

**Analysis of Miocene Primates:
Kenyapithecus, Sivapithecus, and Proconsul**

by

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**ANALYSIS OF MIOCENE PRIMATES:
*KENYAPITHECUS, SIVAPITHECUS, AND PROCONSUL***

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Introduction

The emergence of bipedal hominids have long captivated paleoanthropologists as they begin to understand human evolution. The constant discovery of new fossils and the identification of new species of hominids steadily pushes the date for the emergence of hominids back further and further. As the discovery of new hominid fossils continues, the questions as to the means of their evolution grow more curious and pertinent. Hominids have been discovered in the Pliocene epoch (5-1.8 mya). So far, the exclusion of hominids to the Pliocene epoch has directed paleoanthropologists to examine the aspects surrounding the preceding. The Miocene epoch (25-5 ma) is a critical period in geologic time. It is possible that during the Miocene epoch crucial climatic and ecological shifts occurred that affected primate evolution which could lead to the emergence of hominids during the Pliocene epoch.

The focus of this paper is to examine three predominate species of hominoids during the Miocene epoch and review their morphology, dentition, and locomotion via literature reviews to gain an understanding as to their adaptive strategies. Also, predominate hominids from the early

Pliocene epoch will be examined according to their morphology, locomotion, and dentition and compared to that of the Miocene hominoids in an attempt to demonstrate the shared and derived characteristics between hominoids and hominids as well as a comparison to extant apes.

The predominate hominoids of the Miocene epoch that will be examined in this paper are the hominoids *Kenyapithecus*, *Sivapithecus*, and *Proconsul*. The collection of fossils dating to the Miocene epoch represent an important and highly valued series of hominoid specimens that contribute to the understanding of human evolution. Over thirty species lived in African, Asia, and Europe during the Miocene epoch and there holds a possibility that one of those thirty species is the ancestor to modern hominids (Menon, 1997).

Early Miocene hominoids (23-16 ma) are smaller in size and appear to be restricted to the African continent, specifically abundant in east Africa. By the middle Miocene epoch (15-12 ma) fossils have been discovered from regions other than Africa (Benefit et al., 1995). The first appearance of large-bodied hominoids generally associated with the middle Miocene can be linked with the climatic and environmental adaptation which results with shifting their diet from soft fruit and plant consumption to hard seeds and nuts (Benefit et al., 1995). By examining a variety of Miocene hominoids, a clearer understanding of the factors

that attributed to adaptation and mass speciation can be obtained.

The paleo-environments of *Kenyapithecus*, *Sivapithecus* and *Proconsul* had a tremendous affect upon the diversity of the species. *Proconsul* represents an early Miocene hominoid from Africa, *Kenyapithecus* represents a middle to late Miocene hominoid from Africa, and *Sivapithecus* represents a middle to late Miocene hominoid from Southeastern Asia (Nakatsukasa et al., 1998; Beynon, 1998). The distinctions between each of these genera results from adaptation to their paleo-environments and the success or failure of adequately adjusting to the climatic shifts that occurred in the middle of the Miocene epoch.

The effect of environment on the evolution of hominoids in the Miocene epoch is apparent through the analysis of morphology, locomotion, and diet of *Kenyapithecus*, *Sivapithecus*, and *Proconsul*. This analysis allows for speculation upon how the emergence of new evolutionary trends in the late Miocene produces a probable cause for the shift from quadrupedal hominoids to bipedal hominids in the Pliocene epoch (5 - 1.8 mya). The contributions of Miocene hominoids to human evolution can be analyzed by comparing the morphology, locomotion, and diet of *Kenyapithecus*, *Sivapithecus*, and *Proconsul* to early Pliocene hominids. Comparing the morphology, locomotion, and dentition of *Kenyapithecus*, *Sivapithecus*, and *Proconsul* to the early Pliocene hominids *Ardipithecus ramidus*, *Australopithecus*

anamensis, and *Australopithecus afarensis* allows for an analysis and perspective view on how Miocene hominoids possibly contributed to the human evolutionary line.

Background

Paleo-environment

Proconsul:

One of the most well researched Miocene hominoids is *Proconsul* which is a small-bodied early Miocene (22-12 ma) hominoid (Rose, 1994; MacLatchy et al., 1996; Benefit et al., 1995). Three subspecies of *Proconsul* are *P. heseloni* 9 kg, *P. nyanzae* 31 kgs, and *P. major* 50 kgs (Rose, 1983; Rose, 1994). *Proconsul* has been found mostly in East Africa with the largest collection of remains discovered on Rusinga Island, Kenya (MacLatchy et al., 1996; Retallack et al., 1995; Beynon 1998). The paleo-environment for *Proconsul* in East Africa during the early Miocene is generally considered a more lush and tropical setting than later Miocene and Pliocene primates (Rose, 1994). Carbon isotope values from pyroclastic deposits indicate that Rusinga Island displayed a semi-arid environment that ranged from a woodland to a closed canopy evergreen forest (Bestland et al., 1999). A wet forest environment for *Proconsul* is currently under speculation as new reinterpretation places evidence for a

more wet forest ecosystem as restricted to localized areas in low-lying, more moist landscapes (Bestland et al., 1999; Rose, 1994). The most significant aspect concerning Rusinga Island is the constant catastrophic sufferings of the land from Kisingiri volcano. Throughout the excavation sites in Rusinga, pyroclasts from the volcano indicate that this area was incredibly unstable due to constant eruptions from the volcano (Bestland et al., 1999).

