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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 quadratirostris*? (2) Is the primitive fossil genus *Parapapio*¹ 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

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 quadratirostris*, *Theropithecus baringensis*, *T. brumpti*, *T. oswaldi darti*, *Victoriapithecus*

¹ 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.

macinnesi). These fossils represent all of the currently described fossil African papionin genera and species that we recognize as valid taxa at the species level, and we include *P. angusticeps* (sometimes classified as a subspecies of the extant *P. hamadryas* using the Biological Species Concept; e.g., Delson, 1988) because it is often recognized at the species level as well (see Gilbert et al., 2018 for more complete discussion). The chronosubspecies *T. o. darti* was chosen to represent the *T. oswaldi* lineage because it is an early, morphologically primitive form that is well-documented with both craniodental and postcranial material, and it is therefore likely to be more informative regarding the phylogenetic position of the lineage. Later occurring forms of *T. oswaldi* reach very large sizes (up to the size of a female gorilla; e.g., see Delson et al., 2000), introducing the problem of allometric changes outside any regression of extant papionins along with the appearance of numerous other derived features, increasing the probability of autapomorphies, homoplasy, parallelisms, and long-branch attraction that can negatively affect analyses. For these reasons, it seems prudent to use a more primitive member of a chrono-lineage rather than a later-occurring, more derived one in broad-level phylogenetic analyses.

The matrix comprises qualitative, quantitative, ordered, and unordered characters scored separately for males and females, with the general allometric coding method applied to allometrically-influenced quantitative characters (see Gilbert et al., 2009a; Gilbert, 2013 for details). Relative to the previous analyses of

Gilbert and colleagues (Gilbert and Rossie, 2007; Gilbert et al., 2009a, 2016a; Gilbert, 2013), the current analysis is distinct in that it considers extant species rather than genera as the operational taxonomic units (OTUs), includes additional quantitative data from the PRIMO online database and Frost (2001a), and includes additional data and scorings from recent observations by the second author (CCG). For full sample sizes of craniodental characters by taxon, see Tables 1 and 2. In addition to the 318 craniodental characters listed in Gilbert (2013) (See Supplementary Online Material [SOM] Table S1), 44 postcranial characters (22 for each sex) previously noted to be phylogenetically informative were also added to the current matrix (SOM Table S2; see also Gilbert et al., 2016a,b, 2018). Postcranial samples for extant taxa are given in the references listed in SOM Table S2 with the exception of *Allenopithecus*, which was scored on the basis of three males (one adult, two subadults with most epiphyses fused to increase sample size) and one female. For any given character where postcranial character states were consistent among extant species within sampled genera, the genus average was used for any unsampled congeneric extant species. Fossil taxa with sampled postcrania include *T. o. darti*, *T. brumpti*, *Pp. jonesi*, *Pr. antiquus*, *?P. izodi*, *Pp. ado*, *Pp. lothagamenensis*, and *V. macinnesi*. The matrix used in this study is provided as a nexus file in the SOM.

A parsimony analysis of this character matrix (“morphology-only”) was executed in TNT (Goloboff et al., 2008) using traditional search methods (subtree pruning and regrafting [SPR] and tree

Table 1

Extant Taxa/OTUs included in this study.

Taxon	Quantitative character sample size (Mean, Median, Mode, Range)	Qualitative character sample size (Mean, Median, Mode, Range)
<i>Allenopithecus nigroviridis</i> Males	4.8, 5, 5, 0–5	5.9, 6, 6, 0–7
<i>Allenopithecus nigroviridis</i> Females	4.8, 5, 5, 0–7	6.4, 7, 7, 0–7
<i>Cercocebus agilis</i> Males	10.0, 8, 0, 0–23	14.2, 16, 16, 0–16
<i>Cercocebus agilis</i> Females	6.6, 8, 3, 0–13	11.5, 13, 13, 0–13
<i>Cercocebus atys</i> Males	5.6, 4, 11, 0–12	1.9, 2, 2, 0–4
<i>Cercocebus atys</i> Females	9.1, 5, 0, 0–21	1.8, 2, 2, 0–2
<i>Cercocebus chrysogaster</i> Males	3.3, 0, 0, 0–9	5.6, 6, 6, 0–6
<i>Cercocebus chrysogaster</i> Females	2.3, 0, 0, 0–6	3.6, 4, 4, 0–4
<i>Cercocebus torquatus</i> Males	16.5, 20, 20, 0–32	30.9, 32, 33, 0–35
<i>Cercocebus torquatus</i> Females	13.1, 16, 18, 0–18	12.9, 14, 15, 0–16
<i>Lophocebus albigena</i> Males	18.1, 18, 18, 0–32	29.5, 31, 32, 0–33
<i>Lophocebus albigena</i> Females	15.6, 17, 17, 0–36	30.1, 35, 36, 0–36
<i>Lophocebus aterritus</i> Males	1.5, 1, 1, 0–29	26.9, 29, 29, 0–29
<i>Lophocebus aterritus</i> Females	2.2, 2, 2, 0–22	19.7, 22, 22, 0–22
<i>Macaca</i> spp. ^a Males	20.5, 19, 20, 6–79	72.5, 78, 79, 0–80
<i>Macaca</i> spp. ^a Females	19.0, 18, 19, 0–73	60.3, 68, 73, 0–74
<i>Mandrillus leucophaeus</i> Males	24.1, 25.5, 31, 0–35	13.6, 15, 15, 0–17
<i>Mandrillus leucophaeus</i> Females	14.6, 17, 18, 0–20	17.5, 20, 20, 0–21
<i>Mandrillus sphinx</i> Males	6.7, 6, 6, 4–18	11.4, 12, 12, 0–14
<i>Mandrillus sphinx</i> Females	2.9, 2, 2, 0–15	7.9, 9, 9, 0–10
<i>Papio anubis</i> Males	9.0, 8, 7, 0–39	33.8, 36, 39, 0–39
<i>Papio anubis</i> Females	8.9, 10, 11, 2–17	13.5, 16, 17, 0–17
<i>Papio cynocephalus</i> Males	11.0, 13, 13, 0–17	13.7, 15, 15, 0–15
<i>Papio cynocephalus</i> Females	6.9, 8, 9, 0–11	5.2, 6, 6, 0–6
<i>Papio hamadryas</i> Males	1.2, 1, 0, 0–13	12.1, 13, 13, 0–13
<i>Papio hamadryas</i> Females	0.5, 0, 0, 0–2	1.4, 2, 2, 0–2
<i>Papio kindae</i> Males	4.3, 6, 0, 0–13	11.1, 13, 13, 0–13
<i>Papio kindae</i> Females	4.0, 6, 0, 0–17	13.8, 15, 17, 0–17
<i>Papio papio</i> Males	1.6, 1, 1, 0–10	9.4, 10, 10, 0–10
<i>Papio papio</i> Females	0.0, 0, 0, 0–1	0.9, 1, 1, 0–1
<i>Papio ursinus</i> Males	3.1, 4, 0, 0–36	32, 34.5, 36, 0–37
<i>Papio ursinus</i> Females	2.1, 3, 3, 0–11	8.1, 9, 11, 0–11
<i>Theropithecus gelada</i> Males	17.7, 19, 21, 0–22	16.6, 17, 17, 0–17
<i>Theropithecus gelada</i> Females	16.9, 20, 21, 0–22	5.4, 6, 6, 0–6
MALES AVERAGE	9, 9, 9, 1–25	20, 22, 22, 0–23
FEMALES AVERAGE	8, 8, 8, 0–18	13, 15, 15, 0–16

Notes: See also Table 2 and SOM Tables S1 and S2 for fossil OTU sample sizes and lists of characters and character states.

^a *Macaca* spp. was scored based on *Mc. mulatta*, *Mc. fascicularis*, *Mc. nemestrina*, and *Mc. sylvanus* (Gilbert, 2013).

Table 2
Fossil Taxa/OTUs recognized and used in this study.

