

“Ecomorphological analyses of a late Oligocene catarrhine-bearing community from Kenya”
Final Report
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Introduction

The Tertiary fossil record of Africa has offered several important primate species relevant to understanding crucial moments in primate evolution. Regrettably, the origin of apes has not been one of them. The reason for this has been a large temporal gap of African fossil mammals that would theoretically provide information on the origin of apes and the faunal interchange between Africa and Eurasia that reshaped the continent’s species diversity.

For millions of years, Africa was isolated from Eurasia by the Tethys Sea, at least from the Mid-Cretaceous through the Early Tertiary (Rögl 1999) even though some scholars agree there may have been some specific and short connections with other continents during this time (Mourer-Chauvire 1982; but see also Mourer-Chauvire 1999; Martin 2000; Mehrotra 2003; Yoder et al. 2003). The early Oligocene faunas of Africa were dominated by endemic and archaic groups, while the early Miocene was dominated by an entirely new set of immigrant taxa. This fundamental transition occurred sometime between ~30 and ~20 Ma, and has been called the African Mid-Tertiary Event (AMTE) (Rasmussen and Gutierrez 2009).

When the African and Turkish plates collided, it is hypothesized that a land-bridge between Africa and Eurasia was formed, resulting in a major faunal turnover throughout Africa near the Oligocene-Miocene boundary (Potts and Behrensmeyer 1992; Rögl 1999; Harrison 2005). But the details of this faunal transition have remained unclear due to the lack of relevant fossils (Fleagle and Reed 1999; Seiffert 2006).

Fortunately, the description of two Late Oligocene faunas from Kenya (Losodok and Nakwai) in 2006 and the paleontological reconnaissance undertaken at these sites during June 2007 with funds awarded by the L.S.B. Leakey Foundation and the American Philosophical Foundation helped reformulate some long standing questions in African paleoanthropology and offered the opportunity to fill in an important gap in our understanding of faunal dynamics in Africa during the middle part of the Tertiary, providing an environmental context for the earliest ape-like catarrhine primates of East Africa. Further discoveries in the field allowed us to ask questions such as: what is the taxonomic structure of the late Oligocene fauna in relation to that of earlier and later faunas from Africa? What is the ecological structure of the late Oligocene fauna from Kenya? And how does it compare to other African faunas?

For my doctoral dissertation, I intended to analyze those late Oligocene Kenyan fossil assemblages (Nakwai/Losodok, 24 – 27 Ma; Boschetto 1998, Boschetto et al. 1992) that fall, according to current radiometric dating, within a temporal gap between the famous faunas from the Fayum (early Oligocene, 29-30 Ma, Egypt; Seiffert 2006) and

Songhor (early Miocene, 20-18 Ma, Kenya; Pickford and Andrews 1981, Andrews et al. 1981). Nakwai/Losodok is particularly important because it has the oldest large body-sized ape-like catarrhine known (Leakey et al 1995). My appeal for funds to the L.S.B. Leakey Foundation was intended for: 1) visiting relevant museums to collect data on taxonomy, diet, locomotion, and body mass, and 2) conducting the comparative analyses between the late Oligocene Kenyan faunas and other African primate bearing localities (such as the above mentioned Fayum and Songhor), with the intention of using these tools to understand the faunal transition and the context in which large-bodied catarrhines evolved.

Objectives

The objectives of my research proposal were to: 1) describe the taxonomic and ecological structure of the late Oligocene fauna from Nakwai/Losodok, 2) to compare it taxonomically and ecologically to both early Oligocene and early Miocene faunal proxies (Fayum and Songhor), and 3) to use these comparisons to better understand the timing of the faunal interchange and the effects of environmental factors, if any, on the origin and evolution of typical Miocene apes. I planned to accomplish these by: 1) gathering information about the ecological structure of primate-bearing mammalian communities from the early Oligocene to the early Miocene of Africa, in terms of mammalian guilds, as interpreted by functional variables: diet, locomotion and body size; 2) evaluating taxonomical and ecomorphological variation over time in the faunas of Africa, before and after the AMTE, in order to answer questions such as: did guilds remain similar over time? Did immigrant taxa replace archaic taxa in some guilds? Which new guilds appeared?; and 3) generating an accurate characterization of the community structure of the late Oligocene fauna from Kenya in relation to the other faunal proxies.

