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Cladistic analysis of extant and fossil African papionins using craniodental data

Christopher C. Gilbert^{a,b,c}^a Department of Anthropology, Hunter College of the City University of New York, 695 Park Avenue, New York, NY 10065, USA^b Department of Anthropology, the Graduate Center of the City University of New York, 365 Fifth Avenue, New York, NY 10016, USA^c New York Consortium in Evolutionary Primatology, USA

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ABSTRACT

This study examines African papionin phylogenetic history through a comprehensive cladistic analysis of extant and fossil craniodental morphology using both quantitative and qualitative characters. To account for the well-documented influence of allometry on the papionin skull, the general allometric coding method was applied to characters determined to be significantly affected by allometry. Results of the analyses suggest that *Parapapio*, *Pliopapio*, and *Papio izodi* are stem African papionin taxa. Crown Plio-Pleistocene African papionin taxa include *Gorgopithecus*, *Lophocebus* cf. *albigena*, *Procercocobus*, *Soromandrillus* (new genus defined herein) *quadratiostris*, and, most likely, *Dinopithecus*. Furthermore, *S. quadratiostris* is a member of a clade also containing *Mandrillus*, *Cercocebus*, and *Procercocobus*; *?Theropithecus baringensis* is strongly supported as a primitive member of the genus *Theropithecus*; *Gorgopithecus* is closely related to *Papio* and *Lophocebus*; and *Theropithecus* is possibly the most primitive crown African papionin taxon. Finally, character transformation analyses identify a series of morphological transformations during the course of papionin evolution. The origin of crown African papionins is diagnosed, at least in part, by the appearance of definitive and well-developed male maxillary ridges and maxillary fossae. Among crown African papionins, *Papio*, *Lophocebus*, and *Gorgopithecus* are further united by the most extensive development of the maxillary fossae. The *Soromandrillus*/*Mandrillus*/*Cercocebus*/*Procercocobus* clade is diagnosed by upturned nuchal crests (especially in males), widely divergent temporal lines (especially in males), medially oriented maxillary ridges in males, medially oriented inferior petrous processes, and a tendency to enlarge the premolars as an adaptation for hard-object food processing. The adaptive origins of the genus *Theropithecus* appear associated with a diet requiring an increase in size of the temporalis, the optimal placement of occlusal forces onto the molar battery, and an increase in the life of the posterior dentition. This shift is associated with the evolution of distinctive morphological features such as the anterior union of the temporal lines, increased enamel infoldings on the premolars and molars, a reversed curve of Spee, and delayed molar eruption.

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Introduction

The extant African papionins (Subtribe Papionina sensu Strasser and Delson, 1987) are medium-to-large-sized cercopithecine primates, including the mangabeys (*Lophocebus* and *Cercocebus*), baboons (*Papio*), geladas (*Theropithecus*), mandrills/drills (*Mandrillus*), and kipunjis (*Rungwecebus*). They represent a highly successful group of monkeys that is found throughout sub-Saharan Africa and into the Arabian Peninsula. In addition to the large distribution and diversity of extant taxa, African papionins are widely present and abundant members of the Plio-Pleistocene African fossil record (e.g., Szalay and Delson, 1979; Grine and Hensley, 1981; Fleagle,

1999; Jablonski, 2002; Jablonski and Frost, 2010). However, despite being one of the best documented primate radiations, questions still exist over which fossil taxa are legitimate species, the phylogenetic relationships of fossil taxa amongst themselves, as well as the phylogenetic relationships of fossil taxa to extant taxa. Given the relatively rich fossil record of this group, an analysis of morphological data in a phylogenetic framework seems to be a promising way to test a series of evolutionary hypotheses.

While earlier phylogenetic analyses of African papionin morphological data produced phylogenies incongruent with molecular data (e.g., Szalay and Delson, 1979; Strasser and Delson, 1987; Delson and Dean, 1993; Collard and Wood, 2000, 2001), more recent studies note morphological characters whose distributions support relationships similar to those suggested by molecular data (Fleagle and McGraw, 1999, 2002; Groves, 2000; McGraw and Fleagle, 2006; Gilbert, 2007a). Most recently, Gilbert

E-mail addresses: cgilbert@hunter.cuny.edu, ccgilbs@gmail.com.

and Rossie (2007) and Gilbert et al. (2009a) have demonstrated that, when allometry is accounted for in phylogenetic analysis of African papionin craniodental anatomy, morphological and molecular data suggest congruent phylogenetic hypotheses. Thus, the results of these most recent studies confirm that craniodental anatomy is a valuable source of phylogenetic information and remove the basis for considering hard tissue anatomy 'unreliable' in phylogeny reconstruction using extant and/or fossil taxa.

Given the increased confidence in African papionin morphological data, this study presents a comprehensive phylogenetic analysis based on the craniodental morphology of both extant and fossil African papionin taxa. A major goal of this analysis is to place problematic fossil taxa in a more firm phylogenetic context. In addition, it should provide a clearer understanding of character evolution as well as behavioral and ecological adaptations during their highly successful Plio-Pleistocene radiation.

Taxonomic issues

Before performing a phylogenetic analysis, operational taxonomic units (OTUs) must be defined. Table 1 lists the fossil taxa recognized and used in this study. Many of these taxa are universally accepted; however, the status of some fossil taxa is disputed. With regard to these disputed taxa, I will briefly justify the alpha taxonomy advocated here.