Kenyapithecus:

Kenyapithecus is the most common large-bodied hominoid of the middle Miocene (16-14 ma) (Nakatsukasa et al., 1998; Rose, 1994). The main site of discovery for *Kenyapithecus* is in Kenya, East Africa, most notable Ft. Ternan (MacLatchy et al., 1996; Scott et al., 1999). Two species of *Kenyapithecus* are *K. africanus* with a body weight of around 30 kg and *Kenyapithecus nachola* (Rose, 1994; MacLatchy et al., 1996). The diet for *Kenyapithecus* consisted of nuts and seeds (Nakatsukasa et al., 1998). The paleo-environment for *Kenyapithecus* was an intermediate mix of closed forest and open woodland (Nakatsukasa et al., 1998; Rose, 1994; Scott et al., 1999). A major difference between Rusinga Island and Ft. Ternan is the stress on rainfall water rather than an emphasis on altitude. Ft. Ternan and the paleo-environment for *Kenyapithecus* is considered less lush than Proconsul and more towards a woodland ecosystem (Bestland et al., 1999).

Sivapithecus:

Sivapithecus is a large-bodied middle to late Miocene (12.5 -7 ma) hominoid found in Southern Asia including the Siwalik Nagri formation in Pakistan (Benefit et al., 1995; Rose, 1994). Four species of *Sivapithecus* are *S. indicus* 50 kg, *S. parvada* 69 kg, *S. simonsi*, and *S. sivalensis* [GSP 11876] (Cameron et al., 1999; Rose, 1994; Scott et al., 1999; MacLatchy et al., 1996). The paleo-environments for *Sivapithecus* have been described as a subtropical seasonal evergreen forest (Rose, 1994; Scott et al., 1999), as well as a hot, moist, tropical rain forest similar to present day Burma (Cameron et al., 1999). The subtropical evergreen forest is generally attributed to *Sivapithecus parvada* in the Siwalik Nagri formation in Pakistan and the more moist and lush environment is usually associated with the other three subspecies (Scott et al., 1999; Cameron et al., 1999).

A major focus of reconstructing paleo-ecology in the Siwalik Nagri formation in Pakistan where the species *Sivapithecus parvada* is found is through bovid fossil analysis of the same age as the *Sivapithecus* fossils (Scott et al., 1999). The isotopic values gathered from the bovid fossils as well as the analysis of why certain species of bovids lived in these particular areas were reviewed (Bestland et al., 1999). There appears to have been a gradual shift in the Siwalik Nagri formation from a more lush forest to a more arid grasslands as early as 9.4 mya

(Scott et al., 1999). The paleo-environment for *Sivapithecus* differs from that of *Kenyapithecus* by varying degrees of vegetation cover (Bestland et al., 1999).

Morphology

Skull Morphology

An analysis of the skull morphology of *Sivapithecus*, *Kenyapithecus*, and *Proconsul* illustrates a series of common characteristics as well as distinguishing traits that help separate the three genera from each other and possibly link them as ancestral hominoids to more modern primates.

Proconsul:

The skull morphology of *Proconsul* demonstrates craniodental features such as a frontal air sinus, a wide frontal bone at the bregma, and the development of a maxillary jugum (Beynon, 1998). *Proconsul* has a massive superior transverse tori and no simian shelf (Benefit et al., 1995; Nakatsukasa et al., 1998). *Proconsul* has a more vertically oriented symphyseal axes (Benefit et al., 1995). *Proconsul* has a large angle formed between the long axis of the symphysis and the tooth row (Benefit et al., 1995; MacLatchy et al., 1996; Beynon 1998).

Kenyapithecus:

Distinctive characteristics of *Kenyapithecus* lower jaw morphology can be distinguished from *Sivapithecus* and *Proconsul* in that the symphysis is extremely long and inclined forward. Although *Kenyapithecus* has a robust lower jaw morphology, the upper jaw shape and palate are similar to those of modern humans (Menon, 1997). *Kenyapithecus* demonstrates a distinct simian shelf (inferior transverse torus) (Benefit et al., 1995; Nakatsukasa et al., 1998). *Kenyapithecus* has a very robust lower jaw morphology, similar to those of extant apes (Benefit et al., 1995). In spite of *Kenyapithecus*' long symphysis, the angle formed between the long axis of the symphysis and the tooth row is only around 30-40 degrees (Benefit et al., 1995; MacLatchy et al., 1996; Beynon 1998).

Sivapithecus:

The cranial morphology of *Sivapithecus* include a supraorbital costae, lack of supraorbital torus, frontal trigon formed by the anterior coalescence of the temporal muscles marking the orbital rims, narrow interorbital septum, the presence of an incisive canal, and the curving of the subnasal alveolar process to join with the palatal process of the maxilla (Benefit et al., 1995). These characteristics were once interpreted as a direct ancestry link between *Sivapithecus* and the *Pongo* clade, however,

further discoveries of middle-late Miocene hominoids (*Afropithecus* and *Dryopithecus*) suggest that these characteristics are rather primitive traits of many large-bodied Miocene apes (Benefit et al., 1995; Andrews et al., 1982). *Sivapithecus* has a distinct simian shelf (inferior transverse torus) (Benefit et al., 1995; Nakatsukasa et al., 1998). Also in common, the lower jaw morphology of *Sivapithecus* shares a common lower jaw morphology with *Kenyapithecus* are, in that it is very robust and characteristic to those found in extant apes (Benefit et al., 1995).

