsul africanus</i>	120	146
<i>Proconsul nyanzae</i>	109	104
<i>Proconsul major</i>	81	75
Pongidae indet.	5	16
TOTAL	700	735

To Andrews' (1978) total should be added the ≥ 20 specimens of *Micropithecus clarki*, which he provisionally recognized as *Limnopithecus legetet*. In 1981, Harrison (p. 133) noted 78 specimens that might be *Micropithecus* from Koru, but Pickford (1986) listed only one specimen of *Micropithecus clarki* at Koru, with the bulk of specimens being from Chamtwara ($n = 49$) and Legetet ($n = 14$), in the Koru area, and Napak ($n = 13$), Uganda.

In 1970, Andrews drew some novel inferences about pongid phylogeny on the basis of 2 previously undescribed specimens from Kenya. He concluded that a mandibular fragment [KNM-RU 900], which was discovered in 1956 on Rusinga Island, should be referred to *Aegyptopithecus*. He concluded that *Aegyptopithecus zeuxis*, his new *Aegyptopithecus* sp., and *Limnopithecus legetet* belonged to the same phylogenetic lineage. In 1978, he sank his *Aegyptopithecus* sp. in the hypodigm of *Dendropithecus macinnesi*.

Andrews (1979) proposed that a reasonably complete palate containing all teeth except the incisors, from Songhor [KNM-SO 700], should be referred to *Proconsul* sp. indet. and that it probably represented ancestral *Pongo*. The tips of its canines are broken off; Andrews (1979) surmised that they had not fully erupted. He noted that, both in size and morphology, its closest affinities were with *Proconsul africanus*.

As part of a major taxonomic reshuffling and preliminary accommodation of the newer specimens from Kenyan Miocene localities, Andrews transferred *Limnopithecus legetet* from the Hylobatidae into the Dryopithecinae, but he left *Limnopithecus macinnesi* in the Hylobatidae. He continued to recognize the three species of *Dryopithecus* (*Proconsul*), viz. *D. (P.) africanus*, *D. (P.) nyanzae*, and *D. (P.) major*, and proposed two new species: *Dryopithecus gordonii* and *Dryopithecus vancouveringi*, in a new subgenus *Rangwapithecus*.

The holotype of *Dryopithecus (Rangwapithecus) gordonii* is the Songhor-700 palate (Andrews, 1974), which Andrews (1970) previously had referred to *Proconsul* sp. indet. The hypodigm consisted of 79 specimens, mostly from Songhor, but there were also purported specimens from Rusinga and Mfangano Islands. Some specimens in the hypodigm were undescribed, while others had been assigned to *Limnopithecus macinnesi*, *Proconsul africanus*, and *P. nyanzae*.

In 1974, the hypodigm of *Dryopithecus (Rangwapithecus) vancouveringi* consisted of 7 specimens, including only the upper postcanine dentition and parts of the maxilla (Andrews, 1974). It is distinguished from *D. (R.) gordonii* chiefly in its somewhat smaller size. Judith and John Van Couvering found the type specimen [KNM-RU 2058] on Rusinga Island in 1968. It purportedly occurred also on Mfangano Island and perhaps also on Maboko Island (Andrews, 1978). Pickford (1986) listed only 5 specimens total from Hiwegi and Songhor.

Andrews ended his brief 1974 report with the following pessimistic comment: "In my opinion it is no longer feasible to suggest direct ancestral-descendent relationships between fossil and living species. Presumably one or more of the Miocene species was ancestral to the later pongids, but which this was, and whether one or more species was also ancestral to the Eurasian dryopithecines, can not be known from the available evidence (p. 190)." Apparently, this sober thought did not deter him (Andrews, 1978, p. 210), his contemporaries, his students and other successors from proffering speculative phylogenetic models, which are now arrogantly termed "phylogeny (or phylogenetic) reconstructions."

In a 1978 monograph based on his doctoral thesis, Andrews reiterated that *Dendropithecus macinnesi* belonged in the Hylobatidae, and he placed 6 species of African

Miocene Hominoidea in the Dryopithecinae of the Pongidae: *Limnopithecus legetet*, *Proconsul (Proconsul) africanus*, *Proconsul (Proconsul) nyanzae*, *Proconsul (Proconsul) major*, *Proconsul (Rangwapithecus) gordonii*, and *Proconsul (Rangwapithecus) vancouveringi*.

Although Andrews (1978) endeavored to find clear-cut morphological features that separate these species, most of them are differentiated on the basis of relative size (and perhaps also by site). Andrews (1978) sank *Sivapithecus africanus* into *Proconsul nyanzae*, stating that they may well be ancestors to later *Sivapithecus sivalensis*. He agreed with Pilbeam (1969) that Leakey's specimens of *Kenyapithecus africanus* could be referred to *Proconsul nyanzae* or *Proconsul major*.