Parapapio Six species of *Parapapio* have been widely recognized: *Parapapio jonesi*, *Parapapio broomi*, *Parapapio whitei*, *Parapapio antiquus*, *Parapapio ado*, and *Parapapio lothagamensis* (e.g., Szalay and Delson, 1979; Leakey and Delson, 1987; Fleagle, 1999; Jablonski, 2002; Leakey et al., 2003). Heaton (2006) has recently argued that *Pp. whitei* is invalid, and that the specimens formerly included in this taxon are best assigned to *Pp. broomi* and *Papio izodi*. I find these arguments unconvincing for a number of reasons.

Table 1
Fossil taxa/OTUs recognized and used in this study.

Fossil taxon/OTU	Sample size (males, females)	Key specimens	Source
<i>Dinopithecus ingens</i>	(4, 8)	SB 7, SK 401, SK 542a, SK 546, SK 548, SK 553, SK 554, SK 574, SK 599, SK 600, SK 603, SK 604a, KA 150, KA 153, KA 192, KA 524/676, KA 605, KA 944	Freedman, 1957; This study
<i>Gorgopithecus major</i>	(5, 1)	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	Freedman, 1957; This study
<i>Lophocebus cf. albigena</i>	(6, 8)	CO 100, CO 101, CO 102, CO 115/103, CO 135A, KA 156, KA 161, KA 165, KA 166, KA 167C, KA 168, KA 194, KB 94, GV 4040	Jablonski et al., 2008; This study
<i>Papio angusticeps</i>	(7, 7)	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; This study
<i>Papio izodi</i>	(2, 9)	NME USNO, NME Omo 47-1970-2008, NME Omo 42-1972-1, NME Omo L 185-6, NME Omo 75N (71)-C2, DGUNL LEBa02, DGUNL LEBa03, DGUNL LEBa06	Freedman, 1957, 1961, 1965; Heaton, 2006; This study
<i>Soromandrillus quadratirostris</i>	(4, 4)		Eck, 1977; Iwamoto, 1982; Eck and Jablonski, 1984; Delson and Dean, 1993; This study
<i>Parapapio ado</i>	(4, 5)	BMNH M14940, EP 700/00, EP 1579/98, LAET 74-223, LAET 74-242/243/244, LAET 74-322, LAET 75-483, LAET 75-1209, LAET 75-2966, LAET 77-4595, MB Ma 42441, MB Ma 42444/42445/42458	Leakey and Delson, 1987; Harrison, 2011; This study
<i>Parapapio broomi</i>	(17, 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	Freedman, 1957, 1960; Maier, 1970; Freedman and Stenhouse, 1972; Eisenhart, 1974; This study
<i>Parapapio jonesi</i>	(3, 11)	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	Freedman, 1957, 1960, 1976; Maier, 1970; Freedman and Stenhouse, 1972; Eisenhart, 1974; Frost and Delson, 2002; This study
<i>Parapapio 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, 1976; Maier, 1970; Freedman and Stenhouse, 1972; Eisenhart, 1974; 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; This study
<i>Procercopithecus antiquus</i>	(4, 14)	SAM 4850, SAM 5356, SAM 5364, M3078, M3079, T11, T14, T17, T18, T20, T25, T21, T89-154, TP8, TP9, TP13, UCMP 56624, UCMP 56653, UCMP 56694, UCMP 56821/125956	Gilbert, 2007a; This study
<i>?Theropithecus baringensis</i>	(2, 0)	KNM-BC 2, KNM-BC 1647	Leakey, 1969; 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., 2011a; This study
<i>Theropithecus oswaldi darti</i>	(12, 5)	M2974, 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	Freedman, 1957; Maier, 1970; Eck and Jablonski, 1987; Eck, 1993; 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, 1993; Benefit and McCrossin, 1991, 1997; This study

Notes: Sample sizes are listed for key specimens, identifiable to sex, used in character analyses. Measurements and character state assignments were made and supplemented with additional data from the major sources listed for each taxon.

First, Heaton's (2006) analysis was based almost solely on specimens from Sterkfontein. The most distinctive specimens of *Pp. whitei* come from Makapansgat (e.g., MP 221, MP 223) and consist of fairly complete male crania that are, in my opinion, clearly different from the most complete male crania typically assigned to *Pp. broomi* (e.g., STS 564, M202). While *Pp. broomi* males display features such as flattened muzzles, relatively straight to slightly concave nasal profiles, relatively short and broad muzzles, and well-defined, pinched temporal lines, *Pp. whitei* males contrastingly display features such as peaked nasals and muzzles, slightly concave and often concavo-convex nasal profiles, a relatively long skull, a relatively long and narrow muzzle, and pinched but less distinct temporal lines (see Fig. 1).

Second, Heaton's (2006) taxonomic assignments were largely based on analyses of dental dimensions combined with the assessment of only five qualitative craniodental characters. No extant sample was provided for comparison. Since dental dimensions as well as the qualitative characters used in Heaton's (2006) analysis overlap extensively among extant papionin taxa, especially at the species level, their taxonomic value is probably limited until demonstrated otherwise. In addition, previous analyses of dental dimensions have, in fact, upheld the view of *Pp.*

whitei as a valid taxon at Sterkfontein and elsewhere (Freedman, 1957; Freedman and Stenhouse, 1972).

