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Allometry, sexual dimorphism, and phylogeny: A cladistic analysis of extant African papionins using craniodental data

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ABSTRACT

This study conducts a phylogenetic analysis of extant African papionin craniodental morphology, including both quantitative and qualitative characters. We use two different methods to control for allometry: the previously described narrow allometric coding method, and the general allometric coding method, introduced herein. The results of this study strongly suggest that African papionin phylogeny based on molecular systematics, and that based on morphology, are congruent and support a *Cercocebus*/*Mandrillus* clade as well as a *Papio*/*Lophocebus*/*Theropithecus* clade. In contrast to previous claims regarding papionin and, more broadly, primate craniodental data, this study finds that such data are a source of valuable phylogenetic information and removes the basis for considering hard tissue anatomy "unreliable" in phylogeny reconstruction. Among highly sexually dimorphic primates such as papionins, male morphologies appear to be particularly good sources of phylogenetic information. In addition, we argue that the male and female morphotypes should be analyzed separately and then added together in a concatenated matrix in future studies of sexually dimorphic taxa. Character transformation analyses identify a series of synapomorphies uniting the various papionin clades that, given a sufficient sample size, should potentially be useful in future morphological analyses, especially those involving fossil taxa.

Introduction

The Tribe Papionini (Order Primates; Family Cercopithecidae; Subfamily Cercopithecinae) is a successful group of medium-to-large-sized cercopithecine primates including the living macaques (*Macaca*), mangabeys (*Lophocebus*, *Cercocebus*), baboons (*Papio*), geladas (*Theropithecus*), mandrills, and drills (*Mandrillus*). As a testament to their adaptability and evolutionary success, papionins are geographically distributed throughout the Old World, with macaques (*Macaca*) occupying North Africa and Asia, and the rest of the papionins being spread throughout sub-Saharan Africa (*Cercocebus*, *Lophocebus*, *Mandrillus*, *Papio*, and *Theropithecus*). This latter group of taxa is identified here as the African papionins (Subtribe Papionina, *sensu* Strasser and Delson, 1987).

For much of the past half-century, three groups of African papionins were commonly recognized on the basis of morphological comparisons: mangabeys (*Cercocebus* and *Lophocebus*, often placed in a single genus, *Cercocebus*), baboons (*Papio* and *Mandrillus*, sometimes placed in a single genus, *Papio*), and geladas (*Theropithecus*) (e.g., Buettner-Janusch, 1963; Thorington and Groves, 1970; Jolly, 1972; Szalay and Delson, 1979; Strasser and Delson, 1987; Delson and Dean, 1993). The phylogenetic relationships among these groups were considered unclear, with some studies placing the mangabeys and baboons as sister taxa (e.g., Szalay and Delson, 1979; Strasser and Delson, 1987) and other studies hypothesizing geladas and baboons as sister taxa (e.g., Delson and Dean, 1993; Fig. 1). More recently, this view has changed dramatically, due in large part to the results of molecular studies (Barnicot and Wade, 1970; Barnicot and Hewett-Emmett, 1972; Cronin and Sarich, 1976; Hewett-Emmett et al., 1976; Disotell et al., 1992; Disotell, 1994, 2000; Harris and Disotell, 1998; Tosi et al., 1999, 2003; Harris, 2000). Rather than recognizing the mangabeys and baboons as monophyletic groups, molecular studies strongly argue that both groups are, in fact, diphyletic. Specifically, the terrestrial mangabeys (*Cercocebus*) are inferred to be closely related to the forest baboons (mandrills and drills, *Mandrillus*), and the arboreal mangabeys (*Lophocebus*) are inferred to be closely related to the savannah baboons (*Papio*) (Disotell et al., 1992; Disotell, 1994, 2000; Harris and Disotell, 1998; Tosi et al., 1999, 2003; Harris, 2000; Fig. 2a). The geladas, *Theropithecus*, are