Schedule and Activities

I traveled to a number of institutions around the globe in order to access the relevant collections. Originally, I intended to include the Oligocene fossil mammals from Chilga, Ethiopia, but a brief examination of the fossil remains revealed several problems: a) the number of recovered specimens was very limited, b) the site showed a clear bias against small mammals; and c) no fossil primates had been recovered from the site. Excluding Chilga, the comparisons were left between the upper-level quarries of the Fayum, Egypt, the Nakwai/Losodok fauna from Kenya, and the early Miocene site of Songhor, also in Kenya. The following is a list of the institutions visited for each fauna:

Fayum – The Fayum fossil collections examined for this research were housed in two institutions: the Duke University Lemur Center, Division of Fossil Primates, in Durham, North Carolina, USA, and the Geological Museum in Cairo, Egypt.

Nakwai/Losodok – The fossil collections from Northwest Kenya were housed in the National Museums of Kenya, Nairobi. Many of the fossils from Losodok and Nakwai had been collected in previous years by different researchers and some of the very early material from Losodok was registered as being housed at the Museum of Zoology, Division of Paleontology, at Berkeley University, California. I traveled to this institution to study these fossils, but many of them had been returned to the museum in Nairobi and had not properly been labeled as such. What was left behind in Berkeley were only casts, and the few original fossils that remained were too fragmentary to be included in this study.

Songhor– Most of the fossils from the Songhor collection was housed in the National Museums of Kenya, although some of the early collections were housed at the Natural History Museum in London, UK. Of great importance here are many of the early primates recovered from these sites.

I traveled to all these institutions between 2008 and 2010. At each institution I attempted to examine and identify every well preserved mammalian dental specimen with one or more teeth from all collections. I identified the fossils to the lowest possible taxonomic level, and in occasions in which I found identification difficult, I consulted other specialists. I also photographed good specimens from most species to facilitate the identification of species and to visually compare collections located in different institutions. In the cases where postcrania were available, I identified the element and attempted to assign them to possible taxa. Unfortunately most of the available postcrania were not associated with dentition, which made taxonomic allocation more difficult. A number of standard measurements were taken on the fossils. Sometimes, these depended on diagnostic characteristics of the order to which the remains belonged. In general, I recorded mesio-distal length and bucco-lingual width for all teeth. I also recorded height for those teeth that were unworn or whose wear was minimal. In addition, for carnivores and creodonts, as well as for proboscideans additional measurements were taken due to the morphology of their teeth. To record the measurements I used digital calipers.

During 2010, I dedicated most of my time to writing my dissertation and successfully defended it at the beginning of 2011. In analyzing the data collected, I accomplished my proposed objectives by 1) comparing the taxonomic profile of all three faunas in terms of richness and diversity measures, 2) reconstructing body mass, dietary preference, and locomotion patterns for all mammals, and finally 3) characterizing all assemblages in terms of environmental attributes to better understand the evolutionary patterns in play.

Results

Taxonomic Findings – I was originally expecting to see taxonomic similarities between Fayum and Nakwai/Losodok and significant differences between both of them and Songhor. This was based on the fact that it is well established that sometime during the late Oligocene to early Miocene, the continental plates of Africa and Eurasia collided, giving way to a mainly unidirectional influx of new mammal groups from Eurasia into Africa. This hypothesis was well supported by the data I collected, suggesting that, just as previously thought, the endemic archaic African fauna of the Oligocene indeed was not just a local occurrence in North Africa, but was also found in East Africa a few million of years later. The taxonomic distinctness of Songhor in comparison to the Oligocene faunas showed that a broad replacement of taxa occurred close to the Oligocene-Miocene boundary, and I was able to limit the timing of this event to ~24 - 20 Ma (pending further dating of the sediments).