Finally, some of the sex assignments made by Heaton (2006) are almost certainly incorrect, and these incorrect assignments appear to have distorted the analysis. For example, Heaton (2006) assigns STS 563, an unambiguous female mandible that Broom (1940) designated as the type specimen of *Pp. whitei*, as a *Pp. broomi* male. This is not a credible assignment because the specimen clearly displays small canines as well as P₃s with reduced honing flanges, features that are exclusively found in female papionins (Fig. 2). These incorrect sex assignments lead to problematic taxonomic conclusions. For these reasons, Heaton's (2006) taxonomy is not accepted here and *Pp. whitei* is recognized as a valid taxon (Table 1).

More recently, the *Parapapio* taxon at Taung, *Pp. antiquus*, has been reassigned into its own genus, *Procercocobus*, on the basis of numerous derived features shared with the extant genera *Cercopithecus* and *Mandrillus* (Gilbert, 2007a). This assignment is accepted here and elsewhere (e.g., see Jablonski and Frost, 2010; Harrison, 2011). Further support for this hypothesis will be provided if the current analysis determines *Pr. antiquus* to have a phylogenetic position distinct from *Parapapio* taxa.

Figure 1. Comparison of *Parapapio* taxa. Top: Dorsal view, from left to right, male cranial specimens of *Pp. jonesi* (AL 363-15), *Pp. broomi* (M202), and *Pp. whitei* (MP221). Bottom: Lateral view, from left to right, male cranial specimens of *Pp. jonesi* (AL 363-15), *Pp. broomi* (M202), and *Pp. whitei* (MP221). Note the peaked/raised nasals, slightly concavo-convex nasal profile, relatively long skull, relatively long muzzle, and pinched but less well-defined temporal lines of *Pp. whitei* compared with *Pp. broomi*. Scale in each panel = 1 cm.

Figure 2. Comparison of *Pp. whitei* type specimen, STS 563, with extant papionin male and female specimens. Top: *P. h. ursinus* adult male mandible; Middle: *Pp. whitei*, STS 563; and Bottom: *P. h. ursinus* adult female mandible. Note that STS 563 is an unambiguous papionin female displaying small canines and a reduced P_3 honing flange. Scale = 1 cm.

In contrast to the South African *Parapapio* taxa, the status of the East African species *Pp. ado* has not been recently challenged, and Harrison (2011) has described additional material from Laetoli attributable to this taxon. However, Harrison (2011) argues that *Pp. ado* is best recognized from specimens found at Laetoli and possibly the Kaiyumung Member at Lothagam, rather than the more expansive hypodigm traditionally recognized including specimens from Kanapoi and Allia Bay. Instead, Harrison (2011) suggests that the Allia Bay and Kanapoi specimens, along with a partial mandible from the lower Lomekwi Member (Harris et al., 1988), probably represent the same genus as the hypodigm currently referred to as *Pp. lothagamensis* (see discussion below). Harrison's taxonomy is followed here, and *Pp. ado* is therefore accepted as a valid taxon (restricted to Laetoli) and included in this analysis.

Finally, a sixth *Parapapio* taxon, *Pp. lothagamensis*, has recently been described from Late Miocene deposits at Lothagam (Leakey et al., 2003), with additional material possibly documented at Allia Bay, Kanapoi, the Lomekwi Member of the Nachukui Formation, and in the Lukeino Formation of the Tugen Hills, Kenya

(Gilbert et al., 2010; Harrison, 2011). While *Pp. lothagamensis* currently shares its generic name with other *Parapapio* taxa, it is clear from its published description (Leakey et al., 2003) as well as my own personal observations that this taxon is the most primitive papionin described in the fossil record (see also Harrison, 2011). *Pp. lothagamensis* shares a number of features with *Victoriapithecus* (including dP_4 s lacking complete bilophodonty and expressing a weakly developed hypoconulid, dP_4 s with variable expression of a crista obliqua, the common occurrence of a metaconid on the P_3 , very broad P_3 s relative to their length, an obliquely oriented P_4 , flaring molars, a buccolingually wide M_1 , and distally constricted M^3 s with the variable absence of a distal shelf), and these features suggest that *Pp. lothagamensis* is probably more primitive than *Macaca*. It is almost certain that *Pp. lothagamensis* is both primitive and distinct enough from later *Parapapio* taxa to deserve its own generic rank; however, I will leave this taxonomic decision up to the original authors of *Pp. lothagamensis* (Leakey et al., 2003). For these reasons, *Pp. lothagamensis* is assigned as an outgroup rather than included with its congeners as an ingroup for the current analysis.

Theropithecus baringensis In 1969, Leakey described a partial papionin cranium with associated mandible (KNM-BC 2) from the Chemeron Formation as *Papio baringensis* (Leakey, 1969). A second specimen, a partial mandible (KNM-BC 1647A), was later also assigned to this taxon (Leakey and Leakey, 1976). Eck and Jablonski (1984, 1987) subsequently questioned the validity of these specimens as *Papio*, and instead argued that they represented a member of the genus *Theropithecus*, specifically an early representative of the *Theropithecus brumpti* lineage. Delson and Dean (1993) provided yet another reassessment, concluding that the assignment to *Theropithecus* was questionable.

