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## Phylogenetic relationships of living and fossil African papionins: Combined evidence from morphology and molecules

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## ABSTRACT

African papionins are a highly successful subtribe of Old World monkeys with an extensive fossil record. On the basis of both molecular and morphological data, crown African papionins are divided into two clades: *Cercocebus/Mandrillus* and *Papio/Lophocebus/Rungwecebus/Theropithecus* (P/L/R/T), though phylogenetic relationships in the latter clade, among both fossil and extant taxa, remain difficult to resolve. While previous phylogenetic studies have focused on either molecular or morphological data, here African papionin molecular and morphological data were combined using both supermatrix and molecular backbone approaches. *Theropithecus* is supported as the sister taxon to *Papio/Lophocebus/Rungwecebus*, and while supermatrix analyses using Bayesian methods are largely unresolved, analyses using parsimony are broadly similar to earlier studies. Thus, the position of *Rungwecebus* relative to *Papio* and *Lophocebus* remains equivocal, possibly due to complex patterns of reticulation. *Parapapio* is likely a paraphyletic grouping of primitive African papionins or possibly a collection of stem P/L/R/T taxa, and a similar phylogenetic position is also hypothesized for *Pliopapio*. *?Papio izodi* is either a stem or crown P/L/R/T taxon, but does not group with other *Papio* taxa. *Dinopithecus* and *Gorgopithecus* are also stem or crown P/L/R/T taxa, but their phylogenetic positions remain unstable. Finally, *T. baringensis* is likely the most basal *Theropithecus* taxon, with *T. gelada* and *T. oswaldi* sister taxa to the exclusion of *T. brumpti*. By integrating large amounts of molecular and morphological data, combined with the application of updated parsimony and Bayesian methods, this study represents the most comprehensive analysis of African papionin phylogenetic history to date.

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### 1. Introduction

African papionins (subtribe Papionina) are a highly successful and well-studied group of Old World monkeys comprising six extant genera: *Papio*, *Mandrillus*, *Cercocebus*, *Lophocebus*, *Theropithecus*, and the recently discovered *Rungwecebus*. In addition to these living taxa, the African papionins have an abundant and speciose fossil record stretching back to the late Miocene (Szalay and Delson, 1979; Jablonski, 2002; Leakey et al., 2003; Frost et al., 2009; Jablonski and Frost, 2010; Harrison, 2011; Gilbert, 2013). Despite a long history of study, the genus-level relationships among living taxa remained ambiguous for many years due to gross morphological similarities that unite both the small-bodied mangabeys (*Cercocebus* and *Lophocebus*) and the large-bodied

“baboons” (*Papio*, *Theropithecus*, and *Mandrillus*). As molecular data became available, it was apparent that phylogenetic hypotheses based on these new data were incongruent with long held notions of relationships within the clade. Molecular studies have consistently indicated that both mangabeys and “baboons” are paraphyletic groupings, with *Cercocebus* shown to be more closely related to *Mandrillus*, and *Lophocebus* more closely related to *Theropithecus* and *Papio* (Cronin and Sarich, 1976; Disotell et al., 1992; Disotell, 1994; Harris and Disotell, 1998; Harris, 2000; Tosi et al., 2003; Perelman et al., 2011). Subsequently, with renewed evaluations of anatomy and corrections for the effects of allometry on cranial features, phylogenetic inferences stemming from morphological data came into alignment with those from molecular data, providing strong support for their shared phylogenetic hypothesis (Groves, 1978; Fleagle and McGraw, 1999, 2002; McGraw and Fleagle, 2006; Gilbert, 2007; Gilbert and Rossie, 2007; Gilbert et al., 2009a).

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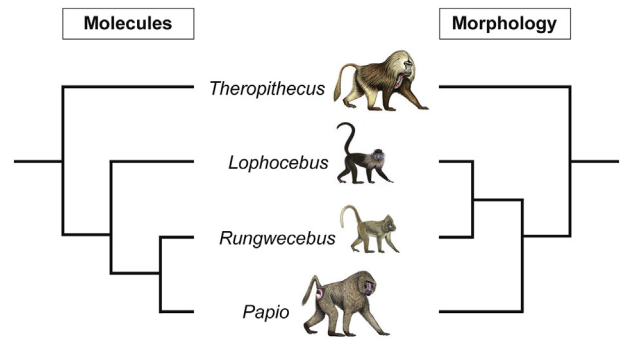
Despite this progress, agreement has yet to be reached on relationships among *Theropithecus*, *Papio*, and *Lophocebus*, although consensus is growing for *Theropithecus* as the basal member of the clade, sister to *Papio/Lophocebus* (Perelman et al., 2011; Gilbert, 2013; Guevara and Steiper, 2014). The addition of *Rungwecebus kipunji*, a rare and critically endangered African papionin discovered in 2005 (Jones et al., 2005; Davenport et al., 2006, 2008), to phylogenetic analyses has provided additional support for this topology. The *kipunji* is hypothesized to be closely related to either *Lophocebus* or *Papio*, to the exclusion of *Theropithecus*, though molecular and morphological data are currently in conflict with regard to its placement (Fig. 1). Morphological descriptions and analyses indicate that the *kipunji* is most similar to *Lophocebus* (Jones et al., 2005; Davenport et al., 2006; Gilbert et al., 2011a; Gilbert, 2013), while molecular analyses have found a closer relationship to *Papio* (Davenport et al., 2006; Olson et al., 2008). Subsequent molecular analyses support a topology where at least one population of *Rungwecebus* is nested within *Papio*, a result which has been interpreted as evidence of introgressive hybridization or that this taxon is hybrid in origin (Burrell et al., 2009; Zinner et al., 2009a; Roberts et al., 2010).