Fossil taxon/OTU	Sample size (M, F)	Key specimens	Source
<i>Dinopithecus ingens</i>	(4, 7)	SB 7, SK 401, SK 542a, SK 546, SK 548, SK 553, SK 554, SK 574, SK 599, SK 600, SK 603	Freedman 1957; Gilbert, 2013; this study
<i>Gorgopithecus major</i>	(6, 4)	KA 150, KA 153, KA 154, KA 192, KA 524/676, KA 605, KA 944, KA 1148, SK 604a, OLD 1962/S.196, FLK NNI 1011	Freedman 1957; Gilbert et al., 2016a; this study
<i>Lophocebus</i> sp. nov.	(6, 8)	KNM-ER 594, KNM-ER 595, KNM-ER 827, KNM-ER 898, KNM-ER 965, KNM-ER 1661, KNM-ER 3090, KNM-ER 6014, KNM-ER 6063, KNM-ER 18922, KNM-ER 40476, KNM-ER 44260, KNM-ER 44262, KNM-ER 44317	Jablonski et al., 2008; Gilbert, 2013; this study
<i>Papio angusticeps</i>	(9, 9)	CO 100, CO 101, CO 102, CO 115/103, CO 134B/D, CO 135A, KA 156, KA 161, KA 165, KA 166, KA 167C, KA 168, KA 188, KA 194, KB 94, GV 4040, UW 88-886, UCMP 56767	Freedman, 1957; McKee and Keyser, 1994; Gilbert et al. 2015, in press; this study;
? <i>Papio izodi</i>	(3, 9)	SAM 11728, SWP Un 2, T13, T89-11-1, TP4/M681/AD946, TP7/M684/AD992, TP10, TP11, TP12, UCMP 125854, UCMP 125855, UCMP 125856	Freedman, 1957; Freedman, 1961; Freedman, 1965; Heaton, 2006; Gilbert, 2013; Gilbert et al., 2015, in press; this study
<i>Papio robinsoni</i>	(8, 15)	SK 406, SK 407, SK 408, SK 409, SK 416, SK 421, SK 549, SK 555, SK 557, SK 558, SK 560, SK 562, SK 565, SK 566, SK 571B, SK 602, SK 3211B, SB 2, M3147, UCMP 56797, UCMP 56786, BF 38, SK II 25	Freedman, 1957; Freedman, 1965; Freedman and Brain, 1977; Gilbert et al., 2015, in press; this study
<i>Soromandrillus quadratirostris</i>	(4, 5)	NME-USNO, NME Omo 47-1970-2008, NME L 4-13b, NME Omo 42-1972-1, NME Omo L-185-6, NME Omo 75N (71)-C2, DGUNL LBA02, DGUNL LBA03, DGUNL LBA06	Iwamoto, 1982; Eck, 1977; Eck and Jablonski, 1984; Delson and Dean, 1993; Gilbert et al., 2009b; Gilbert, 2013; this study
<i>Parapapio ado</i>	(2, 4)	BMNH M14940, EP 1579/98, LAET 74-242/243/244, LAET 75-483, LAET 75-1209, LAET 78-5269, MB MA 42444/42445/42458	Leakey and Delson, 1987; Harrison, 2011; this study
<i>Parapapio broomi</i>	(18, 17)	M202/MP2, M211/MP11, M2961, M2962/MP76, M2978/MP92, M3037, M3067, STS 254, STS 255, STS 258, STS 264, STS 267, STS 297, STS 331, STS 332, STS 335, STS 337, STS 338, STS 339, STS 360, STS 363, STS 378A, STS 379, STS 390A, STS 393, STS 396A, STS 397, STS 409, STS 411A/B, STS 469, STS 534, STS 542, STS 562, STS 564, BF 43	Freedman, 1957; Freedman, 1960; Maier, 1970; Freedman and Stenhouse, 1972; Eisenhart, 1974; Gilbert, 2013; this study
<i>Parapapio jonesi</i>	(4, 12)	AL 363-15, AL 363-1, M215/MP15, M218/MP18, M3051/MP 165, STS 250, STS 284, STS 313, STS 355, STS 372, STS 547, STS 565, SWP (STW) 27, SWP 389, SWP 1728, SWP 2947	Freedman, 1957; Freedman, 1960; Maier, 1970; Freedman and Stenhouse, 1972; Eisenhart, 1974; Freedman, 1976; Frost and Delson, 2002; Gilbert, 2013; this study
" <i>Parapapio</i> " <i>lothagamensis</i>	(5, 2)	KNM-LT 419, KNM-LT 448, KNM-LT 449, KNM-LT 23065, KNM-LT 23091, KNM-LT 24111, KNM-LT 24136	Leakey et al., 2003; this study
<i>Parapapio whitei</i>	(5, 5)	M3072, MP221, MP223, STS 259, STS 266, STS 352, STS 359, STS 374, STS 389, STS 563	Freedman, 1957; Maier, 1970; Freedman, 1976; Freedman and Stenhouse, 1972; Eisenhart, 1974; Gilbert, 2013; this study
<i>Pliopapio alemui</i>	(4, 6)	AME-VP-1/64, ARA-VP 1007, ARA-VP 1723, ARA-VP 1/73, ARA-VP 1/133, ARA-VP 1/563, ARA-VP 1/1006, ARA-VP 1/2553, ARA-VP 6/437, ARA-VP 6/933	Frost, 2001b; Frost et al., 2009; Gilbert, 2013; this study
<i>Procercocobus antiquus</i>	(5, 14)	SAM 4850, SAM 5356, SAM 5364, M3078, M3079, T11, T14, T17, T18, T20, T25, T21, T89-154, T88-17, TP8, TP9, TP13, UCMP 56624, UCMP 56653, UCMP 56694, UCMP 56821/125956	Gilbert, 2007; Gilbert, 2013; this study
<i>Theropithecus baringensis</i>	(2, 0)	KNM-BC 2, KNM-BC 1647	Leakey, 1969; Delson and Dean, 1993; Eck and Jablonski, 1984; this study
<i>Theropithecus brumpti</i>	(12, 6)	NME L17-45, NME 32-154, NME L32-155, NME L122-34, NME L338Y-2257, NME L345-3, NME L345-287, NME L576-8, KNM-TH 46700, KNM-WT 16749, KNM-WT 16806, KNM-WT 16808, KNM-WT 16828, KNM-WT 16888, KNM-WT 17571, KNM-WT 17555, KNM-WT 17560, KNM-WT 39368CX	Eck and Jablonski, 1987; Jablonski et al., 2008; Gilbert et al., 2011b; this study
<i>Theropithecus oswaldi darti</i>	(12, 6)	M2974, M3073, MP44, MP217, MP222, NME AL 58-23, NME AL 134-5, NME AL 142-19, NME AL 144-1, AL 153-14, NME AL 163-11, NME AL 186-17, NME AL 187-10, NME AL 196-3, NME AL 205-1, NME AL 208-10, NME AL 321-12, NME AL 416-2	Eck, 1993; Eck and Jablonski, 1987; Freedman, 1957; Maier, 1970; Maier, 1972; this study
<i>Victoriapithecus macinnesi</i>	(4, 2)	KNM-MB 18993, KNM-MB 21027, KNM-MB 27876, KNM-MB 29100, KNM-MB 29158, KNM-MB 31281	Benefit, 1987; Benefit, 1993; Benefit and McCrossin, 1991; Benefit and McCrossin, 1997; this study

Notes: Sample sizes are listed for key specimens, identifiable to sex, used in character analysis. For each taxon, measurements and character state assignments were made and supplemented with additional data PRIMO from (access courtesy of Eric Delson) and the major sources listed for each taxon.

bisection and reconnection [TBR]). Heuristic searches were performed across 10,000 replicates. *Victoriapithecus macinnesi*, *Allenopithecus nigroviridis*, *Pp. lothagamensis*, and *Macaca* were sequentially constrained as outgroups. Outgroup selection is critically important for setting the polarity of character states in the analysis and multiple outgroups have been demonstrated to increase phylogenetic accuracy (Strait and Grine, 2004). Morphologically, these outgroups are the most complete fossil and extant taxa that are widely recognized as being phylogenetically close to the African papionins, representing primitive cercopithecoids (*Victoriapithecus*), primitive cercopithecins (*Allenopithecus*), and primitive papionins (*Pp. lothagamensis* and *Macaca*). Bremer branch supports and bootstrap values (1000 replicates) were calculated in TNT to summarize node support. Bremer supports were calculated by searching incrementally for suboptimal trees up to 15 steps longer than the most parsimonious trees.

2.2. Molecular data and analysis

The loci and taxa sampled to create the molecular character matrix follow those used in Guevara and Steiper (2014), which itself was primarily composed of sequences deposited by Perelman et al. (2011). Sequence data for 57 independent loci for *Mc. mulatta*, *P. anubis*, *P. hamadryas*, *P. papio*, *L. aterrimus*, *L. albigena*, *T. gelada*, *C. agilis*, *C. chryogaster*, *C. torquatus*, *Mn. leucophaeus*, and *Mn. sphinx* were compiled from GenBank using the accession numbers provided in Guevara and Steiper (2014) and Perelman et al. (2011). *R. kipunji* and *A. nigroviridis* were added to this matrix. Sequence data for *R. kipunji* is scarce, with only five of 57 loci available on GenBank (CD4 [EU600174]; COII [DQ381471.1]; IntX [EU600173]; LPA [EU600172]; TSPY [DQ381472]). A multiple sequence alignment was performed on each locus using the online interface of the program MUSCLE (Edgar, 2004a,b). Minimal by-eye corrections were made. All aligned sequences were then concatenated into a single matrix (61,809 bp) using SequenceMatrix v.1.7.8 (Vaidya et al., 2011). To accommodate for non-conformity in sequence lengths among taxa, long gaps at the beginning and ends of individual sequences were scored as missing when the file was exported from SequenceMatrix.

A partitioned analysis was performed in MrBayes v3.2 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012) using Bayesian optimization (“molecular-only”). Models of evolution for each sequence and selection of priors followed those specified in Guevara and Steiper (2014). Model parameters were allowed to vary across partitions and all parameters except tree topology and branch lengths were unlinked across partitions. *A. nigroviridis* and *Mc. mulatta* were constrained as successive outgroups. Two runs, each with 4 chains, were executed for 50 million Markov chain Monte Carlo (MCMC) generations. Parameters were sampled every 2000 generations. A halfcompat consensus tree was constructed after discarding the first 35% of trees produced by each run. Convergence of the runs was evaluated using average standard deviations of split frequencies along with a combination of diagnostics from the MrBayes sump and sumt outputs, including chain swap information and potential scale reduction factors (PSRFs). Posterior probabilities were used to assess node support.