As Delson and Dean (1993) point out, part of the problem lies in the uncertainty of grouping the cranium and associated mandible with an unassociated mandibular fragment displaying relatively unworn teeth (KNM-BC 1647A). While the worn dentition of the type specimen makes it difficult to discern a distinctive *Theropithecus* molar pattern (increased enamel infoldings, columnar cusps, etc.), the unworn dentition preserved in the mandibular fragment appears very *Theropithecus*-like in its dental features (Delson and Dean, 1993). Thus, Delson and Dean (1993) argue that it is possible that the isolated mandibular fragment belongs instead to *T. brumpti*, which is possibly documented in earlier strata (Delson et al., 2000; Jablonski et al., 2008). Since it can be difficult to distinguish between worn dentitions of *Theropithecus* and other papionins, the alternative hypothesis is that the worn dentition of KNM-BC 2 simply obscures its *Theropithecus*-like morphology.

I have had the opportunity to study the specimens in question, and the similarity of the KNM-BC 1647A partial mandible to the type specimen (KNM-BC 2) is striking (Fig. 3). Given the overall similarity of the specimens and the fact that they were found at the same site (BPRP #97, aka JM/90), it is most parsimonious to assume they represent the same taxon. Therefore, KNM-BC 1647 is included in the *T. baringensis* hypodigm in this analysis. Pending the results of the current analysis, the taxonomic and phylogenetic status of *T. baringensis* will be reassessed.

Theropithecus oswaldi Nearly all authors recognize that *Theropithecus darti* and *T. oswaldi* represent an evolving lineage through time (e.g., Jolly, 1972; Dechow and Singer, 1984; Eck and Jablonski, 1987; Delson, 1993; Eck, 1993; Leakey, 1993; Frost, 2001a, b, 2007; Frost and Delson, 2002; Jablonski, 2002; Gilbert, 2007b; Jablonski et al., 2008). I have previously argued that it is best to recognize the earlier and smaller-bodied populations as a separate chronospecies (*T. darti*) from the larger and morphologically distinct later populations (*T. oswaldi*) (Gilbert, 2007b). However, Leakey (1993), and most recently Frost (2007), make excellent

Figure 3. Direct comparison of the type mandible of ?*T. baringensis*, KNM-BC 2B (left), with the mandibular fragment with relatively unworn teeth, KNM-BC 1647A (right). Both specimens were found at the same site, BPRP #97. Scale = 1 cm.

arguments that it is best to divide the entire chronolineage into three chronosubspecies of *T. oswaldi*: *Theropithecus oswaldi darti*, *Theropithecus oswaldi oswaldi*, and *Theropithecus oswaldi leakeyi*. Given the continuous nature of the morphological transformations through time, this taxonomic scheme is probably the most biologically meaningful and informative. I follow this arrangement here. For the analysis, I use only specimens of *T. o. darti* because these represent the most conservative specimens of the lineage and they are more likely to be phylogenetically informative than the extremely large and derived later chronosubspecies *T. o. oswaldi* and *T. o. leakeyi* (see Table 1).

Small-bodied *Papio* taxa Multiple species of small-bodied *Papio* have been recognized previously in the South African Plio-Pleistocene record: *P. izodi*, *Papio angusticeps*, and *Papio wellsi* (e.g., Gear, 1926; Broom, 1940; Freedman, 1957, 1961, 1965). In my view, Delson (1984, 1988) and McKee (1993) make convincing arguments that *P. angusticeps* is best recognized as a separate taxon from *P. izodi*. This arrangement is followed here. Furthermore, *P. angusticeps* has been suggested to be a subspecies of the modern *Papio hamadryas* with particular morphological affinities to the modern small-bodied baboon *Papio hamadryas kindae* (Delson,

1988). Both taxonomic possibilities will be considered by the analyses conducted in this study (i.e., *P. angusticeps* as a distinct taxon and as a subset of the modern *P. hamadryas* population). *P. wellsi*, on the other hand, is best considered as a junior synonym of *P. izodi* at this time (Szalay and Delson, 1979), and *P. izodi* is widely recognized as a distinct species from the modern *P. hamadryas* populations (e.g., Szalay and Delson, 1979; Delson, 1988; McKee, 1993; Jablonski, 2002; Jablonski and Frost, 2010).

Papio robinsoni In addition to *P. izodi* and *P. angusticeps*, a larger *Papio* taxon has been recognized in the South African Plio-Pleistocene, namely *P. robinsoni*. Szalay and Delson (1979), Jablonski (2002), and Jablonski and Frost (2010) recognize *P. robinsoni* only as a

Figure 4. Comparison of (a) DGUNL LEB05, a presumed adult male frontal from the Angolan Humpata Plateau, with (b) the Usno specimen from the Ethiopian Omo group. Note the widely divergent temporal lines and more posterior union of the temporal lines in the Usno specimen. Photo in part a) courtesy of E. Delson.

subspecies of the living *P. hamadryas* (*Papio hamadryas robinsoni*). I follow this assignment here and only recognize *P. hamadryas* (including all extant subspecies) as an OTU for phylogenetic analysis. *Papio quadratiostris* In 1982, a fairly complete cranium of a large papionin from the Usno Formation of the Ethiopian Omo Group was described as *P. quadratiostris* (Iwamoto, 1982). Similar to the situation with KNM-BC 2, this specimen was soon reallocated to *Theropithecus* by Eck and Jablonski (1984, 1987), and it was also suggested to be an early member of the *T. brumpti* lineage. Delson and Dean (1993) challenged this assignment and argued that the Usno specimen was best left in the genus *Papio*, and noted particular affinities to *Dinopithecus*, which they recognized as a subgenus of *Papio*. Delson and Dean (1993) also went a step further and assigned a number of papionin specimens from the geologically younger Omo Shungura Formation (some of which were originally assigned to *Papio* sp. by Eck, 1977) as well as papionin material from Leba Cave and Fissures on the Humpata Plateau in Angola, to *P. quadratiostris*. In contrast, Jablonski (1994, 2002) recognized the later Omo material and all of the Angolan papionin material (from the sites of Cangalongue, Malola Kiln, Tchiua, and Leba) as *Theropithecus*, grouping it with the KNM-BC 2 specimen as *T. baringensis*.