Post-cranial Morphology

Upper Limb Morphology

The morphology of the articulation of the humerus and the scapula provides insight as to what form of locomotion used by Miocene primates. Typical traits concerning the upper limb morphology of Miocene hominoids is that they all have a broad humeral trochlea and predominant lateral trochlear keel similar to extant hominoids (Benefit et al., 1995). *Kenyapithecus*, *Sivapithecus*, and *Proconsul* have a reasonable range of pronation-supination movement in the elbow (Rose, 1983).

Proconsul:

Proconsul has several distinctions in the elbow (Nakatsukasa et al., 1998; Benefit et al., 1995). *Proconsul* has a deep olecranon fossa. The troclear surface of the proximal ulna is particularly long compared to the width (Rose, 1983). The combination of a moderately beaked olecranon beak and a deep olecranon process suggests the predominate movement in elbow is that of flexion-extension (Rose, 1983; Benefit et al., 1995). *Proconsul* shoulder movement is not reflected in extant primate (Rose, 1983).

Kenyapithecus:

Analysis of *Kenyapithecus* upper limb morphology is considerable (MacLatchy et al., 1996; Rose, 1994). Even though *Kenyapithecus* is a large-bodied hominoid, much of its upper limb morphology is related closely to that of semiterrestrial monkeys (Benefit et al., 1995; MacLatchy et al., 1996; Menon, 1997). *Kenyapithecus* proximal humerus lacks modern hominoid features corresponding to agile climbing and facultative arm-swinging (Benefit et al., 1995). The humeral head of *Kenyapithecus* is monkey-like in that it differs from extant hominoids because it is directed backward for an articulation with a ventrally directed scapular glenoid fossa (Benefit et al., 1995). The humeral head of *Kenyapithecus* is proximally flat and low which is similar to Old World Monkeys (Benefit et al., 1995). The greater tubercle is large and anteriorly placed and extends

above the level reached by the humeral head which resembles a semiterrestrial monkey or macaque. Opposite to the humeral head of *Kenyapithecus* is that of extant great apes and arboreal monkeys which have a humeral head that projects above the level of the greater tubercle (Benefit et al., 1995).

Sivapithecus:

Further distinction between the three hominoid's upper limb morphology is apparent in the lower portions of the upper limbs. The medial epicondyle of the humerus in *Kenyapithecus* is different from other Miocene hominoids in that it is strongly inclined posteriorly, where as *Sivapithecus* and *Proconsul* have a medially directed epicondyle.

Lower Limb Morphology

Lower limb fossil remains have not been discovered for many of the subspecies of *Kenyapithecus*, *Proconsul*, and there are none available for *Sivapithecus*. The few discovered lower limb bones for *Proconsul* demonstrates a number of characteristics common with that of *Kenyapithecus* (Rose, 1994). These characteristics consist of a moderately wide articular surface of the femoral head, a high femoral

neck angle, a low greater trochanter, a laterally flared insertion of *m. gluteus minimus*, a large lesser trochanter, a wide deep fibular notch on the distal tibia, a thick fibular shaft, and a large fibular malleolus (Benefit et al., 1995; Nakatsukasa et al., 1998; Rose, 1994).

Kenyapithecus femur is slender and slightly longer than the humerus as well as more gracile than *Proconsul* (Benefit et al., 1995; Rose, 1994).

Spinal Column and Pelvic Girdle Morphology

Proconsul:

Spinal column and pelvic girdle morphology has been predominately discovered in *Proconsul*. The long extension of *Proconsul* trunk functions to increase the length of the strides which reduces the possibilities of its long limbs interfering with its stride (Rose, 1994; Benefit et al., 1995). *Proconsul* also has a mobile hip similar to apes but unlike cercopithecoids, concerning a prolongation of the femoral articular surface on the superior aspect of the neck (MacLatchy et al., 1996; Benefit et al., 1995; Sanders et al., 1994). *Proconsul's* ribs are monkey-like with the vertebral column rather long craniocaudally and the pelvis narrow.

Kenyapithecus:

The few discoveries of *Kenyapithecus* spinal column and pelvic girdle appear to share many characteristics with *Proconsul*. *Kenyapithecus* and *Proconsul* both have craniocaudally long lumbar vertebral centra, ventrally keeled vertebral bodies, transverse process arising from the vertebral body (Nakatsukasa et al., 1998; Rose, 1994). Which suggests a long trunk with a strong erector spinae muscle and a relatively mobile hip joint (Nakatsukasa et al., 1998; Benefit et al., 1995; Sanders et al., 1994).

Knee Morphology

The morphology of the knee provides a great deal of insight concerning locomotion. The patellar morphology of *Proconsul* and *Kenyapithecus* tends to resemble extant great ape morphology in that quadrupedalism was a typical behavior both semiterrestrally and arboreally. There is no information available concerning the knee morphology of *Sivapithecus*.

Proconsul:

The patellar morphology for *Proconsul* is closer to great apes than monkeys, emphasizing a variety of knee postures (Rose, 1994; MacLatchy et al., 1996). Like the great apes, it is probable that *Proconsul* did not rely heavily on

extensive running and leaping. *P. heseloni* and *P. nyanzae* patellas resemble that of great apes which do not rely heavily on running and leaping frequently (MacLatchy et al., 1996; Ward et al., 1995).