2.3. Combined molecular and morphological data and analysis

Two methods, the molecular backbone and the supermatrix, were used to analyze molecular and morphological data together. In order to create the “molecular backbone,” extant taxa were constrained to reflect the topology of the Bayesian consensus tree resulting from the molecular-only analysis. Seven ingroup constraints were enforced in TNT: (1) *Cercocebus/Mandrillus* (C/M), (2)

Cercocebus, (3) *Mandrillus*, (4) P/L/R/T, (5) P/L/R, (6) *Lophocebus*, and (7) *Papio/Rungwecebus*. A constrained parsimony analysis of the morphology-only matrix, using the same parameters as outlined above, was then performed to place the fossil taxa among these constraints. The placement of fossil taxa relative to extant taxa was not fixed, leaving them to move freely within the ingroup constraints.

The matrix for the supermatrix analysis was created by merging the morphological and molecular data into a single matrix, resulting in a total of 62,171 characters. All molecular characters were scored as missing (?) for fossil taxa. The molecular dataset has fewer species of *Papio* represented than does the morphological dataset, so *P. ursinus*, *P. cynocephalus*, and *P. kindae* were also scored as missing for all molecular characters, making the inferred relationships of these taxa reliant on morphological data. This may affect relationships within the *Papio* clade, especially with regard to the fossil *Papio* taxa *P. angusticeps* and *P. robinsoni*, which have been suggested to share primitive baboon morphology with *P. kindae* and/or *P. cynocephalus* in particular (e.g., Delson, 1988; Gilbert et al., 2018), and on the position of *Rungwecebus*, which among species of *Papio* may be most closely related to, or have hybridized with, *P. cynocephalus* (Burrell et al., 2009; Zinner et al., 2009a; Roberts et al., 2010).

The supermatrix was analyzed in both TNT and MrBayes, using parsimony and Bayesian criteria, respectively. Two versions of the matrix were created to permit for different treatment of gaps in TNT: one that treated mid-sequence gaps in molecular data as missing data points, and one that scored gaps as a fifth character state. The latter treatment accounts for any phylogenetically-informative information that may be garnered from the insertion and deletion events that gaps represent (Giribet and Wheeler, 1999). The treatment of gaps did not influence tree topology or support, and will not be discussed further. MrBayes treats mid-sequence gaps as missing data points by default. Again, *V. macinnesi*, *A. nigroviridis*, *Pp. lothagamensis*, and *Macaca* were constrained as successive outgroups. The Bayesian analysis has 58 partitions, accounting for each of the 57 independent molecular loci and the morphological dataset. Settings for molecular partitions follow those used in the molecular-only analysis. The morphology partition was run under the Mk model (Lewis, 2001).

Trees were visualized and edited using FigTree v.1.4.3 (Rambaut, 2016), and character transformation analyses were then performed on the consensus trees in Mesquite v. 3.31 (Maddison and Maddison, 2017).

3. Results

Overall, the results presented here are largely congruent with those of previous studies and with one another. Consensus trees are presented in Figures 2–5 and the most parsimonious trees (MPTs) are available in the SOM. All analyses resolved the extant C/M clade, and all but the Bayesian supermatrix resolve the extant P/L/R/T clade. Species of the extant genera *Cercocebus*, *Mandrillus*, and *Lophocebus* form well-supported monophyletic clades in all analyses. Resolution and support are consistently poor within *Papio*, and extant members of the genus do not form a monophyletic clade in the morphology-only analysis (Fig. 3), Bayesian supermatrix analysis (Fig. 5c), or in the strict consensus tree of the parsimony supermatrix analysis (Fig. 5b). *Papio* is monophyletic in the majority-rule consensus tree of the parsimony supermatrix analysis (Fig. 5a) and in the molecular backbone trees (Fig. 4), though in the latter it has been constrained that way to reflect the topology of the molecular-only analysis (Fig. 2). Bootstrap and Bremer support values, as well as posterior probabilities, are generally low for morphology-only and combined analyses, with the exception of

Figure 2. Results of the molecular-only partitioned Bayesian analyses. Posterior probabilities are shown above nodes. Blue circles indicate the clades that are constrained in the molecular backbone analysis: (1) C/M, (2) Cercopithecus, (3) Mandrillus, (4) P/L/R/T, (5) P/L/R, (6) Lophocebus, and (7) Papio/Rungwecebus. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

clades composed of species of the extant genera mentioned above and *Theropithecus*. The topology of the molecular-only analysis mirrors that of Guevara and Steiper (2014), and posterior probabilities are high for most nodes, though the addition of *Rungwecebus* reduces resolution and support within *Papio*.

Theropithecus, composed of *T. gelada* and the fossil species *T. brumpti*, *T. o. darti*, and *T. baringensis*, is among the most highly supported of clades, and the only clade mainly composed of fossil taxa with high support in combined and morphology-only analyses. *Theropithecus* is resolved as the sister taxon to a clade comprised of *Papio*, *Lophocebus*, *Rungwecebus*, and their fossil relatives in the majority-rule consensus trees of the morphology-only and parsimony supermatrix analyses (and is constrained as such in the backbone analysis following the results of the molecular-only analysis), adding to the growing body of support for this branching pattern. In the strict consensus trees this node collapses and a polytomy is formed by *Theropithecus*, the P/L/R clade, ?*P. izodi*, *D. ingens*, and *G. major* (and several other fossil taxa, varying by tree). Review of the MPTs (SOM) for each analysis indicates that the likely reason for the collapse of this basal node is not related to a lack of support for a (*Theropithecus* (*Papio*/*Lophocebus*/*Rungwecebus*)) topology, but rather the uncertain placement of several fossil taxa relative to this node. The Bayesian supermatrix analysis provides very low resolution among taxa generally inferred to be stem or crown members of P/L/R/T, though the monophyly of *Theropithecus* is well-supported.

Rungwecebus is found to group with *Lophocebus* on the basis of morphological data, and with *Papio* on the basis of molecular data, as in previous studies from which these data were drawn. The molecular-only analysis places *Rungwecebus* within *Papio*, in a clade with *P. hamadryas* and *P. anubis*. The molecular backbone analysis was constrained to reflect this *Rungwecebus*/*Papio* grouping at the genus level, however, this node collapses in the consensus trees and *Rungwecebus* is part of a polytomy formed by

Lophocebus sp. nov., extant *Lophocebus*, and *Papio*. The collapse of this node reflects the fact that *Rungwecebus* is grouping with *Lophocebus* sp. nov. in the majority of MPTs, and in turn, the relationship of this clade to extant *Lophocebus* or *Papio* is poorly resolved. A similar topology is inferred from the parsimony supermatrix analysis, while in the Bayesian supermatrix consensus tree *Rungwecebus* is part of a large polytomy that includes all members of the ingroup.

In the C/M clade, *Soromandrillus quadratirostris* is invariably placed as sister to *Mandrillus* in consensus trees resulting from parsimony inference. The position of *Pr. antiquus* relative to *Cercocebus* and *Mandrillus*/*Soromandrillus* is equivocal. This taxon is part of a polytomy with *Cercocebus* and *Mandrillus*/*Soromandrillus* in the morphology-only consensus trees as well as the strict consensus trees for the molecular backbone and parsimony supermatrix analyses. In the majority of MPTs resulting from these combined analyses, *Pr. antiquus* is the sister taxon to the latter clade. In the Bayesian supermatrix analysis, the positions of these fossil taxa are unresolved, and they fall outside the extant C/M clade as part of the ingroup polytomy.

The remaining ingroup fossils, aside from *Pp. ado*, are generally inferred to be stem or crown members of the P/L/R/T clade. *Dinopithecus ingens* falls within the P/L/R/T clade, but its relationships to other taxa within the clade are equivocal. In the morphology-only, molecular backbone, and supermatrix strict consensus trees it forms a polytomy with some configuration of *Theropithecus*, *Lophocebus*, *Papio*, *Rungwecebus*, and *Gorgopithecus*; however, in the majority-rule consensus trees of the combined analyses it is the sister taxon to *Theropithecus*. *Gorgopithecus major* is also placed within the P/L/R/T clade as part of the same polytomy as *D. ingens* in the strict consensus trees. In the majority-rule trees, *G. major* is found to be either a stem member of the P/L/R/T (morphology-only) or the P/L/R clade (molecular backbone and parsimony supermatrix).