In addition to hypotheses regarding genus-level relationships among extant *Papio/Lophocebus/Rungwecebus/Theropithecus* (P/L/R/T) taxa, this study will further examine hypotheses put forth in the recent morphological analyses of extant and fossil African papionins by Gilbert and colleagues (Gilbert, 2013; DeVreese and Gilbert, 2015; Gilbert et al., 2016a, 2018). As with the extant taxa, most of the remaining phylogenetic uncertainty regarding fossil African papionins is among stem and crown members of the P/L/R/T clade (e.g., *Dinopithecus*, *Gorgopithecus*, and *?P. izodi*). The precise relationships of fossil *Cercocebus/Mandrillus* (C/M) taxa (*Soromandrillus* and *Procercocebus*) relative to the extant genera as well as relationships among the extant *Cercocebus* mangabeys are also not well-resolved. Likewise, when the fossil taxa are considered, relationships within the genus *Theropithecus* are still debated (e.g., Eck and Jablonski, 1984; Delson and Dean, 1993; Jablonski, 1993, 2002; Frost, 2001a; Jablonski et al., 2008). Finally, questions also remain at the base of the crown African papionin clade, particularly in regards to which fossil taxa are stem African papionins and which are members of the crown (e.g., *Parapapio* and *Pliopapio*).

Therefore, this paper will attempt to address the following major questions about fossil African papionin phylogeny: (1) What are the more detailed species-level relationships within the C/M clade, including the fossil taxa *Procercocebus antiquus* and *Soromandrillus quadratiostris*? (2) Is the primitive fossil genus *Parapapio*<sup>1</sup> a stem or crown African papionin taxon, and is it paraphyletic as suggested by Gilbert (2013)? (3) Are *Pliopapio* and *?P. izodi* stem African papionin taxa or members of the P/L/R/T clade? (4) What are the phylogenetic positions of *Gorgopithecus major* and *Dinopithecus ingens* relative to extant P/L/R/T taxa? (5) What are the relationships within the *Theropithecus* clade?

This study builds upon previous studies by utilizing available morphological and molecular data together to explore relationships among extant and fossil African papionins, focusing on those within the more poorly resolved P/L/R/T clade and on the placement of fossil taxa relative to each other and to living taxa. Two methods will be used to integrate previously published molecular and morphological datasets. The first method is the supermatrix approach (also called total evidence analysis), where all available

<sup>1</sup> Due to numerous primitive features shared with *Victoriapithecus*, "*Parapapio lothagamensis* is considered here and elsewhere (e.g., Gilbert, 2013) as a separate taxon relative to its congeners. Thus, we consider *Pp. ado*, *Pp. broomi*, *Pp. whitei*, and *Pp. jonesi* as constituting the genus *Parapapio* in this study.



**Figure 1.** Phylogenetic hypotheses stemming from morphological and molecular data disagree over the placement of *Rungwecebus*. Illustrations ©2013 Stephen D. Nash/IUCN SSC Primate Specialist Group. Used with permission.

character data for fossil and extant taxa is concatenated into a single matrix and analyzed simultaneously (Eernisse and Kluge, 1993; Gatesy et al., 2002; de Queiroz and Gatesy, 2007). The second is the molecular backbone approach (also called molecular scaffolding), in which the position of extant taxa are constrained based on the results of an analysis of molecular data, and a parsimony analysis of morphological data is used to determine the position of fossil taxa relative to those constraints (Springer et al., 2001). In addition to utilizing molecular and morphological data together, this study differs from the previous morphology-only analyses of fossil and extant papionins of Gilbert (2013) in that it analyzes data at the species rather than genus level. These methodological advancements make this analysis the most comprehensive evaluation of African papionin phylogeny to date.

A well-resolved phylogeny provides the necessary foundation for many of the evolutionary questions we seek answers to in paleoanthropology and evolutionary biology, more broadly. For example, the timing and order of appearance of key morphological features, an understanding of homology vs. homoplasy, and biogeographic hypotheses for any taxonomic group are reliant on the underlying hypotheses of evolutionary relationships (e.g., Hennig, 1966; Nelson and Platnick, 1981; Lockwood and Fleagle, 1999; Strait and Wood, 1999). Thus, to ask more detailed and interesting evolutionary questions about one of the best-studied extant primate radiations, the African papionins, a well-supported estimate of phylogenetic relationships in the groups is required. This study aims to provide the best estimate of fossil and extant African papionin phylogeny, with an updated interpretation of what the resulting trees might mean for the evolution of the clade.

## 2. Materials and methods

### 2.1. Morphological data and analysis

The morphological character matrix used in the present study is modified from Gilbert (2013) and Gilbert et al. (2016a) (see also Gilbert et al., 2018). Three hundred and sixty two morphological characters were scored for 18 extant species from eight genera (*Allenopithecus*, *Macaca*, *Cercocebus*, *Mandrillus*, *Lophocebus*, *Papio*, *Rungwecebus*, and *Theropithecus*) and 18 fossil taxa (*Dinopithecus ingens*, *Gorgopithecus major*, *Lophocebus* sp. nov. [a new large species of *Lophocebus* from Koobi Fora, previously referred to as *L. cf. albigena* by Jablonski et al. (2008) but almost double the size of the extant taxon], *Papio angusticeps*, *P. robinsoni*, *?P. izodi*, *Parapapio ado*, *Pp. broomi*, *Pp. jonesi*, *Pp. lothagamensis*, *Pp. whitei*, *Pliopapio alemui*, *Procercocebus antiquus*, *Soromandrillus quadratiostris*, *Theropithecus baringensis*, *T. brumpti*, *T. oswaldi darti*, *Victoriapithecus*

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