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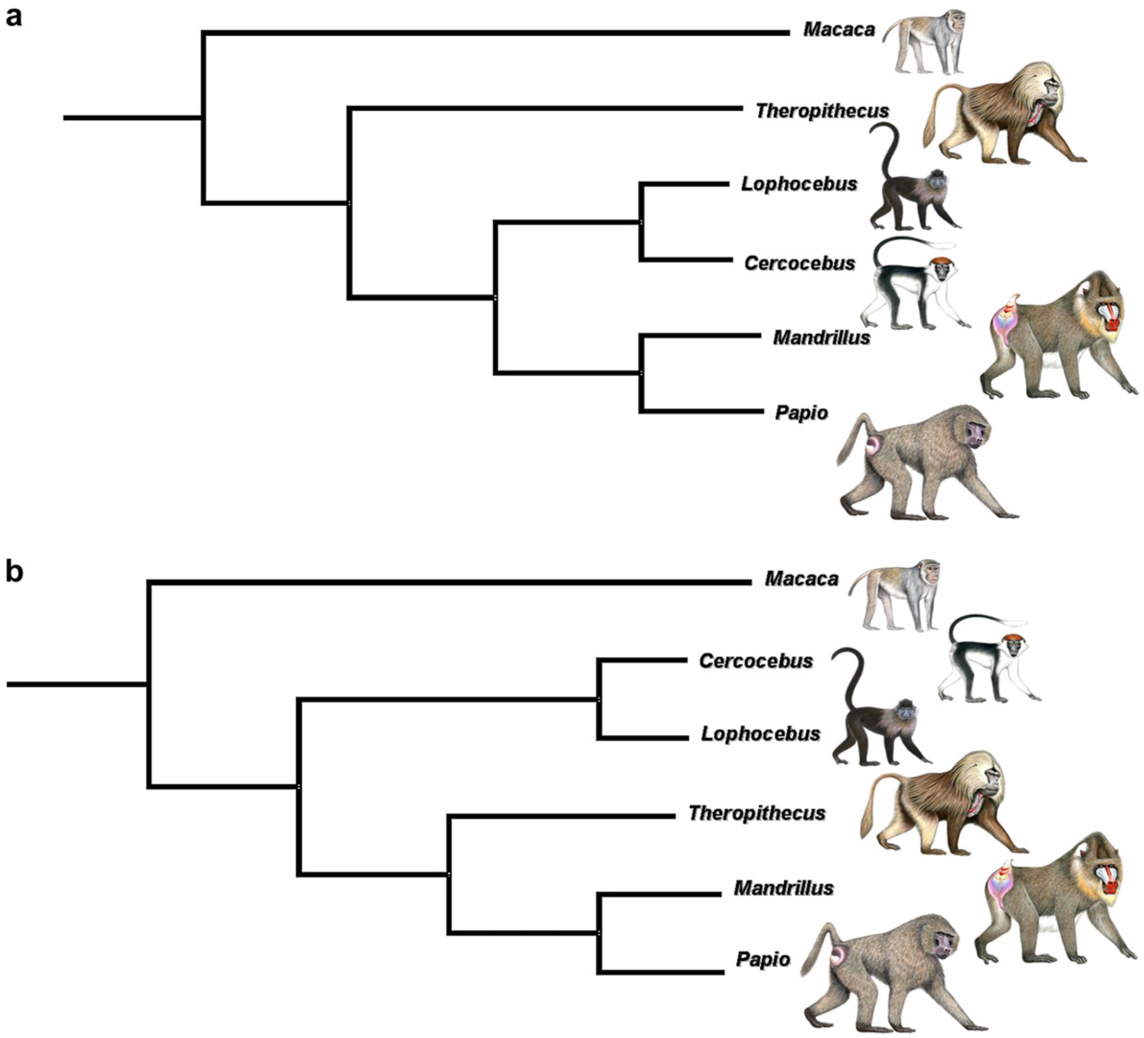

Figure 1. Traditionally hypothesized phylogenetic trees of the extant Papionini from morphological data. (a) Szalay and Delson (1979), Strasser and Delson (1987). (b) Delson and Dean (1993). Illustrations by Stephen Nash.

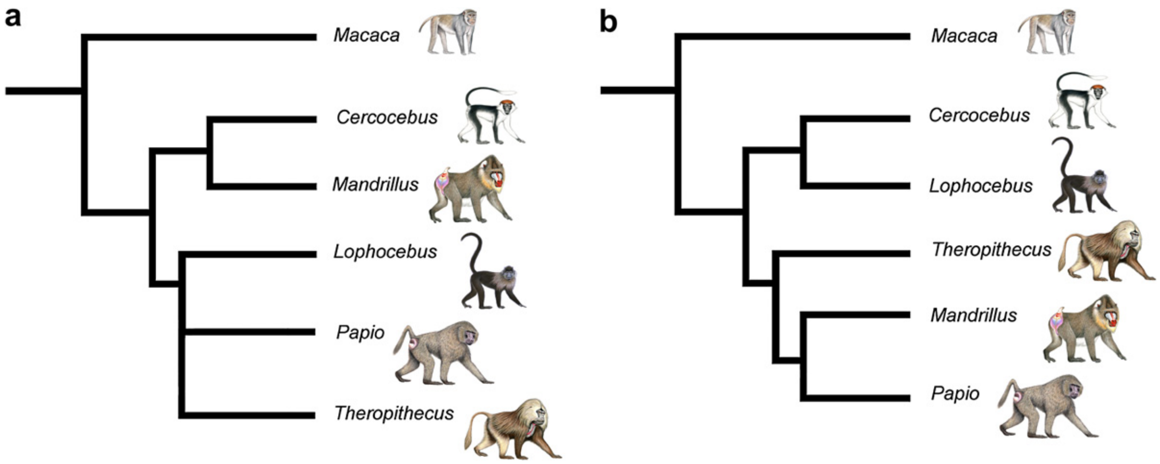

Figure 2. (a) Hypothesized consensus phylogenetic tree of the extant Papionini from molecular (mtDNA and Y-chromosome) data (Disotell et al., 1992; Disotell, 1994, 2000; Harris and Disotell, 1998; Tosi et al., 1999, 2003) compared with (b) the most parsimonious tree derived from the craniodental data set of Collard and Wood (2000, 2001), using *Macaca* rather than *Pan* as the outgroup. Illustrations by Stephen Nash.