In all analyses performed here, *Parapapio* is paraphyletic. *Pp. ado* is consistently the sister taxon to all African papionins, while *Pp. broomi*, *Pp. whitei*, and *Pp. jonesi* are typically stem members of the P/L/R/T clade. In all MPTs resulting from the parsimony supermatrix and all but two MPTs in the molecular backbone analysis, *Pp. ado* is supported as the only stem African papionin in the analysis. In two of 14 MPTs resulting from the molecular backbone analysis, *Pp. ado* is inferred to be the sister to *Pl. alemui*. *Parapapio whitei* and *Pp. jonesi* invariably form a clade, even in the otherwise poorly resolved Bayesian supermatrix consensus tree, while *Pp. broomi* branches earlier. In the strict consensus tree resulting from the molecular backbone analysis, *Pp. broomi* and *Pp. whitei*/*Pp. jonesi* are part of a polytomy at the base of the African papionin clade. *Pliopapio alemui* and ?*P. izodi* follow a similar pattern, diverging after *Pp. broomi* and *Pp. whitei*/*Pp. jonesi* sequentially as stem members of the P/L/R/T clade in the majority-rule trees derived from the morphology-only and combined analyses.

The fossil taxa *P. angusticeps* and *P. robinsoni* are nested within the *Papio* clade in the combined analyses where extant *Papio* is found to be monophyletic. Both fossil taxa are inferred to be members of the crown *Papio* clade in all of the supermatrix and backbone MPTs, however this node collapses in the strict consensus tree of the parsimony supermatrix analysis as a result of the uncertain position of *Lophocebus* sp. nov. and *Rungwecebus* relative to this node. Within *Papio*, *P. robinsoni* is always found to be the sister to *P. hamadryas*, while the position of *P. angusticeps* is more variable. In the backbone analysis, *P. angusticeps* is inferred to be the sister to the *P. robinsoni*/*P. hamadryas* clade in all MPTs. *Papio* is not monophyletic in the morphology-only analysis, and in the resulting consensus trees *P. angusticeps* is sister to *P. kindae*, while *P. robinsoni* is more basal.

Figure 3. Results of the morphology-only analysis. a) Majority-rule (>50%) and b) strict consensus tree summarizing 6 MPTs from the parsimony analysis of the morphology-only dataset (TL = 2104, CI = 0.286, RI = 0.446). Bremer support values and bootstrap support values (1000 replicates; >50%) are shown above and below nodes, respectively. * indicates fossil taxa.

Figure 4. Results of the backbone analysis. a) Majority-rule and b) strict consensus trees summarizing 14 MPTs resulting from the molecular backbone analysis (TL = 2125, CI = 0.289, RI = 0.455). Seven constraints were enforced in TNT to reflect the topology of the molecular-only tree shown in Figure 2: (1) C/M, (2) *Cercocebus*, (3) *Mandrillus*, (4) P/L/R/T, (5) P/L/R, (6) *Lophocebus*, and (7) *Papio/Rungwecebus*. Some of these clades have collapsed in the consensus trees due to the uncertain placement of fossil taxa around constrained nodes. Bremer support values and bootstrap support values (1000 replicates; >50%) are shown above and below nodes, respectively. * indicates fossil taxa.

Figure 5. Results of the supermatrix analyses. a) Majority-rule consensus tree of the maximum parsimony analysis, b) strict consensus tree of the maximum parsimony analysis, and c) Bayesian majority consensus tree. For the maximum parsimony analysis, consensus trees are summarizing 13 MPTs resulting from simultaneous analysis of molecular and morphological data (TL = 4228, CI = 0.594, RI = 0.562). Bremer support values and bootstrap support values (1000 replicates; >50%) are shown above and below nodes, respectively. Posterior probabilities are shown above nodes in the Bayesian majority consensus tree. * indicates fossil taxa.

4. Discussion

4.1. Combined methods of phylogenetic analysis

As genetic sequence data have become increasingly easy to access, the popularity of molecular systematics has swelled and, with it, the perception that hard tissue morphology is an unreliable tool

for phylogenetic inference (e.g., [Pilbeam, 2000](#); [Collard and Wood, 2000, 2001](#); [Scotland et al., 2003](#)). Regardless of the issues that exist with morphological characters, they remain our best and in many cases only means of forming phylogenetic hypotheses for the relationships between fossil and extant taxa ([Gauthier et al., 1988](#); [Donoghue et al., 1989](#); [Wiens, 2004](#); [Gilbert and Rossie, 2007](#)). Additionally, multiple studies suggest that the inclusion of fossil

taxa, even when fragmentary, may reveal patterns of character change and unique combinations of primitive and derived characters that are not observed in extant taxa, thereby improving tree resolution (e.g., Springer et al., 2001; Wiens, 2003a; Strait and Grine, 2004; de Queiroz and Gatesy, 2007). This utility is not limited to fossil taxa; increasing the absolute number of taxa in an analysis, fossil or extant, has been shown to have favorable effects in diminishing the strength of long branch attraction (Wheeler, 1992; Rannala et al., 1998; Zwickl and Hillis, 2002; Kearney and Clark, 2003; Wiens, 2003a, 2005; Pattinson et al., 2015). This result holds true even when sampled taxa have large amounts of missing data (Wiens, 1998; Wiens, 2003a,b; 2006; Wiens and Morrill, 2011; Pattinson et al., 2015), and thus the benefits of increased taxon sampling outlined above generally outweigh any arguments for their exclusion. For these reasons, if the overall goal is phylogenetic accuracy, it is advisable to sample taxa as densely as possible even when data are missing for many characters, as in the case of *Rungwecebus* and many fossil papionins.

The use of all available information in hypothesis formation is a fundamental concept in science, and has the capacity to increase the explanatory power of resulting hypotheses (Kluge, 1989; Nixon and Carpenter, 1996; DeSalle and Brower, 1997). In an effort to include as many independent lines of evidence for the maximum number of taxa, methods that combine molecular data with traditional morphological characters have been devised. By combining multiple types of data, it is possible to employ the vast amount of sequence data available for extant taxa and anatomical features for both extant and fossil taxa simultaneously. Integrating molecular and morphological character data has been accomplished using a variety of approaches, including the supermatrix and molecular backbone methods utilized here. The supermatrix approach concatenates large amounts of data together into a single character matrix and analyzes them simultaneously using parsimony or model-based optimization criteria (Eernisse and Kluge, 1993; Gatesy et al., 2002; de Queiroz and Gatesy, 2007). The major advantage of this method is that it allows for simultaneous analysis of diverse character data, including data drawn from fossils. Because data are analyzed simultaneously, there is potential to maximize weak phylogenetic signals that are not expressed when partitions (e.g., molecular and morphological) are analyzed separately (de Queiroz and Gatesy, 2007). Even when there are conflicting signals caused by convergence or incomplete lineage sorting among gene sequences, the use of multiple lines of evidence has the propensity to increase the signal to noise ratio, thereby increasing the likelihood of converging on the “true” tree (e.g., Rokas et al., 2003).

Criticisms of this method include concerns that the phylogenetic signal from potentially vast amounts of sequence data will “swamp” any signal coming from the smaller morphological character sets (Bull et al., 1993; but see de Queiroz et al., 1995). It has also been noted that a single point mutation is likely not equivalent to a state change in a morphological character (say presence or absence of a maxillary sinus), which raises the question of how characters should be weighted (Springer et al., 2001, 2004). Another potential problem is the high proportion of missing data in combined character matrices, which may lead to spurious resolution and inflated support (e.g., Simmons, 2011; Simmons and Norton, 2013). Analyses of fossil taxa often already have large amounts of missing data due to the fragmentary nature of the fossil record, and this problem is magnified when molecular and morphological characters are combined, as fossil taxa cannot be scored for molecular characters. However, as discussed above, it has been demonstrated that missing character data may not be as detrimental as is typically assumed, and the inclusion of incomplete taxa may be beneficial to the analysis, so long as the scored

characters are informative (Wiens, 2003a, 2006; Fulton and Strobeck, 2006; de Queiroz and Gatesy, 2007; Wiens and Morrill, 2011). The potential issues stemming from incompleteness are arguably not due to the absolute amount of missing data, but rather that the character data available for each taxon may not overlap, making it impossible to directly compare certain taxa (de Queiroz and Gatesy, 2007; Wolsan and Sato, 2010). The artifacts of sparse supermatrices can be reduced by partitioning Bayesian analyses, or by using methods that calculate support without resampling (e.g., Bremer support; Simmons and Norton, 2013), as was done here.

Springer et al. (2001) suggested the use of a molecular backbone constraint to avoid the issue of character weighting and possible complications related to large amounts of missing data, while still utilizing both molecular and morphological data. In order to create a molecular backbone, relationships among extant taxa are first inferred from analysis of molecular data, usually using a model-based approach, and then a constrained parsimony analysis is performed using the morphological matrix, thereby allowing placement of fossil taxa among the branches of the extant tree. Note that this approach still allows fossil data to drive relationships and may result in trees that break down sister relationships among extant taxa. For example, *Soromandrillus* is found to be the sister taxon to *Mandrillus* even though *Cercocebus* and *Mandrillus* were constrained as sisters; the backbone analysis does not force a C/M sister relationship to the exclusion of fossil taxa. In other words, fossil taxa are not merely “hung” onto constrained branches of extant relationships, but rather fossil taxa are able to move among the constraints imposed on extant taxa.