Delson and Dean (1993) make a convincing argument that the later Omo material and some of the Angolan material from Leba are extremely similar to each other. However, the later Omo material and some of the Leba specimens are dentally distinct from the type Usno specimen in that they display very large premolars. In addition, there is no good overlapping male craniofacial material that allows a proper comparison between the Usno skull and the later Omo and Angolan material (although comparable male palates and female partial crania exist). The only overlapping craniofacial material is a partial male frontal from Leba, Angola (DGUNL LEBA05), that clearly displays a different temporal line morphology

compared with that of the type Usno specimen (Fig. 4). Whereas the Angolan specimen displays pinched temporal lines that appear to converge anteriorly quite quickly, the Usno specimen displays widely divergent temporal lines that do not converge until the posterior end of the cranium (Fig. 4).

While Jablonski (1994) recognized only one papionin taxon (*T. baringensis*) among the Plio-Pleistocene sites in Angola, I believe that a minimum of two papionin taxa (and one colobine) are represented among the Angolan specimens, and possibly more. As mentioned above, some of the craniodental material from the Leba assemblage resembles the later Omo material, particularly a couple of craniodental specimens with large premolars and a partial female cranium (see Table 2 for list of specimens). However, other Leba specimens are dissimilar to those from the Omo, such as the partial male frontal DGUNL LEBA05, and the CAN 30 '90 partial mandible from Cangalongue, which displays a *Theropithecus*-like dentition. Many of the other Angolan specimens appear to be large non-*Theropithecus* papionins perhaps unidentifiable to a more specific taxon at this time, in large part because a disproportionately large number of the specimens are subadults (Gilbert et al., 2009b). In these cases, it is not possible to be confident about many adult morphological features and make lower-level taxonomic assignments (Gilbert et al., 2011b). Given the clear affinities between some of the dental material as well as the partial adult female cranium preserved in the Leba assemblage to the late Omo material, I recognize the adult papionin specimens with large premolars and other diagnostic morphologies similar to the Omo material as one taxon, and the remaining material as cf. *Theropithecus* (CAN 30 '90), Papionini sp. indet., *Cercopithecoides* sp., or *Cercopithecidae* sp. indet. (see Table 2). Additional study of the Angolan material may result in more definitive assignments for some of the adult and more advanced juvenile specimens (e.g., LEBA 04, TCH 38 '90).

Table 2
Cercopithecoid specimens from the Humpata Plateau, Angola.

Specimen	Site	Taxon	Brief description	Estimated age (Ma)	Reference
TCH 38 '90	Tchiua	Papionini sp. indet.	Partial juvenile M1 cranium	~2.0–3.0	Jablonski, 1994
TCH 19 '90	Tchiua	Papionini sp. indet.	Partial infant cranium	~2.0–3.0	Jablonski, 1994
TCH 25 '90	Tchiua	Papionini sp. indet.	Partial male cranium	~2.0–3.0	Jablonski, 1994
TCH 41 '90	Tchiua	Papionini sp. indet.	Female partial cranium	~2.0–3.0	Jablonski, 1994
TCH 42 '90	Tchiua	Papionini sp. indet.	Isolated lower central incisor	~2.0–3.0	Jablonski, 1994
TCH 96 '90	Tchiua	Papionini sp. indet.	Crushed partial subadult cranium	~2.0–3.0	Jablonski, 1994
TCH TEMP1 '90	Tchiua	<i>Cercopithecidae</i> sp. indet.	Isolated glenoid fossa	~2.0–3.0	Jablonski, 1994
TCH TEMP2 '90	Tchiua	<i>Cercopithecidae</i> sp. indet.	Subadult occipital and parietal fragment	~2.0–3.0	Jablonski, 1994
MAL 19 '90	Malola Kiln	Papionini sp. indet.	Partial male symphysis	~2.0–3.0	Jablonski, 1994; Pickford et al., 1994
CAN 30 '90	Cangalongue	cf. <i>Theropithecus</i> sp.	Partial male mandible	~1.8–1.3	Jablonski, 1994; Pickford et al., 1994
MCZ 19870	Leba	Papionini sp. indet.	Partial M1 juvenile cranium	~2.0–3.0	Minkoff, 1972
LEBA 01	Leba	<i>Cercopithecoides</i> sp.	Partial mandible	~2.0–3.0	Pickford et al., 1992; Gilbert et al., 2009b
LEBA 04	Leba	Papionini sp. indet.	Maxillary fragment	~2.0–3.0	Unpublished photos
LEBA 05	Leba	Papionini sp. indet.	Partial male neurocranium	~2.0–3.0	Delson and Dean, 1993
LEBA 08	Leba	Papionini sp. indet.	Partial juvenile female mandible	~2.0–3.0	Gilbert et al., 2009b
LEBA 09	Leba	Papionini sp. indet.	Partial juvenile cranium	~2.0–3.0	Gilbert et al., 2009b
LEBA 10	Leba	Papionini sp. indet.	Partial juvenile cranium	~2.0–3.0	Gilbert et al., 2009b
LEBA 11	Leba	Papionini sp. indet.	Partial juvenile cranium	~2.0–3.0	Gilbert et al., 2009b
LEBA 12	Leba	Papionini sp. indet.	Partial juvenile cranium	~2.0–3.0	Gilbert et al., 2009b
LEBA 13	Leba	Papionini sp. indet.	Partial juvenile cranium	~2.0–3.0	Unpublished photos
LEBA 14–17	Leba	Papionini sp. indet.	Isolated teeth	~2.0–3.0	Gilbert et al., 2009b
LEBA 02	Leba	<i>Soromandrillus quadratiostris</i>	Partial female cranium/basicranium	~2.0–3.0	Delson and Dean, 1993
LEBA 03	Leba	<i>Soromandrillus quadratiostris</i>	Partial female mandible	~2.0–3.0	Delson and Dean, 1993
LEBA 06	Leba	<i>Soromandrillus quadratiostris</i>	Partial male maxilla	~2.0–3.0	Delson and Dean, 1993
LEBA 07	Leba	<i>Soromandrillus quadratiostris</i>	Partial maxilla	~2.0–3.0	Gilbert et al., 2009b