3.7 Taxonomic trials of the 1980s and 1990s

The trend toward splitting, resurrecting taxa, and naming new ones accelerated during the 1980s and 1990s. Pickford's 1986 compilation is a prime example. He listed no fewer than 15 African Miocene anthropoid species binomially and noted 8 more that awaited full and formal nomination. He raised *Rangwapithecus* and the newly revived *Xenopithecus* from subgeneric to generic rank, resurrected *Kenyapithecus*, and accepted several new species, including *Mabokopithecus clarki*, *Micropithecus songhorensis*, and *Limnopithecus evansi*. Concurrently, Harrison (1986a, 1989) added a new species, *Nyanzapithecus pickfordi*, and changed *Proconsul (Rangwapithecus) vancouveringi* to *Nyanzapithecus vancouveriorum*. Harrison (1986b) proposed that *Nyanzapithecus* is an earlier Miocene ancestor for the Late Miocene European oddball, *Oreopithecus bambolii*. Harrison (1986a) sustained *Rangwapithecus gordonii*, which might approach the Early Miocene ancestor of *Nyanzapithecus*.

In 1993, Walker and coworkers named a new species, *Proconsul heseloni*, for the smaller specimens of *Proconsul* from Rusinga and Mfangano, but retained the nomen *Proconsul africanus* for specimens from Koru and Songhor.

Harrison (1988) also implemented a major taxonomic revision of the smaller Early Miocene catarrhine primates from western Kenya and Uganda. He not only sustained *Dendropithecus macinnesi*, *Micropithecus clarki*, and *Limnopithecus legetet* but also recognized *Limnopithecus evansi* and a new species, *Kalepithecus songhorensis* (formerly *Micropithecus songhorensis*), which is represented at Koru and Songhor. Moreover, Harrison (1988) referred some Middle Miocene specimens from Moboko Island to a new species, *Micropithecus leakeyorum*, but Benefit (1991) sank them in *Simiolus*.

Having yielded several thousand primate specimens, Maboko is one richest paleoprimatological sites in East Africa. It is the type-site of *Kenyapithecus africanus*, *Mabokopithecus clarki*, *Nyanzapithecus pickfordi*, and *Victoriapithecus macinnesi*. During a 6-week excavation in 1997, Gitau and coworkers (1998) recovered 22 specimens of *Kenyapithecus africanus*, 45 each of *Mabokopithecus clarki* and *Nyanzapithecus pickfordi*, 17 of *Simiolus leakeyorum*, and 327 of *Victoriapithecus macinnesi*. Based on postcranial specimens, McCrossin and Benefit (1994) concluded that *Kenyapithecus africanus* was adapted to terrestrial pronograde digitigrade quadrupedal locomotion, which set them apart from other Miocene species.

In 1998, Benefit and coworkers concluded that *Mabokopithecus clarki* is at least congeneric, and perhaps conspecific, with *Nyanzapithecus pickfordi*. Accordingly, *Nyanzapithecus pickfordi* becomes *Mabokopithecus pickfordi* (or *M. clarki*, if conspecific

with *M. pickfordi*) and Nachola *Nyanzapithecus harrisoni* becomes *Mabokopithecus harrisoni*.

In northern Kenya, Kalodirr is the 16–18Ma type site of *Afropithecus turkanensis*, *Turkanapithecus kalakolensis*, and *Simiolus enjiessi* (R. Leakey and M.G. Leakey, 1986a,b; R. Leakey et al., 1987; R. Leakey et al., 1988a,b; Boschetto et al., 1992). The former two species are cranially among the best-known Miocene anthropoids. Postcranial features of *Afropithecus* and *Turkanapithecus* appear to be logical precursors for those in later ape skeletons, though they lack special features related to obligate suspensory feeding and knuckle-walking (Rose, 1993). *Afropithecus turkanensis* was probably also present at Buluk in northern Kenya (R. Leakey and Walker, 1985; McDougall and Watkins, 1985).

Two sites—Nachola and Namurungule—in the Samburu Hills, south of Lake Turkana, have provided intriguing hominoid specimens due to the efforts of the 1980 and subsequent Japan/Kenya Expeditions (Ishida, 1984).

Primate remains ($n > 200$) are common components of the Nachola fauna (Sawada et al., 1998). Pickford (1986) proposed that *Kenyapithecus* cf. *africanus*, *Micropithecus* sp., and perhaps *Xenopithecus* sp. are represented in the 15–14Ma Nachola collection. However, Kunimatsu (1997) and Sawada et al. (1998) noted that the Nachola anthropoids are *Nyanzapithecus harrisoni*, *Kenyapithecus* sp., and *Victoriapithecus*. Postcranial remains indicated that Nachola *Kenyapithecus* were accomplished arboreal quadrupeds and climbers that engaged in little suspensory behavior (Rose et al., 1996; Nakatsukasa et al., 1996, 1998).