“Swamping” of morphological characters and relative weighting of molecular and morphological characters are not concerns in molecular backbone analyses since these different data types are not analyzed simultaneously. This method does not benefit from the maximization of otherwise weak phylogenetic signals, but can be useful for placing fossil taxa within a well-supported framework of living taxa. However, in circumstances where morphological and molecular data are incongruent over the placement of a specific extant taxon, as is the case for *Rungwecebus*, this method will only reflect the signal of the molecular data due to enforced topological constraints.

4.2. African papionin phylogeny

The application of combined methods generally supports earlier findings and adds several new hypotheses regarding African papionin phylogeny. The Bayesian supermatrix approach, however, is aberrant in this regard, returning a virtually unresolved tree with the exception of a few extant molecular and morphologically supported clades (Fig. 5c). In fact, recent studies indicate that, while generally more accurate, lower levels of resolution can often be expected in Bayesian analyses versus parsimony, particularly for relatively small morphological character matrices (O'Reilly et al., 2016; Puttick et al., 2017). Thus, while one can perhaps have more confidence in the accuracy of the few well-supported clades in the Bayesian trees (see O'Reilly et al., 2016; Puttick et al., 2017), this may come at the expense of phylogenetic resolution for fossil taxa. Equal-weights parsimony analyses, such as those employed in this study, can be nearly as accurate as Bayesian analyses and offer more resolution (O'Reilly et al., 2016; Puttick et al., 2017), making them advantageous when working with fragmentary fossil taxa. Furthermore, during simulations most accuracy problems in parsimony seem concentrated at the tips (O'Reilly et al., 2016), increasing confidence for well-supported major clades even if weakly supported lower-level relationships should be viewed as more uncertain. Thus, we view the major clades consistently

supported in our parsimony analyses as likely to be accurate pending additional information and the inclusion of new fossil taxa.

Beyond the intrinsic value of generating new hypotheses, the optimal trees recovered here also offer the opportunity to assess previous questions regarding generic-level relationships among the extant members of the P/L/R/T clade and phylogenetic relationships of the fossil taxa outlined in the Introduction. As we review the results of the current analyses, beginning with the base of the trees and moving towards the extant tips, we attempt to address these questions and highlight any new phylogenetic hypotheses to be evaluated and tested in the future. In addition, we also note selected morphological synapomorphies for the major recovered clades as indicated by character transformation analyses (Table 3).

Stem African papionins *Pp. ado* is consistently inferred to be a stem African papionin (93% of MPTs from combined analyses), as in previous analyses (Gilbert, 2013). *Pp. ado* is known from its type locality of Laetoli and sometimes recognized at similar-aged sites in the Turkana Basin, but compared to the other named *Parapapio* taxa, this species is not well-known anatomically (e.g., see Leakey and Delson, 1987; Harrison, 2011). Furthermore, at Laetoli, its hypodigm is currently under revision, and specimens attributable to an early *T. oswaldi* subspecies comparable to that seen at Woranso-Mille have likely been misassigned to *Pp. ado* in the past (S. Frost and C. Gilbert, pers. obs.; see also Frost et al., 2014, 2018). The morphology known for *Pp. ado* is certainly generalized enough to be ancestral to the rest of the African papionins, but it remains difficult to know the likely phylogenetic placement of this taxon in the absence of more complete cranial material. For these reasons, we prefer to maintain *Pp. ado* in the genus *Parapapio* for the time being, even though the position of *Pp. ado* in the analyses here and elsewhere (Gilbert, 2013; Gilbert et al., 2016a, 2018) suggests that *Parapapio* may be a paraphyletic genus.

P/L/R/T clade Numerous fossil taxa (*Pp. jonesi*, *Pp. broomi*, *Pp. whitei*, *Pl. alemui*, *?P. izodi*) are most often inferred to be stem members of the P/L/R/T clade in the current analyses, differing from earlier assessments suggesting these taxa were instead stem African papionins (e.g., Szalay and Delson, 1979; Frost, 2001b; Jablonski, 2002; Gilbert, 2013). Intuitively, either position for these taxa seems reasonable (and this is reflected in the strict consensus trees). Molecular data suggests the split between the C/M and P/L/R/T clades occurred in the Late Miocene ~6.7 Ma (95% confidence interval ~5.4–8.1 Ma; Perelman et al., 2011), and since it is now clear that *Theropithecus* first appears by at least ~4.2 Ma (e.g., see Frost, 2001a; Frost et al., 2014, in revision), there is also paleontological support for a crown African papionin divergence date sometime in the latest Miocene to early Pliocene. The *Parapapio* species found to be stem P/L/R/T members here all derive from deposits younger than 4.0 Ma, and the same is true of *?P. izodi*. *Pl. alemui* is the only species falling within the estimated divergence date range, in the latest Miocene (~5.7–5.2 Ma) to early Pliocene (~4.4–4.2 Ma; see Frost, 2001b; Frost et al., 2009), and even in this case, if the molecular estimates are correct it is still likely to have evolved after the split. Therefore, hypotheses including these taxa as stem members of the P/L/R/T clade are consistent with currently estimated divergence dates, even though the list of morphological features uniting the entire clade is relatively short and contains no unambiguous synapomorphies that cannot be found elsewhere in the tree or are generally uncertain due to a lack of preservation in many taxa (Table 3). Moreover, all of these putative stem P/L/R/T taxa retain numerous African papionin symplesiomorphies (e.g., the lack of consistent, definitive facial fossae), making their position inside or outside of the crown clade difficult to determine with confidence, but they are most often found at the base of the P/L/R/T clade here.

As previously noted (Gilbert, 2013), *Parapapio* seems to be a paraphyletic grouping of primitive African papionins (excluding *Pp. lothagamensis*, which is most likely a separate genus; see Leakey et al., 2003; Gilbert, 2013). More material of *Pp. ado* is needed to definitively assess its phylogenetic position and make a determination of its status within the genus (see above). While previous analyses have typically found a monophyletic clade formed by *Pp. whitei*, *Pp. jonesi*, and *Pp. broomi*, and some have even suggested they represent a single, highly variable taxon (Monson et al., 2017), *Pp. broomi* is separated out here as branching before a *Pp. whitei*/*Pp. jonesi* clade in the vast majority of MPTs, with only one of the supermatrix MPTs recovering a *Pp. broomi*/*Pp. whitei*/*Pp. jonesi* clade. *Pp. broomi* is, in fact, distinctive in having a relatively short snout and palate for an extant African papionin of its size, particularly in comparison to *Pp. jonesi* and *Pp. whitei*, and these and other features may account for its position outside of the other two *Parapapio* taxa (e.g., see Fig. 1 in Gilbert, 2013; Gilbert et al., 2018). Given that previous analyses have hypothesized a close relationship between *Pp. broomi* and *Pp. whitei* to the exclusion of *Pp. jonesi* (e.g., Gilbert, 2013), the arrangement recovered in this study is interesting. Features uniting *Pp. jonesi* and *Pp. whitei* include a low cranial vault index (bregma-basion/glabella-inion), a relatively narrow superior facial breadth (bi-frontomaletemporale), a narrow bimaxillary breadth (bizygomaxillare), a peaked muzzle dorsum, a more concavo-convex lateral nasal profile, a higher incidence of nasal bone projection above the frontal-maxillary suture, relatively longer (MD) upper molars, a slight extension of the nasal bones over the nasal aperture in males, a more medial inferior petrous (Eustachian) process, peaked muzzle dorsum, mesiodistally longer mandibular molars, and a more inclined ascending ramus in females (see also Gilbert et al., 2018). Thus, a close relationship between *Pp. whitei* and *Pp. jonesi* seems relatively well-supported at this time, but whether or not *Pp. broomi* is more closely related to *Pp. whitei*/*Pp. jonesi* than to other African papionins (i.e., additional evidence of *Parapapio* parphyly) requires further testing.

Also in contrast to Gilbert (2013), the phylogenetic hypotheses posited here suggest that *Pl. alemui* is most likely a stem member of the P/L/R/T clade, rather than a stem African papionin. This position was also suggested by Frost (2001b). As mentioned above, in two of the MPTs from the backbone analysis, *Pl. alemui* is the sister taxon to *Pp. ado* and placed within a larger clade with the other *Parapapio* taxa, and in one parsimony supermatrix MPT it is placed at the base of a clade containing *?P. izodi*, *Dinopithecus*, and the *Theropithecus* taxa (see MPTs in SOM). However, this taxon most often branches right after *Pp. whitei*/*Pp. jonesi* and right before *?P. izodi* (Figs. 4a and 5a), and this position seems most likely at this time.

?P. izodi is most often inferred to be a stem member of the P/L/R/T clade, typically the last taxon to branch off before the crown group, similar to other recent analyses (Gilbert, 2013; Gilbert et al., 2016a, 2018). In a few MPTs, it is regarded as being a stem member of the P/L/R clade, but it is never found as a member of the crown *Papio* group. Thus, there is a consistent signal to indicate that *?P. izodi* is more primitive than other *Papio* species and should possibly be reassigned to a new genus (see also Gilbert et al., 2018). However, *?P. izodi* shares enough features with *Papio* to make it a reasonable candidate as a baboon ancestor, and so until a more targeted morphological analysis is performed, we follow the recent suggestion by Gilbert et al. (2018) to formally question its inclusion in *Papio* by using the *?Papio* designation, but refrain from erecting a new genus.