Ecological Findings – I studied several ecological attributes of these faunas based on the idea that, even when taxonomic composition changes, guilds of mammals might remain unchanged if the environments are comparable. My comparisons revealed an interesting and cautionary aspect of paleoecological reconstructions: with the currently available data collected for the three horizons, the faunas are not ecologically comparable in terms of biodiversity. Nakwai/Losodok emerged as the most effectively diverse community of all three; however diversity indices are not only based on species richness but also on abundance of species, which is greatly compromised in the fossil record. This finding was clearly dominated by the even distribution of the sample across all species (a typical phenomenon found during the first stages of collection in a new place). Because I found that the sample size is currently too small to reconstruct the true biodiversity of Nakwai/Losodok, other means of comparison were used. An assessment of body mass representation, dietary preferences, and locomotion patterns also revealed differences among the faunas. In terms of ecological structure, I was expecting to find more differences between Fayum and Nakwai/Losodok than between the latter and Songhor. This was based on the fact that similarities between the primate fauna of Nakwai/Losodok and Songhor could be indicating environmental changes that affected both communities favoring the evolution of large-sized primates. This was not supported by my data. Nakwai/Losodok and Fayum emerged as more similar to each other than either one is to Songhor. The distribution of body mass across the different faunas did not reveal any particular patterns when compared to each other, however it showed a clear pattern when compared in terms of taxonomic groupings: an increment in the average body mass of almost all higher taxonomic groups was evident from the early Oligocene to the early Miocene. In terms of positional behavior, Fayum and Nakwai/Losodok showed almost identical proportions of terrestrial animals versus arboreal ones, but that pattern was found to be almost the exact opposite at Songhor. Lastly, the distribution of dietary preferences in the

communities remained fairly similar, possibly representing similarity of available resources, with only a few notable cases: there is an increase in the proportion of small herbivorous mammals towards the Miocene with a concomitant decrease in large-sized herbivores; and there is a significant increase in the number of insectivorous mammals at Songhor.

These findings suggest that Songhor is indeed sampling a relatively different environment: one in which small mammals and arboreal ones dominate the community. Characteristics such as those presented above are normally found in densely forested environments, and a comparison of published data of four different types of environments (forest, closed woodland, woodland/bushland transition, and bushland) with my data not only agrees with that position, but also places the Oligocene faunas more closely to closed woodland than to dense forest.

The Primates – It was a major goal of this study to understand the differences and similarities between the three horizons in terms of primate composition. Taxonomically, there is no specific overlap among the primates for each of the three faunas; however the primate composition of Nakwai/Losodok shows taxa that relate this fauna to both the earlier Fayum and the later Songhor (i.e. *Propliopithecus* sp. and *Kamoyapithecus*). Because the comparisons shown earlier place Nakwai/Losodok more closely to the Fayum than either one is to Songhor, I was interested in understanding if the differences observed for other mammals also held for primates.

The proportion of primate species relative to the total number of mammals remained nearly constant throughout time, but other attributes did not. Early Oligocene catarrhines were no larger than 10 kg, while the body mass of the late Oligocene *Kamoyapithecus* overlaps with the body mass ranges of larger Miocene apes. The trend toward larger body size in catarrhine primates had started by the late Oligocene, and it cannot be linked to competition with immigrant taxa, since no evidence of a full-fledged AMTE is recorded for this time period. Furthermore, in all three faunas, 75% of the recorded primates are frugivorous with the rest being mostly insectivorous, and all of them are reconstructed as arboreal animals with relatively similar locomotion patterns. No clear environmental evidence has emerged that can be attributed to the differences in body size distribution of primates. Nonetheless, general phyletic increase in size through time that characterizes other mammals may apply to primates as well.

The relative stability of Nakwai/Losodok compared to Fayum in terms of species diversity may indicate little change in the environment inhabited by those taxa. There may instead be a gradual conquering of new or previously vacant niches that starts in the late Oligocene with the large-sized *Kamoyapithecus* and reaches a peak during the early Miocene with the occupation of empty niches by rodents and a higher diversity of primates.

Conclusions

The generous grant provided by the L.S.B. Leakey Foundation helped me accomplish my main research objective of understanding the ecological context of evolution of the first large body-sized catarrhines.

The results I obtained agree on a reorganization of the Miocene community, with immigrants competing with some endemic mammals for their niches (e.g. new artiodactyls and perissodactyls vs. the endemic hyracoids and embrithopods, new carnivores vs. endemic creodonts), and both endemic and new mammals filling available niches, either new or previously unoccupied ones (e.g. explosive radiation of rodents and other small mammals, and new primate types).

By comparing the faunas, I was also able to constrain the timing of the AMTE to a few million years (24 – 20 Ma). I also found that Songhor stands out as a fauna that is environmentally different from the other two – a more forested environment with a higher proportion of arboreal and insectivorous mammals. Thus, the later radiation of apes during the Miocene is potentially related to more forested environments, such as Songhor. However, no environmental correlation or evidence for niche competition was found that would explain the appearance of the first large body-sized catarrhine, *Kamoyapithecus hamiltoni*, in the late Oligocene of Kenya. Yet, a phyletic tendency of higher groups to evolve into larger body sizes was observed across the spectrum of Oligocene mammals.

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