Notes: This table includes only those specimens of which I have seen photographs, have personally examined, or which have been published. Other specimens remain undescribed.

If Delson and Dean's (1993) hypothesis is correct, then the Usno specimen, later Omo material, and selected Angolan material, as recognized here (see below and Table 2), should be reconstructed as a single clade. A previous analysis suggested that this is indeed the case (Gilbert, 2008). Thus, at this point in time, I consider it best to recognize *P. quadratiostris* as a chronolineage spanning the Usno Formation, Omo Shungura Formation, and Leba Cave and Fissures on the Humpata Plateau. In other words, I consider a situation where the USNO specimen/population is directly ancestral to the later Omo and Angolan material as the most likely scenario given the available morphological, geological and geographical evidence. The Usno specimen is dated to approximately 3.4 Ma (millions of years ago) (Delson and Dean, 1993), and the Omo and Angolan material are ~0.5–1.5 Ma younger. In the case of the Omo material, my own measurements suggest that fourth premolar size increases through time from their small size in the Usno specimen (3.4 Ma) with progressive enlargement in Members E through G (2.5–2.3 Ma; see specimens NME L 185–6, NME L 4–13b, NME Omo 42–1972–1, NME Omo 47–1970–2008; see Table 3). If the Usno specimen and the later Shungura E–G material indeed represent an evolving lineage, then they should probably be recognized as the same species with different chronological (anagenetic) subspecies. I would also include the Angolan material in the same subspecies as the later Omo material based on the similarities noted by Delson and Dean (1993) as well as myself (see above; Table 3).

Throughout the study of the *P. quadratiostris* material from Usno, Omo, and Leba, I was struck by the number of derived similarities the *P. quadratiostris* specimens share with the *Cercocebus*/*Mandrillus* clade, particularly with *Mandrillus*. At the time of Delson and Dean's (1993) study, mandrills and drills were widely considered species within the genus *Papio* rather than placed within their own genus, *Mandrillus*. Delson and Dean (1993) also considered mandrills and drills to be members of the genus *Papio*, and many of the morphological similarities they noted between the Usno specimen and *Papio* were, in fact, similarities more specifically with mandrills and drills (e.g., see Fig. 5). *P. quadratiostris* shares many features with mandrills and drills to the exclusion of savannah baboons: a long and low neurocranium, widely divergent temporal lines that meet at the posterior of the skull to form an extensive temporonuchal crest, an upturned nuchal crest in the midline, relatively shallow maxillary fossae restricted to the area just above the alveoli, and large premolars in the geologically younger specimens. All of these features suggest that *P. quadratiostris* is, in fact, not a member of the genus *Papio* at all. Instead, the entire hypodigm

should be transferred to a new genus to reflect its morphological similarities to the *Cercocebus*/*Mandrillus* clade and probable phylogenetic relationship to that group.¹

Systematic paleontology

Order Primates Linnaeus, 1758
Infraorder Catarrhini É. Geoffroy St. Hilaire, 1812
Family Cercopithecidae Gray, 1821
Subfamily Cercopithecinae Gray, 1821
Tribe Papionini Burnett, 1828
Soromandrillus, gen. nov.

[= or including *Papio* Erxleben, 1777 (in part); Iwamoto, 1982. *Theropithecus* I. Geoffroy St. Hilaire, 1843 (in part); Eck and Jablonski, 1984; Jablonski, 1994. *Papio* (*Dinopithecus*) Broom, 1937 (in part); Delson and Dean, 1993.]

Type species

Soromandrillus quadratiostris (Iwamoto, 1982)

Etymology

In reference to its hypothesized sister relationship to the extant African papionin clade containing the genera *Cercocebus* and *Mandrillus*, or, more specifically, a sister relationship with *Mandrillus*. From the latin root for sister, Soro-, combined with the extant genus *Mandrillus*.