The placement of *D. ingens* as sister to *Theropithecus* in the majority of MPTs from each combined analysis is more consistent in the current analyses than in previous studies (Gilbert, 2013). However, *D. ingens* remains (along with *G. major*, and to a lesser

Table 3
Selected synapomorphies suggested by character transformation analyses.

	Reconstructed synapomorphies	Character number
CLADE 1: African Papionins	†*Longer postglabella-bregma chord in males, †*Longer parietal-lambdoid chord in females, †*More anterior orientation of the foramen magnum relative to biporion in males (i.e. more posteriorly oriented EAM), †* Maxillary fossae at least variably present , *Nasal bone projection present in males, *Longer canine interalveolar distance in males, *Taller mandibular corpus at the level of M ₁ in males, * Increased cranial/body size , * Broad ulnar coronoid width	†*C6 (M), †*C8 (F), †*C31 (M), †* F19 , *F28 (M), *P8 (M), *M3 (M), * Gmean , * U1
CLADE 2: C/M (<i>Soromandrillus</i> / <i>Mandrillus</i> / <i>Cercocebus</i> / <i>Procercocebus</i>)	Widely divergent temporal lines , Uprturned nuchal crests across the midline in males, †*Short basisphenoid length in females, * Vomer inflated , *Medially positioned inferior petrous process in females, *Presence of definitive maxillary ridges in males, *Broader mandibular corpus at the level of M ₃ in males, *P ₄ mesiodistally long in males, * Proximally extended humeral supinator crest , Prominent medial trochlear lip in males, † Triangular radial shaft shape , † Weak gluteal tuberosities on the ilium , † Moderately developed medial lip on the femoral patellar groove , †*Moderate to strongly developed lateral lip on the femoral patellar groove in males	C20 , C21 (M), †*C39 (F), * C44 , *C47 (F), *F21 (M), *M6 (M), *M9 (M), * H3 , H5 (M), † R1 , † I2 , † Fe1 , †*Fe2 (M)
CLADE 3: P/L/R/T (<i>Pp. broomi</i> / <i>Pp. whitei</i> / <i>Pp. jonesi</i> / <i>Pliopapio</i> ? <i>P. izodi</i> + Crown P/L/R/T)	†Broad basicranium across the carotid canals in males, *Medially positioned EAM in males, *EAM crest present in females, *Mesiodistally short female canines, *† Unenlarged lateral margin of the oleranon fossa , †Relatively shallow olecranon fossa in males	†C14 (M), *C19 (M), *C29 (F), *P13 (F), †* H7 , †H8 (M)
CLADE 4: Crown P/L/R/T (<i>Papio</i> / <i>Lophocebus</i> / <i>Rungwecebus</i> / <i>Theropithecus</i> / <i>Gorgopithecus</i> / <i>Dinopithecus</i>)	†*Longer neurocranium (glabella-inion) in females, * Taller neurocranium (bregma-basion) , †*Longer parietal-sagittal chord in females, *Sagittal crest present posteriorly in males, * Relatively long foramen magnum , †Broad basioccipital in males, Well-excavated fossae for longus capitis in males, * Definitive maxillary fossae invade to deeply invade the infraorbital plate , *Definitive maxillary ridges present in males, *Wide interalveolar distance at the level of the M ₃ , †*Long premaxilla in females, * Mandibular corpus fossae present (particularly in females) , † 13T:6L vertebral column (at least polymorphic for this count) , †Relatively broad olecranon fossa in males, †*Broad ulnar coronoid process in males, † Rounded radial shaft shape , †*Narrow ilium in males, † Weak gluteal tuberosities , †*Increased tibial compression in males	†*C1 (F), * C2 , †*C7 (F), †*C11 (F), *C17 (M), * C30 , †C37 (M), C48 (M), * F20 , *F21 (M), *P15 (M), †*P19 (F), * M32 , † A1 , †H6 (M), *†U1 (M), † R1 , *†I1 (M), † I2 , *†T1 (M)
CLADE 5: <i>Theropithecus</i>	†*Shorter parietal-lambdoid chord in females, †*Shorter lambda-inion chord in females, Sagittal crest present well anterior to bregma in males, *Increased postorbital constriction in males, *Closely approximated tympanic with postglenoid process in males, *Vomer uninflated in females, *Deeply-excavated fossae for longus capitis in males, *Tall malar height in males, *I ₁ mesiodistally short in males, *Canine mesiodistally long in males, Small I₁ compared to I₂ , * Low degree of molar flare , *M ₃ tuberculum sexum present in males, Increased level of enamel folding in mandibular molars , Relatively oblique lophid orientation , *Extramolar sulcus relatively wide in males, *P ₄ mesiodistally long relative to breadth in females, * M₂ mesiodistally long relative to breadth , *Mandibular corpus shallows posteriorly in males, Reversed Curve of Spee , MC1 elongated compared to MC2 , †*Increased tibial compression in females	†*C8 (F), †*C9 (F), C17 (M), *C24 (M), *C27 (M), *C44 (F), *C48 (M), *F8 (M), †*P4 (F), *P11 (M), *P13 (M), P26 , * P30 , *M21 (M), M22 , M23 , *M33 (M), *M35 (F), * M37 , *M40 (M), M41 , MC1 , †*T1 (F)

(continued on next page)

Table 3 (continued)

	Reconstructed synapomorphies	Character number
CLADE 6: <i>Papio</i> (including <i>P. angusticeps</i> and <i>P. robinsoni</i>)	<p>*Downturned nuchal lines across the midline in females, †*Longer opisthion-inion chord in females, *Tall superior facial height in females, †*Relatively broad nasal aperture in males, †*Relatively tall nasal height in females, †*Relatively long nasal bones (nasion-rhinion) in females, *Long nasal bones relative to facial length (nasion-rhinion/nasion-prosthion), *Relatively high level of M₁ tapering, †*Low scapular index in females, †*Narrow distal articulation on the humerus in females, †*Broad ulnar coronoid process in females, †*Broad ilium in females, †*Weakly developed/rounded lateral lip on the femoral patellar groove in females</p>	<p>*C21 (F), †*C33 (F), *F1 (F), †*F9 (M), †*F10 (F), †*F11 (F), *F35, *M39, †*S1 (F), †*H4 (F), †*U1 (F), †*I1 (F), †*Fe2 (F)</p>

Notes: Listed characters represent those suggesting a character-state transition at the corresponding node. Character states in bold are recognized as notable synapomorphies appearing in both males and females of the clade listed. * = those character-states reconstructed as synapomorphies for a given clade, but also appearing elsewhere on the tree or incurring reversals within the clade. † = reconstructed synapomorphies uncertain due to absence of preservation in most fossil taxa. Character Number refers to the character number in the accompanying nexus data matrix file (see SOM), with (M) referring to the male character and (F) referring to the female character; character states in bold are again found in both males and females. See Figures 3–5 for consensus trees with corresponding clades; synapomorphies reconstructed from most common clades found in the consensus trees. For other potential clades, please see text and Gilbert (2013).

extent, *?P. izodi*) one of the most unstable OTUs in the analyses, and it is also found in positions both outside of the crown P/L/R/T clade and as a stem member of the P/L/R clade, making any inference about its precise phylogenetic position uncertain (see strict consensus trees; Figs. 3–5). Furthermore, there are reasons to be skeptical regarding the veracity of a *Dinopithecus*/*Theropithecus* clade. First, there are no cranial synapomorphies that unite *D. ingens* exclusively with *Theropithecus* other than those also found in other taxa and/or those that are due, at least in part, to overall large size. For example, *D. ingens* shares with *Theropithecus* species a relatively high degree of postorbital constriction, also seen in other papionins (e.g., *Parapapio*, *P. papio*, *Mandrillus*, *Soromandrillus*), and relatively extensive nuchal cresting in both males and females, a feature shared with some *Theropithecus* taxa and likely accentuated due to its very large size outside the range of any extant papionin (Delson et al., 2000). There are other, more subtle character states that *D. ingens* shares with *Theropithecus* (in males, a closely approximated ecto-tympanic to the postglenoid process [also seen in some *Parapapio*, *Cercocebus*, and *Papio* taxa], wide bizygomatic width [also seen in *Gorgopithecus*], tall malar region [also seen in *Papio* species], relatively long zygomaxillare-porion chord [also seen in *P. broomi*, *Lophocebus*, two *Papio* species, *Soromandrillus*, and *Mandrillus*], and a relatively long M₂ shape [also found in some *Papio* taxa and *Gorgopithecus*]; in females, a long basioccipital length [also in some *Lophocebus*], an uninflated vomer [also seen in *Papio* taxa], a laterally positioned inferior petrous [Eustachian] process [also in some *Papio* taxa], and, like in males, a relatively wide bizygomatic breadth [also seen in *P. papio* females]), but again, all of these character states are also found in other papionin taxa, including various *Papio* species, and *Papio* is the taxon with which *Dinopithecus* has traditionally been most closely aligned (e.g., Szalay and Delson, 1979; Delson and Dean, 1993; Frost, 2001a).