Kenyapithecus:

Kenyapithecus has a mediolaterally broad, anteroposteriorly thin, and a short nonarticular extension distally on its patella (Benefit et al., 1995; MacLatchy et al., 1996).

Proconsul and *Kenyapithecus* share a common generalized pattern of knee function and patellar morphology and a wide patella surface, relatively short, thin patellas reflecting a generalized, mobile loading regime (Nakatsukasa et al., 1998; Rose, 1994; MacLatchy et al., 1996). This morphology is typical of Miocene hominoid patellar fossils suggesting that this pattern of patellar morphology and knee function is probably primitive for hominoids (Ward et al., 1995).

Hand and Foot

Hand and foot morphology is important in the analysis of the pattern of locomotion whether palmigrade, digitgrade, or knuckle-walking.

Proconsul:

The proximal and intermediate phalanges of *Proconsul* are long and curved suggesting arboreality (Benefit et al., 1995; Rose, 1983). *Proconsul* demonstrates an African ape-like navicular facet on the ectocuneiform (Benefit et al., 1995). *Proconsul* hand and foot morphology is that of a moderately wedged talar trochlear surface, a developed median keel on the talocrural joint, a lateral trochlear rim on the talus that is higher and distally projecting than the medial rim, deep grooves for the tendon of *m. flexor hallucis longus* on the posterior talar trochlea and inferior to the calcaneal sustentaculum, a laterally expanded styloid process, a distinct *m. peroneus longus* groove on the fifth metatarsal. (Nakatsukasa et al., 1998; Rose, 1994; MacLatchy et al., 1996). *Proconsul* demonstrate an African ape-like navicular facet on the ectocuneiform (Benefit et al., 1995).

Kenyapithecus:

The hand and foot morphology of *Kenyapithecus* has a moderately wedged talar trochlear surface, a developed median keel on the talocrural joint, a lateral trochlear rim on the talus that is higher and distally projecting than the medial rim, deep grooves for the tendon of *m. flexor hallucis longus* on the posterior talar trochlea and inferior to the calcaneal sustentaculum, a laterally expanded styloid process, a distinct *m. peroneus longus* groove on the fifth metatarsal which is also found in *Proconsul* (Nakatsukasa et

al., 1998; Rose, 1994; MacLatchy et al., 1996).

Kenyapithecus displays a strong transverse dorsal ridge associated with that of *Gorilla* and *Pan* knuckle-walking, however, it is also present in semiterrestrial Old World monkeys like mandrills. The ridge maybe representative of a digitgrade hand posture including dorsal digitgrade of knuckle-walking and palmar digitgrade of semiterrestrial Old World monkeys (Benefit et al., 1995; MacLatchy et al., 1996). The strong transverse dorsal ridge indicates hyperextension at the metacarpophalangeal joint. The intermediate phalanx of *Kenyapithecus* are short and stout with little curvature of the shaft indicating semiterrestrial behavior (Benefit et al., 1995). *Kenyapithecus* has a very well developed hallux (Nakatsukasa et al., 1998). The hallux for *Kenyapithecus* is adapted for semiterrestrial behavior with the hallucial metatarsal medial portion of the entocuneiform facet is flat with a large peroneal tubercle indicating that the hallux was habitually adducted (Benefit et al., 1995). *Kenyapithecus* foot is well developed for grasping both vertically and horizontally and supports better than *Proconsul*.

(Nakatsukasa et al., 1998).

Sivapithecus:

Sivapithecus has a separate characteristics than both *Kenyapithecus* and *Proconsul*. *Sivapithecus* has a very well developed hallux (Nakatsukasa et al., 1998). *Sivapithecus*

like *Proconsul* demonstrate an African ape-like navicular facet on the ectocuneiform (Benefit et al., 1995).

Locomotion

Interpreting the morphology of *Kenyapithecus*, *Sivapithecus*, and *Proconsul* an idea as to what type of locomotion was used can be represented. Locomotive behavior also reflects the environment which provides either trees to climb in or ground to walk on. Rose (1983) describes the upper limb morphology of Miocene hominoids as having a forelimb design suitable for palmigrade quadrupedal activity, relatively mobile shoulder girdle, an extensive range of movement at the elbow, and free mobility in the hands.

Proconsul:

Morphologically, *Proconsul* has long limbs, comparable to certain living macaques, the spinal column is long with a narrow pelvis and the scapula is aligned vertically on the side of the thorax. All of these morphological features contribute to the reduction of mechanical interference between limb structure and quadrupedalism (Rose, 1994). The lumbar vertebrae are adapted for dorsoventral flexion of the lower back in a pronograde posture (Sanders et al., 1994). *P. heseloni* and *P. nyanzae* postcranial skeleton does not suggest habitually pronograde postures during locomotion,

with no obvious adaptations for suspension in any parts of their skeletons (Ward et al., 1995; MacLatchy et al., 1996). *Proconsul* exhibits a few of the basic trunk features equal to that of several Old and New world monkeys which contribute a fundamental gait of quadrupedalism (Sanders et al., 1994; MacLatchy et al., 1996).

Examining *Proconsul's* scapula and humerus, the placement of the acromion, which overhangs the glenoid laterally, and the combination of the humeral shaft indicates that there was moderate mobility to the shoulder area (Rose, 1994; MacLatchy et al., 1996). *Proconsul's* humerus is most similar to living *Presbytis* (Rose, 1994). *Proconsul's* humeral and radioulnar joints suggest a somewhat extensive range of pronation-supination in the forearm (Rose, 1994).