Generic diagnosis

A genus of large African papionin, distinguished cranially from other large African papionins such as *Mandrillus*, *Papio*, *Dinopithecus*, *Gorgopithecus*, and *Theropithecus* by its combination of a long, low cranium (particularly in males), a relatively small braincase with strong postorbital constriction, widely divergent temporal lines in both males and females, a sagittal crest forming posterior to bregma in males, an upturned nuchal crest in both males and females, and molars that do not display a high degree of flare. *Soromandrillus* is differentiated from *Theropithecus* by a more posteriorly positioned sagittal crest in males, more widely divergent temporal lines in males and females, maxillary ridges in males that run medially towards the incisors rather than laterally towards the canines, the lack of a reversed curve of Spee, upper central incisors larger than the lateral incisors, and the lack of increased enamel infoldings on the premolars and molars. *Soromandrillus* is most easily differentiated from *Papio*, *Gorgopithecus* and *Dinopithecus* by its small braincase, more widely divergent temporal lines in both males and females, an upturned nuchal crest in both males and females, and male maxillary ridges that run medially towards the incisors. It is further differentiated from *Dinopithecus* by its more posteriorly positioned external auditory meati relative to basion.

In addition to its larger overall size, *Soromandrillus* is distinguished from smaller African papionins such as *Parapapio*, *Cercocebus*, and *Lophocebus* by the presence of an anteorbital drop, the presence of maxillary fossae that are restricted to the region above the maxillary alveoli (rather than extending up to and/or invading

Table 3

S. quadratiostris premolar size through time in the Omo River Basin and Humpata Plateau, Angola.

Specimen	Omo Usno/Shungura Member	Estimated age (Ma)	P ⁴ /M ¹ ratio	P ₄ /M ₁ ratio
Usno	U-8 or U-9	3.3	52.8	X
NME L 185–6	E	2.5	(67.4)	X
NME L 4–13b	E	2.5	67.7	X
NME Omo 207–1973–1762	E	2.5	69.9	X
NME Omo 42–1972–1	F	2.4	71.9	X
NME Omo 75N (71)–C2	G	2.3	X	68.5
NME Omo 47–1970–2008	G	2.3	X	83.0
LEBA 02	X	~2.0–3.0	72.0	X
LEBA 03	X	~2.0–3.0	X	80.1
LEBA 06	X	~2.0–3.0	(67.6)	X
LEBA 07	X	~2.0–3.0	78.3	X

Notes: Premolar ratios = (P₄ area/M₁ area) × 100. Numbers in parentheses represent estimates. Estimated age values from Delson and Dean (1993) and Eck and Jablonski (1984, 1987). X = unavailable.

¹ This publication and the new genus that it contains have been registered in ZooBank, the ICZN online registration system. ZooBank Life Science Identifiers (LSIDs) can be accessed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:57C51D7F-BB4B-4176-8223-D27DBDAFB4E9.

Figure 5. Comparison, in lateral, dorsal, and occipital views, of (top) an adult male *S. quadratiostris* (Usno) with (bottom) adult male *Mandrillus* specimens. *M. sphinx* in dorsal and lateral views modified from Delson and Dean (1993) with permission. *M. leucophaeus* in occipital view modified from Gilbert (2007a).

the infraorbital plate as in *Cercocebus* and *Lophocebus*), the presence of definitive maxillary ridges, a prominent glabella, and a prominent supraorbital region with a postorbital sulcus. It is differentiated from *Pliopapio* by its larger overall size, long and low skull, muzzle with maxillary ridges and maxillary fossae, widely divergent temporal lines, upturned nuchal lines, larger premolars (particularly in the upper Omo and Angolan specimens), and a more upright mandibular symphysis.

The mandible of *Soromandrillus* is large and displays shallow mandibular corpus fossae in males but typically lacks these depressions in females (a pattern similar to modern *Cercocebus* and *Mandrillus*). The symphysis is relatively upright with a median mental foramen and mental ridges present on male specimens. The molars are typically papionin and do not exhibit exaggerated enamel infoldings like *Theropithecus*. The extramolar sulcus is narrow. Where preserved, it appears as if the ascending ramus was posteriorly inclined. The ratio of the P_4 to M_1 appears to have been variable but relatively high, particularly in the later Omo specimens (see Table 3).

Soromandrillus shares multiple craniodental characters with both *Cercocebus* and *Mandrillus*, with particular similarities to *Mandrillus* including large overall size, a long, low male cranium, widely divergent temporal lines in males and female, upturned nuchal crests in males and females, relatively shallow maxillary fossae restricted to the region above the maxillary alveoli, mandibular corpus fossae present in males but shallow to absent in females, maxillary ridges which run medially towards the incisors in males, and large premolars, specifically among Omo Shungura and Leba specimens assigned to *S. quadratiostris*. *Soromandrillus* is differentiated from *Mandrillus* by its smaller braincase, slightly less

divergent temporal lines in both males and females (most likely related to the smaller braincase), unexaggerated and uninflated maxillary ridges in males, shallower mandibular corpus fossae in males, and molars lacking a high degree of flare. Early members of *Soromandrillus* are further distinguished from *Mandrillus* by the possession of smaller premolars relative to the molars. The estimated body size of *Soromandrillus* is 34–48 kg for males and 18–25 kg for females (Delson et al., 2000). If body mass estimates published in Delson et al. (2000) are accurate, then a large degree of sexual dimorphism appears to be present in *Soromandrillus* with a male to female ratio potentially exceeding 2:1 (estimated at 2.3 by Delson et al., 2000). Only *Mandrillus* and *Cercocebus* taxa have a ratio greater than 2:1 among extant papionin taxa (e.g., Gilbert and Grine, 2010).

