

Abstract of the Dissertation

African Papionin Phylogenetic History and Plio-Pleistocene Biogeography

by

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The cercopithecine primate tribe Papionini (Order: Primates; Family Cercopithecidae; Subfamily Cercopithecinae) are an extremely successful group of monkeys including the living macaques (*Macaca*), mangabeys (*Lophocebus*, *Cercocebus*), baboons (*Papio*), geladas (*Theropithecus*), mandrills, and drills (*Mandrillus*). The proliferation of the papionins is a well documented evolutionary phenomenon; in addition to the geographic and taxonomic diversity of the extant taxa, papionin monkeys are widely present and abundant members of the African Plio-Pleistocene fossil record. Despite their evolutionary success and relative abundance, the taxonomic and phylogenetic status of many Plio-Pleistocene papionins remains uncertain. Well supported phylogenetic hypotheses are essential to understanding the origins and evolution of this group: such phylogenetic trees can be used to infer the evolutionary sequence of the key characters in certain lineages as well as assess Plio-Pleistocene

biogeography. Comparative questions regarding biogeography can then be assessed and compared to contemporaneous hominin taxa.

In order to elucidate African papionin phylogenetic history, two main methods of quantitative morphological analysis were used: cladistic analysis of character data using parsimony and 3-D geometric morphometric analysis of the basicranium. In contrast to many previous phylogenetic studies of papionin craniodental data, here the effects of allometry are accounted for by applying the narrow allometric coding method to allometrically influenced morphological characters (Gilbert and Rossie, 2007). The results of the cladistic analysis (Chapter 2) strongly suggest that papionin phylogeny based on analysis of craniodental data and that based on molecular systematics are congruent and support a *Cercocebus/Mandrillus* clade as well as a *Papio/Lophocebus/Theropithecus* clade. In addition, within the *Papio/Lophocebus/Theropithecus* clade, a *Papio/Lophocebus* sister relationship is supported. If congruence between molecules and morphology is considered to be a prerequisite for accepting morphological data as being reliable, then papionin and, more broadly, primate morphology as evidenced by this data set must be considered a reliable source of phylogenetic information. When fossil taxa are added to the analysis, the two most parsimonious trees recovered suggest the following phylogenetic relationships (Chapter 3): *Parapapio*, *Pliopapio* and *Dinopithecus* are stem African papionins, *Theropithecus* is the most primitive crown African papionin taxon and the status of *T. baringensis* as a member of the genus *Theropithecus* is strongly supported, *Gorgopithecus* is closely related to *Papio* and *Lophocebus*, and *Papio quadratiostris*, as defined by Delson and Dean (1993) to include the later Omo Shungura material as well as some of the material from the Angolan Humpata Plateau, is closely related to *Mandrillus*, *Cercocebus*, *Procercocebus*.

To further investigate the potential signal contained within papionin cranial anatomy, I applied 3-D geometric morphometric techniques in a phylogenetic analysis of African papionin basicranial morphology (Chapter 4). Neighbor-joining and UPGMA clustering methods were used to generate phylogenetic hypotheses based on Euclidean distances between the average principal components (PC) matrices compiled by sex for each taxon. To adjust for the effects of allometry, PCs that

were significantly correlated with centroid size were excluded from the analysis. While the basicranium has been suggested to be a highly informative anatomical region in the study of other primate taxa, papionin basicranial shape, as represented by the PC matrices in this study, does not suggest the same phylogenetic relationships among taxa as the more comprehensive craniodental analyses in Chapters 2 and 3. It is difficult to properly adjust for the effects of allometry in multivariate analyses of shape, and it is likely that important phylogenetic information is contained within the information that is excluded on the size-correlated PCs. Further effort should focus on methodologies to adjust for allometric effects in multivariate morphometric analyses.

In light of the phylogenetic relationships hypothesized in Chapter 3, Chapter 5 investigates African papionin biogeography by treating biogeography as an unordered cladistic character and biogeographic regions such as South Africa, East Africa, North Africa, Central Africa, and West Africa as character states. The biogeographic character states for each fossil and extant papionin taxon are then mapped onto a cladogram derived from Chapter 3 and, using logic similar to the “progression rule” (Hennig, 1966), dispersal events are then inferred. The hypothesized biogeographic patterns of the African papionins during the Plio-Pleistocene are then compared to contemporaneous hominin biogeographic patterns. Results indicate that African papionin dispersal patterns largely mirror those of early hominins and, in at least one case, oppose general mammalian trends as well. Suggestions of unique behavioral adaptations to account for early hominin biogeography and dispersal patterns, therefore, seem unwarranted. In addition, African papionin monkeys appear to document a biogeographic connection between West and South Africa ~2.3 - 1.5 Ma.