Proconsul's hand and wrist morphology also matches that of a quadrupedal monkey (Rose, 1994; MacLatchy et al., 1996). *Proconsul's* foot demonstrates good adaptation for arboreal quadrupedal locomotion. The foot pattern appears to indicate a heel-off foot placement which is found in most anthropoids with the exception of humans and great apes (Rose, 1994; Sanders et al., 1994). *Proconsul's* foot pattern also suggest above branch quadrupedalism as opposed to hindlimb suspension below the branches (Rose, 1994). It is possible that *Proconsul* had the ability to engage in leaping and bounding behaviors however without a great deal of efficiency or frequency (MacLatchy et al., 1996) The

positional repertoire is more typical of extant monkeys than extant apes (Sanders et al., 1994).

Kenyapithecus:

Postcranial features of *Kenyapithecus* suggest arboreal quadrupedalism and climbing without frequent suspensory activities (Nakatsukasa et al., 1998; MacLatchy et al., 1996). *Kenyapithecus* and *Proconsul* patellas do not exhibit adaptations to their specialized locomotor activities including quadrumanous climbing, bridging, suspension, or terrestrial knuckle-walking (Ward et al., 1995). There is no reason to exclude terrestriality from *Kenyapithecus* locomotion, however, ground walking and running must have been minor locomotor modes (Nakatsukasa et al., 1998; Menon, 1997). Features of the proximal femur including the head and neck as well as much of the upper body including the humerus which suggests that *Kenyapithecus* predominately used quadrupedal locomotion (Rose, 1994; MacLatchy et al., 1996). Also the feature of *Kenyapithecus* having a strong posteriorly directed medial epicondyle infers semiterrestrial behavior (Nakatsukasa et al., 1998; Rose, 1994).

Sivapithecus:

Sivapithecus hindlimb morphology found only in femoral fragments indicates quadrupedal locomotion with a possible emphasis on climbing and suspensory behavior (Benefit et

al., 1995; Rose, 1994; MacLatchy et al., 1996).

Sivapithecus has a combination of monkey-like proximal humerus and an ape-like distal humerus that suggests either a type of locomotor behavior not seen in living primates or a different functional underpinning to similar types of activity (Rose, 1994). The recent discovery of two humeral shafts with pronounced proximal and lateral curvature are interpreted as incompatible with forelimb suspensory activity. *Sivapithecus* is a quadrupedal primate and climbing is not as strongly emphasized as previously thought (MacLatchy et al., 1996).

Sivapithecus sivalenisi has a proximal femur adapted for wide excursions necessary for climbing (MacLatchy et al., 1996). The foot morphology consists of the talocrural and subtalar joints are similar to those of *Proconsul*, which indicate quadrupedalism (Rose, 1994; MacLatchy et al., 1996). The hallux is very robust and indicates a powerful grasping capability which suggest climbing (Rose, 1994).

Sivapithecus postcranial evidence points towards the main locomotion being quadrupedalism in what could possibly be a variety of locomotion capabilities (Rose, 1994).

Sivapithecus functional interpretations of elements in the hand, foot, forearm, and hip suggests the interpretation of an arboreal quadruped (Rose, 1994; MacLatchy et al., 1996)

Dentition

Dental remains are the most predominate source of fossils due to the ability for teeth to survive the taphonomic process. The information that can be gauged from dental remains directs paleoanthropologists in their understanding of the primates diet. With an understanding of diet comes and understanding of what the surrounding environment was like in which the primate had to choose its foods. Miocene hominoids have several jaw and tooth features that are found in great apes and humans which have been regarded by some anthropologists as a conservative retention from ancestral conditions for living apes (Benefit et al., 1995; MacLatchy et al., 1996; Sanders et al., 1994).

Kenyapithecus, *Sivapithecus*, and *Proconsul* present similar characteristics of dentition with *Australopithecines* and even the genus *Homo*. *Kenyapithecus* and *Sivapithecus* share similar molar morphology with early *Australopithecines*, especially *A. afarensis*. Their morphology consists of lower occlusal relief, a more constricted central basin, and molar cusps similar to extant great apes (Benefit et al., 1995). The thick enamel on the molars, also shared with *Australopithecines*, results from a dietary shift from soft fruits and plants to nuts and grass seed consumption which requires a larger grinding space on the occlusal surface of the molars as well as thicker enamel to endure the constant abrasiveness of the newly adaptive

diet (Beynon 1998). A shared reduction of molar shelves with extant apes and humans is considered derived because all Miocene apes including *Proconsul* share this reduction (Benefit et al., 1995; Beynon 1998; Dean, 1998).

Proconsul:

Proconsul dentition demonstrates a low crowned p3, and a reduced cusp heteromorphology of the upper premolars (Beynon, 1998). *Proconsul* has been described as having thin enamel on its teeth, however recent studies examining *Proconsul* teeth describe the enamel as thicker than previously thought but still more thin than large-bodied middle-late Miocene hominoids (Beynon, 1998). Based on thin enamel, cusp tips position on the crown molars, and occlusal surfaces, *Proconsul* was accustomed to consuming soft foods that did not require cracking hard objects with its teeth or an emphasis on grinding (Benefit et al., 1995; Dean, 1998). The lower incisors of *Proconsul* are vertically implanted (Benefit et al., 1995; Dean 1998).