As indicated in Gilbert (2013), it seems likely that the placement of *D. ingens* is being affected, at least in part, by some of the coding decisions made in this study, particularly the inclusion of polymorphic character states. Because male *D. ingens* is known craniofacially from only a single partial cranium, it eliminates the possibility of recording polymorphisms for many characters. Nearly all *Papio* species are polymorphic for many characters, making it difficult for *D. ingens* and *Papio* to share male character states in many cases and, therefore, probably artificially deflates the probability of the analysis recovering a close relationship between these taxa. Conversely, because *Theropithecus* taxa, particularly the fossil taxa *T. o. darti* and *T. baringensis*, are known from only a few male crania and/or display fewer polymorphisms, it probably artificially increases the probability of the analysis recovering a close relationship between *Dinopithecus* and *Theropithecus* on the basis of subtle, fixed (non-polymorphic) states. Regardless of these potential problems, the benefits to including polymorphisms generally outweigh any negative effects (e.g., see Wiens, 2000), and we still believe the character coding decisions made here are the best ones available given the current data and methodological options. However, the general lack of data available for the male cranium almost certainly has an effect on the instability of *D. ingens* given that male papionin specimens have been demonstrated to likely be more phylogenetically informative than females (Gilbert and Rossie, 2007; Gilbert et al., 2009a). Therefore, due to the combination of allometry, character coding methodology, and low sample size, the precise phylogenetic position of *D. ingens* remains elusive, but a position as either a stem or crown P/L/R/T member close to the origin of the crown group seems well-supported at this time.

Similar to *D. ingens*, *G. major* is relatively unstable in our trees, but most often found as the sister taxon to the P/L/R clade (see

Figs. 3–5). Previous analyses have suggested *G. major* is the sister taxon to extant *Lophocebus*, a position that is still possible, but found in only two of the MPTs from the parsimony supermatrix analysis. Among all other MPTs in the parsimony supermatrix and molecular backbone analyses *G. major* is inferred to be the sister taxon to *Papio* (one MPT), a stem P/L/R/T taxon (the sister to the crown group in three of the backbone MPTs), or at the base of a clade containing ?*P. izodi*, *D. ingens*, and *Theropithecus* (two of the backbone MPTs). This last position seems, to us, quite unlikely, and seems driven by the fact that ?*P. izodi*, *G. major*, and *D. ingens* are all most likely close to the crown group of P/L/R/T taxa but share numerous primitive or fixed character states in the analysis, due in part to small male sample sizes and a general lack of data that is common in fossil taxa (see also above and Gilbert, 2013). In summary, *G. major* is most likely closely related to extant *Lophocebus*, *Rungwecebus*, and *Papio* in some way, but the exact relationships are equivocal.

Excluding the largely unresolved Bayesian analysis, parsimony analyses integrating both morphological and molecular data found *Theropithecus* to be the most basal member of the crown P/L/R/T clade, which adds to the growing body of studies supporting this topology (e.g., Perelman et al., 2011; Gilbert, 2013; Guevara and Steiper, 2014). The inclusion of *Rungwecebus* as a relative of *Papio* or *Lophocebus*, or both, firmly establishes *Theropithecus* as the basal genus of this clade. Within *Theropithecus*, a couple of different phylogenetic hypotheses have been suggested in the literature (reviewed in Jablonski, 1993). Our results generally support the previous suggestions of Delson (1993; see also Gilbert, 2013) and thus recognize a sister relationship between the *T. oswaldi* lineage (here represented by *T. o. darti*) and *T. gelada*, with *T. brumpti* as the sister branch to this clade. In our analyses, there are numerous features supporting a closer relationship between *T. o. darti* and *T. gelada* to the exclusion of *T. brumpti*, including a deeply excavated longus capitis fossae, a relatively wider bizygomatic breadth, a broad ulnar coronoid width, and a relatively narrow ilium in both males and females, combined with the absence of maxillary ridges in males and a tall superior facial height, relatively long maxilla-alveolar length, more vertical ascending ramus, narrower extra-molar sulcus, and mesiodistally long M_1 in females.

In contrast to Delson (1993) and other authors (Eck and Jablonski, 1984, 1987; Jablonski, 2002; Jablonski et al., 2008), we did not find a well-supported relationship between *T. baringensis* and *T. brumpti*; rather, *T. baringensis* is supported here and elsewhere (Gilbert, 2013) as the basal member of the genus. Given that the *T. oswaldi* lineage has been identified at Woranso-Mille ~3.6–3.8 Ma based on good cranial material and that the crania of *T. oswaldi* and *T. brumpti* are quite distinct from each other, the split between the *T. oswaldi* and *T. brumpti* lineages must have taken place earlier than 3.8 Ma, closer to 4 million years ago at a minimum. The split between *T. baringensis* and the rest of the genus must have taken place even earlier still, and there is some preliminary evidence of an unidentified but *T. baringensis*-sized *Theropithecus* population at Kanapoi ~4.2 Ma (Frost, 2001a; Frost and Gilbert, pers. obs., Frost et al., in revision). *T. baringensis* is otherwise only positively identified at site JM 90/91 (BPRP #97) in the Tugen Hills, Kenya at ~3.2 Ma (Deino and Hill, 2002), which would potentially suggest a ghost-lineage of at least one million years between the splitting of *T. baringensis* and its appearance in the fossil record. In any case, if *T. baringensis* is indeed the most basal member of the genus, its morphology implies that the ancestral morphotype for *Theropithecus* is much more in line with a generalized large P/L/R/T papionin monkey, and that *T. brumpti* largely retains this basic cranial shape while significantly modifying the zygomatic arches and other aspects of its anatomy off of this basic cranial morphotype. It is instead the *T. oswaldi* and *T. gelada* clade

that seems more likely to be derived in their overall cranial shape, including the more distinctive airorhynch/facial “dishing”, the loss of maxillary ridges in males, and the other features noted above (see also Delson, 1993; Delson and Dean, 1993). If this phylogenetic inference is correct, the loss of facial fossae and male maxillary ridges in the *T. oswaldi* lineage are particularly noteworthy secondarily derived features. Dentally, as previously noted by Frost et al. (2014), it seems likely that *T. brumpti* and *T. oswaldi*/*T. gelada* evolved or at least became fixed for many of their dental specializations in parallel, and this is consistent with the fact that *T. baringensis* is more variable or does not display many of these features as strongly as seen in the later taxa, particularly the highly derived molar features. Postcranially, both the *T. brumpti* and *T. oswaldi* lineages display the same unique hand proportions present in the extant *T. gelada* (i.e., a high opposability index achieved by elongation of the thumb and reduction of the 2nd and 3rd digits; see Napier and Napier, 1967; Jablonski, 1986; Jablonski et al., 2002; Frost et al., 2014), suggesting that the common ancestor of all three of these taxa also possessed the same proportions. What is not clear is when this unique adaptation evolved; there are no known hand fossils of *T. baringensis*, and it is therefore an open question as to whether or not these distinctive hand proportions were in place even earlier in the *Theropithecus* radiation.

The position of *Rungwecebus* within the P/L/R clade remains equivocal, despite the use of combined methods, which failed to resolve its position relative to extant *Lophocebus* and *Papio*. Morphological studies, including the morphology-only analysis performed here, align *Rungwecebus* with *Lophocebus* (Fig. 3; Gilbert et al., 2011a; Gilbert, 2013), while molecular studies indicate a close relationship to *Papio* (Fig. 2; Davenport et al., 2006; Olson et al., 2008). More recent molecular studies have suggested that there is a complex pattern of hybridization occurring between *Rungwecebus* and *Papio*, specifically *P. cynocephalus*, which has a geographic range that overlaps with that of *Rungwecebus* (Burrell et al., 2009; Zinner et al., 2009a; Roberts et al., 2010). The molecular-only analysis supports these findings, as *Rungwecebus* is nested within *Papio*. However, the Perelman et al. (2011) molecular dataset does not include *P. cynocephalus*, so this specific relationship cannot be evaluated here. Available morphological and molecular data for *Rungwecebus* remains sparse, which exacerbates these issues. Examination of morphology is currently hindered by the dearth of available adult specimens (Davenport et al., 2006; Gilbert et al., 2011a; Gilbert, 2013). Analyses to date have relied on field observations, photographs, and two juvenile male craniodental specimens. Widely available molecular data for *Rungwecebus* are limited to five loci, all from the Southern Highlands population. Until more data become available for *Rungwecebus*, its precise position within the P/L/R clade will remain uncertain. In the majority of the MPTs including fossil taxa, *Rungwecebus* is inferred to be the sister taxon to the fossil *Lophocebus* taxon from Koobi Fora (Figs. 4 and 5). It is possible that the fossil *Lophocebus* taxon and *Rungwecebus* form a clade, based on shared derived dental features not found in extant *Lophocebus* such as longer and narrower upper molars (M^2), a mesiodistally shorter P_4 , and buccolingually narrow lower molars (M_2), as found in the character transformation analyses. However, it is also possible that this association is again driven by general morphological similarities relating to overall similar body size, small sample sizes, and high proportions of missing data for both taxa. The fossil *Lophocebus*, previously referred to as *L. cf. albigena* by Jablonski et al. (2008), is almost twice the size of any living *Lophocebus* species and also displays other characteristics making it likely to be a new species (Frost, 2001a; Gilbert and Frost, pers. obs.), but its overall striking similarity to living *Lophocebus* mangabey in the preserved fragmentary craniofacial features perhaps points to a position within that genus as most likely (found in two

of the backbone MPTs and four of the supermatrix MPTs). Notably, the results of this study and others strongly suggest that the extant *Lophocebus* mangabeys and *Rungwecebus* are secondarily-derived for their smaller body size, a feature also found independently in some *Cercocebus* mangabeys. As has been pointed out previously (Gilbert and Rossie, 2007; Gilbert, 2007, 2013; Gilbert et al., 2009a), this independent shift in body size is almost certainly responsible for many of the similar features observed among mangabey taxa.