Expanded samples of dentognathic (Kunimatsu et al., 1999) and postcranial (Nakatsukasa et al., 1999) remains of the Nachola large hominoid cast doubt on its being a species of *Kenyapithecus*. Accordingly, Ishida et al. (1999) named a new species: *Nacholapithecus kerioi*.

Based on a partial skeleton from Kipsaramon, Tugen Hills, north-central Kenya, Ward et al. (1999) erected a new species, *Equatorius africanus*, into which they sank *Kenyapithecus* sp. from the Aiteputh and Nachola Formations at Nachola and from the Muruyur Formation, Tugen Hills and all specimens of *Kenyapithecus africanus* from the Maboko Formation of Maboko Island, Majiwa, Kaloma, Nyakach, and Ombo.

The Namurungule Formation contains one of the precious few Late Miocene sites in eastern Africa (Sawada et al., 1998). The single hominoid specimen [KNM-SH-8531] is a left maxilla with P³–M³, which Ishida and Pickford (1997) named *Samburupithecus kiptalami*. It is ≈ 9.5 Ma, which makes it the most complete hominoid mandibular specimen from early Late Miocene eastern Africa. Pickford and Ishida (1998) concluded that dentally it is closest to early Hominidae, viz. *Praeanthropus africanus* (*Australopithecus afarensis* and *A. anamensis*).

The Ngorora Formation, in the Baringo Basin, Kenya, which spans a > 2 million year period between 13 and < 10 Ma, yielded 11 primate specimens. In addition to cercopithecoid monkeys, 8 specimens were provisionally assigned to *Kenyapithecus*, *Proconsul*, and a small ape (Hill et al., 1985; Hill and Ward, 1988; Hill, 1994).

3.8 Return of the Proconsulidae

In 1982 (p. 18), Pickford echoed Louis Leakey (1962, 1963) in noting that *Proconsul* and other unspecified African Early Miocene large genera of Catarrhini probably do not belong

in the Pongidae. Harrison (1987) and others resurrected Leakey's (1963) once disregarded family, the Proconsulidae, to accommodate many African Miocene species. For example, in 1988 Fleagle placed *Dendropithecus*, *Limnopithecus*, *Micropithecus*, *Proconsul*, *Rangwapithecus*, and *Simiolus*, together with two Chinese Miocene species (*Dionysopithecus* and "*Platydontopithecus*") in the Proconsulidae. He accepted *Nyanzapithecus* as a member of the Oreopithecidae and left *Afropithecus*, *Kenyapithecus*, and *Turkanapithecus* in Family *incertae sedis* of the Hominoidea. This resembles de Bonis' (1987) scheme, except that de Bonis placed *Rangwapithecus* in the Oreopithecidae and *Turkanapithecus* in the Proconsulidae and did not classify *Dendropithecus* familially.

4. CONCLUSIONS

All in all, despite periodic taxonomic shuffles of specimens, the Miocene dental apes of eastern Africa represent a remarkable adaptive radiation of forest, dense woodland, and perhaps more open habitat species, which has been compared with the radiation of the Cercopithecoidea. The three modern African apes—*Gorilla gorilla*, *Pan troglodytes*, and *Pan paniscus*—are an impoverished faunal component in comparison with their African Miocene cousins and cercopithecoid contemporaries. Premature attempts to link specific African Miocene apes to extant African apes, e.g. *Proconsul africanus* to *Pan troglodytes* and *Proconsul major* to *Pan gorilla*, have been discredited. Indeed, it is difficult even to derive a species of Eurasian Middle Miocene apes directly from the eastern African Miocene species, though it is generally thought that the latter must have evolved from African precursors.

The problem of linking Early and Middle Miocene anthropoids to *Pan*, *Gorilla*, and *Homo* is particularly exacerbated by the poor fossil record of apes during the Late Miocene and Pliocene of Africa. The only informative specimen representing the morphology of a Late Miocene African ape is the maxilla of *Samburupithecus kiptalami*. This has stimulated researchers to look to Europe for proximate Miocene ancestors of African apes and australopiths (de Bonis, 1987; Andrews et al., 1996; Begun and Kordos, 1997; Begun et al., 1997).

5. ACKNOWLEDGEMENTS

I thank Dr. Hidemi Ishida for inviting me to the benchmark symposium in 1999, for which I prepared an earlier version of this paper, and for his gracious hospitality and that of our other hosts and assistants, especially Dr. Masato Nakatsukasa, who faithfully directed me to the right dining room, vehicle, kinen-shashin, and costume.

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Human Origins and Environmental Backgrounds

Ishida, H.; Tuttle, R.; Pickford, M.; Ogihara, N.;

Nakatsukasa, M. (Eds.)

2006, X, 282 p., Hardcover

ISBN: 978-0-387-29638-8