Kenyapithecus:

Kenyapithecus shares dental traits with the genus *Homo*, such as the reduction of incisors and canines and the appearance of thick enamel on the molars associated with molar-grinding (Benefit et al., 1995; Beynon 1998). The uniqueness of the lower jaw morphology of *Kenyapithecus* is related to the specialized lower incisors, demonstrating

tall incisors with thick enamel that lean forward strongly (Benefit et al., 1995; Menon, 1997). Characteristics of tall thick enamel incisors are found in modern South American monkeys such as bearded sakis (Chirotos) and uakaris (Cacajao) which use these specialized teeth to break open hard outer coatings of nuts and fruits (Benefit et al., 1995; Scott, 1999). The association between *Kenyapithecus* and its later descendants suggest that as the diet became more varied the strong inclination of the lower incisors became obsolete however the simian shelf was retained and served as a preadaptation for the evolution of broad lower incisors (Benefit et al., 1995). The dental arcade of *Kenyapithecus* is rectangular and reflects that of extant great apes (Benefit et al., 1995). The upper incisors of *Kenyapithecus* are heteromorphic, which indicates that the central incisors are more broad and spatulate than the lateral incisors which are more conical (Benefit et al., 1995).

Sivapithecus:

The dental arcade of *Sivapithecus* is rectangular and reflects that of extant great apes (Benefit et al., 1995). The upper incisors of *Sivapithecus* are heteromorphic, which like *Kenyapithecus*, indicates that the central incisors are more broad and spatulate than the lateral incisors which are more conical (Benefit et al., 1995). *Sivapithecus* has moderate enamel wrinkling within the occlusal surface (Cameron et al., 1999). The third premolar (p3) for

Sivapithecus represents a difficult problem due to the sexual dimorphism within the tooth (Cameron et al., 1999). The female morphology of p3 is represented by as a broad linguobuccally tooth, though another specimen is needed to determine whether this morphology is a sexually dimorphic or specific characteristic (Cameron et al., 1999).

Kenyapithecus and *Sivapithecus* have very robust male upper canines which are believed to be medially inclined and externally rotated similar to extant great apes and opposite of *Proconsul* (Benefit et al., 1995).

Early Pliocene Hominids

The subfamily of Australopithecines has three genera: *Australopithecus*, *Paranthropus*, and *Ardipithecus*. Two of the genera, *Australopithecus* and *Ardipithecus*, are examined in connection with the Miocene hominoids. An examination of the morphological, locomotive, and dental characteristics of *Australopithecus anamensis* (3.9-4.2 mya), *afrarensis* (3.2-3.5 mya), and *Ardipithecus ramidus* (4.4 mya) allow for a comparison to determine Miocene hominoid contributions to Pliocene hominids (White et al., 1994, Leakey et al., 1995).

Morphology*Ardipithecus ramidus:*

A. ramidus differs from *Kenyapithecus* and *Sivapithecus* in that the foramen magnum is anteriorly placed relative to carotoid foramen, hypoglossal canal anteriorly placed relative to internal auditory meatus, carotid foramen placed posteromedial to tympanic angle (White et al., 1994). The placement of the foramen magnum relates to the morphology of bipedal hominids. *A. ramidus* skull morphology *boisei* has a shortening of the basioccipital (Wood, 1994). The length of the upper limbs in *A. ramidus* are longer than *A. afarensis* (White et al., 1994; Susman et al., 1984). Based on the size of humeral head, the size of *A. ramidus* is over 30 kilograms which is a comparable weight with some members of *A. afarensis* (Wood, 1994). *A. ramidus* has an extensive pneumatization of the squame, a very small external acoustic meatus, and a barely definable articular eminence all located on the left temporal bone (Ward et al., 1999).

Australopithecus anamensis:

A. anamensis has a primitive mandible and maxilla than *A. afarensis*. An extensive pneumatization of the squame, a very small external acoustic meatus, and a barely definable articular eminence all located on the left temporal bone are similar to *A. ramidus* and distinctively different from *A.*

afarensis (Ward et al., 1999). *A. anamensis* has a tibia larger than any from the Hadar sites. The tibia of *A. anamensis* is missing approximately one-third to half of the bone, and using regression equations the weight of *anamensis* is estimated between 47 and 55 kilograms (Leakey et al., 1995). The metaphyses of the tibia are distinctly flared proximally and distally, which is a characteristic found only in bipedal hominids (Ward et al., 1999).

Locomotion

A. ramidus:

The recovery of mostly cranial fossils limits the locomotive identification of *A. ramidus* (White et al., 1994, Ward et al., 1999). Sufficient morphology has not been discovered to determine whether or not *A. ramidus* is bipedal. The morphology of the skull pertaining to the anterior placement of the occipital condyles in conjunction with the spinal column suggests compatibility with bipedalism (White et al., 1994; Leakey et al., 1995).

A. anamensis:

A. anamensis retained some primitive feature in the upper limb morphology which indicates an ability for arboreality as well as habitual bipedalism (Ward et al., 1999).

A. afarensis:

A. afarensis is a biped but presents several characteristics that indicate arboreality. Curved proximal phalanges on the hand and feet, rod-like pisiform, and a robust hamate hook indicate the ability to grasp objects accurately and powerfully which is associated with climbing (Ward et al., 1999). The toes of *A. afarensis* had more mesio-lateral mobility than modern humans suggesting the toe-off motion was less than in modern humans which allows for *A. afarensis* to maintain arboreality (Susman et al., 1984).