There are two fossils confidently assigned to *Papio* included in the present analysis: *P. angusticeps* and *P. robinsoni*. The taxonomic and phylogenetic position of both fossil taxa are discussed extensively in Gilbert et al. (2018), but to summarize our results, both fossil taxa are found to be members of the crown *Papio* clade in all of the supermatrix and backbone MPTs. Using a Biological Species Concept, it can therefore be argued that both should be recognized as subspecies of *Papio hamadryas* (i.e., *P. h. angusticeps*). However, we prefer the Phylogenetic Species Concept and would simply recognize *P. angusticeps* and *P. robinsoni* as likely members of the crown radiation. From morphological data alone, there is some indication that *P. robinsoni* may be more primitive than the extant *Papio* species (see also Gilbert et al., 2018), but it is clear that *P. angusticeps*, at least, is a crown *Papio* species. The association of *P. robinsoni* with *P. hamadryas* may, once again, be an artifact of low sample sizes and missing data (*P. hamadryas* sample sizes are very low for males and females and male *P. robinsoni*, in particular, is not well-represented beyond the palate/muzzle). In any case, both fossil taxa are similar in their estimated first appearance dates (~2.4–2.0 Ma) and seem to establish the modern genus *Papio* in the fossil record by this time, in accordance with molecular clock estimates as well (see also Gilbert et al., 2015, in press).

C/M clade The topology of the C/M clade in the supermatrix and molecular backbone analyses is broadly similar to previous morphology-only studies (Gilbert, 2013; DeVreese and Gilbert, 2015; Gilbert et al., 2016a,b, in press), with differences attributable to the addition of postcranial characters, scoring of extant taxa at the species rather than genus level, and from the use of combined phylogenetic methods. Both combined analyses have added confidence to the results of the morphology-only analysis by Gilbert (2013), and to earlier taxonomic recommendations for fossil African papionins made by Gilbert (2007, 2013). Gilbert (2013) reclassified "*Papio*" *quadratiostris* as *S. quadratiostris* to reflect its close phyletic relationship to *Mandrillus*, a classification that also found strong support here. Combined analyses also support *Pr. antiquus* as a member of the C/M clade, but do not necessarily support a sister relationship between *Pr. antiquus* and *Cercocebus*, as was recovered in Gilbert (2013). Instead, *Pr. antiquus* is positioned as either a stem member of the C/M clade or as the basal member of the *Soromandrillus*/*Mandrillus* clade. Craniodentally, *Pr. antiquus* looks most similar to *C. torquatus* (Gilbert, 2007), but its widely divergent temporal lines and, in particular, robust humerus with strong muscle markings (Gilbert et al., 2016b) are more similar to *Mandrillus*. These competing signals no doubt make it hard to pin down the exact position of *Pr. antiquus*. In total, it seems clear that *Pr. antiquus* is a member of the C/M clade, but its exact position within this clade is equivocal (see also Table 3 for updated list of C/M synapomorphies). Among the extant *Cercocebus* taxa, it is *C. torquatus* that is inferred to branch off first, and its morphological similarities with *Pr. antiquus* and the *Soromandrillus*/*Mandrillus* clade in many features are probably due to primitive retentions from the common ancestor of the clade (see also Fleagle and McGraw, 1999, 2002; Gilbert, 2007; DeVreese and Gilbert, 2015). The successive branching of *C. atys* and then *C. agilis*/*C. chrysogaster* is consistent with the previous suggestions of DeVreese and Gilbert (2015) and molecular analyses by Perelman et al. (2011) and Guevara and Steiper (2014). Similar to the situation with the extant

Lophocebus mangabeys, this arrangement also indicates that the smaller *Cercocebus* taxa (e.g., *C. agilis*) are secondarily derived for their smaller body size and associated shorter faces (see also DeVreese and Gilbert, 2015).

5. Conclusions

In summary, the analyses presented here offer further resolution into the evolutionary history of the African papionins. Taken as a whole, the most confident view of African papionin evolution is presented in the strict consensus trees inferred from the backbone and parsimony supermatrix analyses (Figs. 4b, 5b). All recent phylogenetic analyses, including those presented here, divide crown African papionins into two clades: *Cercocebus*/*Mandrillus* and *Lophocebus*/*Papio*/*Rungwecebus*/*Theropithecus*. Given the results of the present study, and those of other recent studies (Perelman et al., 2011; Gilbert, 2013; Guevara and Steiper, 2014), it also seems reasonable to conclude that *Theropithecus* is the basal taxon within the latter clade, having branched off from the other taxa before ~4.2 Ma and probably closer to at least ~4.5–5 Ma. The addition of *Rungwecebus* to phylogenetic analyses provides additional support for this branching pattern. The integration of morphological and molecular characters for living and fossil taxa in the above analyses provides further support for the position of *Theropithecus*, but does little to clarify the position of *Rungwecebus* within the P/L/R clade. While the scarcity of available specimens and sequence data undoubtedly enhance the difficulties in estimating the phylogenetic position of *Rungwecebus*, relationships within the P/L/R clade may remain ambiguous due to complex patterns of reticulation hinted at by several studies (e.g., Burrell et al., 2009; Zinner et al., 2009a,b; Roberts et al., 2010). Denser genetic sampling of all members of these genera, with a focus on geography rather than morphologically-defined species, may be necessary to resolve the position of *Rungwecebus*, as recommended previously (e.g., Burrell et al., 2009; Roberts et al., 2010). The addition of *P. cynocephalus* to the molecular dataset may also prove useful in evaluating relationships of *Rungwecebus*, since several studies have found *Rungwecebus* nested within the population-level variation of this species (Burrell et al., 2009; Zinner et al., 2009a).

Regarding the broader phylogenetic history of the African papionins, the analyses presented here, including both molecular and morphological data at the species level along with the application of both parsimony and Bayesian inference methods, provide the most comprehensive view to date. The results of these analyses are broadly similar to earlier studies, but offer additional confidence and clarity, particularly for those relationships supported in the strict consensus trees from the parsimony backbone and supermatrix analyses. Regarding the research questions outlined at the beginning of this study, our results suggest that: (1) *Pr. antiquus* is either a stem or crown C/M taxon, and *S. quadratiostris* is the sister to *Mandrillus*; (2) it seems probable that *Parapapio*, as currently constituted, is a paraphyletic grouping of primitive African papionins (either stem African papionins or, based on results presented here, stem P/L/R/T taxa), with *Pp. ado* seemingly distinct from the other three taxa and even *Pp. broomi* possibly being distinct from a *Pp. jonesi*/*Pp. whitei* clade; (3) *Pliopapio* may be a stem member of the P/L/R/T clade, but a position basal to crown African papionins remains possible. *Pp. izodi* is either a stem or crown P/L/R/T taxon and should probably be transferred to a new genus; (4) *Dinopithecus* and *Gorgopithecus* are either stem or crown P/L/R/T taxa, with *Gorgopithecus* more likely to be a P/L/R taxon, but their phylogenetic positions are unstable and their precise positions are difficult to ascertain; and finally, (5) *T. baringensis* is likely the most basal *Theropithecus* taxon, with *T. gelada* and *T. oswaldi*

likely sister taxa to the exclusion of *T. brumpti*. In our view, a number of more specific hypotheses consistent with these basic relationships seem feasible, although some hypotheses appear much more likely than others, as illustrated by the majority-rule trees, various support values, and the points raised above. For example, as suggested by the majority-rule trees, we consider *G. major* as likely to be more closely related to P/L/R than to any other clade, and even a position as the sister taxon to *Papio* or *Lophocebus* seems quite possible.

As is typical for most studies that include fossils, further resolution of African papionin evolutionary history depends on additional data for taxa such as *D. ingens*, *G. major*, *Pp. ado*, and the fossil *Lophocebus* species from Koobi Fora. Specifically, in order to gain a better understanding of these relationships, future studies will need to sample additional fossil specimens preserving missing aspects of the male cranium in several African papionins. Uncertainties about the phylogenetic position of *Rungwecebus* may be a result of more complex factors than simple lack of data, such as introgression, though additional adult specimens and sampled molecular loci will surely be beneficial in attempts to resolve its position relative to *Lophocebus* and *Papio*.

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Supplementary Online Material

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