Dentition*A. ramidus:*

In *A. ramidus*, size of the upper and lower central incisors relative to postcanine teeth is comparable to those of Miocene hominoids (White et al., 1994). Also, the canine is positioned in line with the mesiodental axis of the postcanine axis as found in Miocene hominoids and extant apes (White et al., 1994). *A. ramidus* has different dentition from *Sivapithecus* and *Kenyapithecus* in that the canines are more incisiform, crowns less projecting, relatively higher crown shoulders, cupped distal wear pattern on lower canine, mandibular p3 with weaker mesiobuccal projection of crown base without honing facet,

modally relatively smaller mandibular p3, modally relatively broader lower molars (White et al., 1994). *A. ramidus* possibly shares a hominid derived trait from *A. afarensis* in which the protoconid is reduced occlusally and mesiobuccally probably associated with the loss of honing from the deciduous canine (White et al., 1994). The wear patterns of *A. ramidus* are significantly different from those found in extant apes (White et al., 1994). *A. ramidus* contrasts with extant apes in that its upper canine is buccolingually large and extant apes are mesiodistally elongated (White et al., 1994).

A. anamensis:

A. anamensis can be distinguished from *A. ramidus* by features such as the thicker tooth enamel, buccolingually expanded molars, first and second molars are relatively same size, and a weak lateral trochlear ridge in the humerus (Leakey et al., 1995). *A. anamensis* demonstrates the possibility for sexual dimorphism in the teeth (Leakey et al., 1995).

Discussion

The late Miocene is attributed as the time when a significant shift in climate and environment occurred causing a spread of grasslands, global cooling and the major

changes of faunal diversity (Scott et al., 1999). Global cooling in the late Miocene perhaps lead to the habitat fragmentation which resulted in the isolation of populations and increased speciation. The climate and environmental shifts can be identified as factors in hominoid morphology adaptation and how each species survived in its habitat. This new force in adaption causes an emergence on evolutionary trends and encourages speciation. The increase in speciation due to isolation and adaptation to new environments may have been responsible for resulting in the basal *Australopithecine* diversity (Scott et al., 1999; Susman et al., 1984).

There is a possibility that Miocene hominoids experienced an intermediate habitat as early as 14 ma through 9.4 ma (Bestland et al., 1999; Scott et al., 1999). Geographic differences in paleo-environments between African and Eurasia may have been of considerable importance in determining the course of hominoid evolution in these regions (Scott et al., 1999). The late Miocene represents a time of great hominoid diversity in Eurasia which includes a diverse array of habitats. The association of diverse hominoids with their diverse habitats suggest the impact of environmental diversity is linked to hominoid taxonomic diversity (Scott et al., 1999). Four significant events that occurred in the middle to late Miocene were 1) the spread of grasslands 2) the global cooling event 3) the immigration of hipparionines into Eurasia and their

radiation 4) major changes in faunal diversity (Scott et al., 1999). These four events are a reaction to one another as well as a significant occurrence that begins a chain of shifts and adaptation that allow for new trends in evolution to appear.

Proconsul postcranial morphology suggests a complex mosaic of characteristics that can be interpreted as hominoid-like as well as others that can be viewed as basal catarrhine-like (Beynon, 1998). Evidence from the skull and dentition link *Proconsul* with later hominoids (Beynon, 1998). *Proconsul* displays adapted dental morphology for the consumption of soft foods, which leads to the theory that in the Middle Miocene when the climatic shift occurred that *Proconsul* did not adapt to hard food consumption and thus became extinct (Benefit et al., 1995). *Proconsul* is one of the best represented genus from Early or Middle Miocene hominoids and is also known for its lack of derived hominoid postcranial features (MacLachy et al., 1996).

The habitat of *Kenyapithecus* was a mix of both intermediate (broken cover) and closed cover area including woodlands and forests (Scott et al., 1999). The diversity of habitats from bush, woodland, swamp, tall grass, and hilly areas were available to *Kenyapithecus* (Scott et al., 1999). The diversity of *Kenyapithecus*' environment, especially Ft. Ternan, suggests that the regional environmental differences were critical for the course of hominoid evolution in Africa and Asia (Scott et al., 1999;

Bestland et al., 1999). Recent discoveries of *Kenyapithecus* in Northern Kenya, provide a vast insight into the postcranial aspects which were previously considered scarce (Nakatsukasa et al., 1998). *Kenyapithecus* foot morphology similar to gorillas and chimpanzees along with the modern-looking jaw, face, and teeth have lead scientists to group *Kenyapithecus* as a possible ancestor to modern chimps and gorillas (Menon, 1997).

Based upon the tooth enamel apatite of *Sivapithecus*, an argument has ensued about the gradual shift to grasslands potentially began 9-4 ma and cooling event between 10-9 ma and 9-8 ma (Scott et al., 1999). Flora analysis reveals a hot, moist, tropical forest environment for *Sivapithecus* as well as bovid isotopic analysis concludes evidence for an open savanna-like environment (Scott et al., 1999; Cameron et al., 1999). *Sivapithecus* likely lived in a mosaic like habitat with both closed forest areas as well as open savanna-like areas (Cameron et al., 1999). *Sivapithecus* lived in distinctly different habitat structures than that of *Kenyapithecus* in Africa, a diversity characterized by a variety of diverse vegetative cover (Scott et al., 1999).

The paleo-environments of the early Pliocene hominids affected the morphology, locomotion, and dentition as it did in the Miocene. The suggested paleo-environment for *A. ramidus* is a either closed or semi-open woodland setting (Wood, 1994; Leakey et al., 1995). The paleo-environment of *A. anamensis* is considered dry wooded or bushland with a

gallery forest located near the rivers (Leakey et al., 1995). *A. afarensis* lived in an environment that consisted of a mosaic of forest, woodlands, and open areas (Susman et al., 1984). All three Australopithecines lived in areas consisting of woodland and semi-open to open areas. As the drying trend continues from the Miocene into the Pliocene, the tropical forests continue to dissipate in favor of a more prosperous woodland environment. As in the Miocene, the inhabitants either adapted or became extinct.

A. afarensis narrows the gap between Miocene hominoids and other early hominids through morphology and locomotion (White et al., 1994). The morphology of *A. afarensis* suggests continually arboreality as well as adaptation for bipedalism (Susman et al., 1984). The evidence for Miocene hominoids contributing to the aspect of Australopithecine evolution is found in the ability for early Australopithecines to retain morphology conducive to life in the trees as well as on the ground as long as the environment provides the proper surroundings. Morphology indicates that *A. afarensis* was bipedal, however, the Hadar environment retained many aspects of a forested environment which indicates that once *A. afarensis* could walk bipedally, the species did not abandon the forests for open areas but utilized both aspects (Ward et al., 1999; Susman et al., 1984). What began in the middle Miocene as a drying trend, shifted the environments forcing the inhabitants to adapt to a more dry habitat. The trend of adapting to new

environments in the Miocene is reflected in the Pliocene hominids. A progression of adapting to new environments by utilizing the aspect of bipedalism.

Conclusion

The Miocene epoch (25-5 ma) is the critical time concerning human evolution. A series of dramatic climatic events occurred throughout the Miocene epoch that affected the paleoecology of the earth. These dramatic events served as catalysts that would shape an environment conducive to generate hominids. During the middle Miocene a climatic cooling event occurred worldwide that altered global ecology. This change in the paleoecology produces a shift in the evolutionary course of earth's inhabitants. There are over thirty different species of Miocene hominoids and an analysis of specific species demonstrates how ecological change affects speciation (Benefit et al., 1995). Adaptive strategies that emerge as a result of the paleoecological shift lead to the emergence of new evolutionary trends that impact the Miocene hominoids such as the need for larger body types, dietary changes, and possibly bipedalism. The impact of the global cooling event in the Miocene epoch reflects how ecological change affects speciation and how it set the stage for the emergence of Pliocene hominids.

The morphology, locomotion, and dentition found in *Kenyapithecus*, *Sivapithecus*, and *Proconsul* present a varied look at the Miocene epoch in which twenty million years of speciation, climatic shifts, and adaptation took place. As a result of the events that took place in the Miocene epoch, apes emerged as bipedal in the Pliocene. Vital to the understanding of Miocene hominoid contributions to the human evolutionary line is the comparison of the adaptations occurring in the Miocene to the shifting environment to the adaptations surrounding Pliocene environments.

Further studies into the impact of shifting paleo-environments on the adaptive morphology and behavior is necessary to understand the impact of the Miocene epoch on human evolution. *Proconsul* surviving only in the first half of the Miocene epoch provides insight into the climatic shift from lush closed canopy tropical rain forest environment to a more dry and open woodland environment. The shift in climate can be monitored in the fossil remains that *Proconsul* was adapted for soft foods and habitat compatible with a closed canopy environment, where as *Kenyapithecus* was more adapted for hard food consumption and open woodland habitat apparent in more terrestrial quadrupedalism than *Proconsul*. Also, *Sivapithecus*, which has a mix of traits concerning *Kenyapithecus* and *Proconsul* was adapted for an intermediate environment of both closed canopy subtropical rain forest as well as an open canopy woodland environment apparent in the wide variety of

locomotive abilities and the mixed dentition of grinding surfaces and canine and premolar adaptation.

The tremendous speciation that occurs in the Miocene epoch results from the adaptation of Miocene hominoids to a more dry and open area that leads to geographic isolation and establishes the characteristic traits that are necessary for bipedalism to emerge. The beginning of the Miocene epoch, hominoids were fairly small monkey-like primates, however, apes emerge as bipedal 20 million years later in the Pliocene. Somewhere within that 20 million year epoch rests the answer to understanding why hominoids adapted to bipedalism. The link to understand the nature of bipedalism and the necessary steps acquired to reach a bipedal state is found in the Miocene epoch within the context of adaptation to new food sources and climatic changes as well as vast speciation.

To aid in the quest for the transition from quadrupedalism to bipedalism, further research needs to be conducted over the Miocene hominoid morphology as it applies to environmental adaptation shifts. Analyzing how Miocene hominoids adapted to the new environments and how that adaptation is reflected in their morphology. Measurements and calculations concerning metatarsal and metacarpals, upper and lower limb structures, and the distribution of weight on the foot can lead to a better understanding of what the adaptive shift looks like mathematically. The analysis of Miocene hominoid adaptation can then be applied

to Pliocene adaptation and compared statistically. The largest emphasis on understanding the shift from quadrupedalism to bipedalism is placed on the need for more Miocene excavations. Only when there is more sufficient fossil specimens to analyze will the information become more apparent. The mind-set of current research into the emergence of bipedalism is biased towards the Pliocene epoch. The pitfall of this mind-set is that there are bipeds in the Pliocene, so a logical step is to examine the epoch previous to bipeds and to understand why there are no bipeds in the Miocene epoch and how they emerged in the Pliocene.

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