S. quadratiostris (Iwamoto, 1982)

[= or including *P. quadratiostris* Iwamoto, 1982. *T. quadratiostris* (Eck and Jablonski, 1984). *P. (Dinopithecus) quadratiostris* (in part): Delson and Dean, 1993. *T. baringensis* (in part): Jablonski, 1994.]

Holotype

The Usno cranium, described by Iwamoto (1982), a partial male cranium preserving most of the face, palate, and neurocranium. Much of the basicranium is not preserved. This specimen is curated in the NME (National Museums of Ethiopia), but not formally numbered; Delson and Dean (1993) informally termed it NME Usno.

Hypodigm

I confidently assign only the following specimens to the *Soromandrillus* hypodigm at this time: NME Usno partial male cranium (type specimen), NME L 4-13b (female? maxillary fragment), NME L 173-5 (mandibular fragment), NME L 185-6 (partial male palate), NME Omo 207-1973-1762 (partial female palate/muzzle with frontal and cranial frags), NME Omo 42-1972-1 (partial female cranium), NME Omo 47-1970-2008 (partial female mandible), NME Omo 75N (71)-C2 (partial male mandible), DGUNL LEBA 02 (partial female cranium/basicranium), DGUNL LEBA 03 (partial female mandible), DGUNL LEBA 06 (partial male muzzle/maxilla), DGUNL LEBA 07 (partial maxilla) (Tables 1–3).

Specific diagnosis

Same as for genus.

Horizon

Omo Usno Formation, Omo Shungura Formation, and Leba Cave and Fissures, Humpata Plateau of Angola.

Localities/sites

The NME Usno cranium was found at the White Sands locality of the lower Omo basin, southwest Ethiopia, and is estimated to be ~3.4 million years old (Iwamoto, 1982; de Heinzelin, 1983; Delson and Dean, 1993). NME L 185-6, NME L 173-5 and NME L 4-13b, and NME Omo 207-1973-1762 are from the Omo Shungura Member E (~2.5 Ma), NME Omo 42-1972-1 is from the Omo Shungura Member F (~2.4 Ma), and NME Omo 47-1970-2008, NME Omo 75N (71)-C2 are both from the Omo Shungura Member G (~2.3 Ma). DGUNL LEBA 02, 03, 06, and 07 are all from the site of Leba (cave and fissures), which is estimated to be Plio-Pleistocene in age, ~3–2 Ma (see Delson and Dean, 1993; Gilbert et al., 2009b).

Further support for *Soromandrillus* as a valid taxon will be provided if the analyses presented in this study place *S. quadratostris* in a phylogenetic position close to *Cercocebus*/*Mandrillus* rather than close to *Papio*.

Materials and methods

Complete character lists with definitions and character states are presented in Table 4. Extant taxa and sample sizes are presented in Table 5. Fossil taxa and sample sizes are presented in Table 1.

For analysis, males and females were coded separately and then combined into a larger ‘combined-sex’ matrix, as described by Gilbert et al. (2009a). Phylogenetic analyses involving many fossil taxa often run into problems because of large amounts of missing data. One way to combat these problems is to increase the number of characters used in the analysis (Wiens, 2003a,b, 2006; Wiens et al., 2005). Increasing the number of characters in an analysis has been repeatedly demonstrated to increase overall phylogenetic accuracy and help resolve character conflict that can hamper fossil analyses with large amounts of missing data (Wiens, 2003a,b, 2006; Wiens et al., 2005). In this case, combining characters that have been scored separately for males and females allows for both unique male and female character states that are phylogenetically informative to be sampled together during the analysis and potentially increase the strength and accuracy of the phylogenetic signal (see also Gilbert et al., 2009a). In total, 318 craniodental characters were included: 89 quantitative characters, and 70 qualitative characters coded for each sex (see Table 4 for full character list with sources). This character matrix is based in large part on the

previously published matrices of Gilbert et al. (2009a). Relative to the Gilbert et al. (2009a) analysis, a small number of characters have been added (six quantitative and two qualitative) and a few characters have been redefined to allow for novel character states presented by fossil taxa as well as to more precisely discern synapomorphies (Table 4). In addition, sample sizes among extant taxa have been slightly increased in some cases (Table 5). No postcranial data are included here because most of the postcranial material in the fossil record is unassociated and cannot be attributed to specific taxa.

Victoriapithecus, *Pp. lothagamensis*, and *Macaca* were assigned and constrained as successive outgroups for all analyses. Because many quantitative characters were coded on the basis of allometric corrections, *Victoriapithecus* is not an appropriate outgroup for these characters since the allometric trajectory influencing the craniodental morphology of *Victoriapithecus* is not directly comparable to that observed in papionin monkeys. A phenetically distant taxon such as *Victoriapithecus* should not be used as an outgroup for these quantitative craniometric characters (Gaffney, 1979; Lockwood et al., 2004; Gilbert and Rossie, 2007). However, the inclusion of multiple outgroups has been demonstrated to increase phylogenetic accuracy, and since *Victoriapithecus* is universally recognized as a primitive cercopithecoid monkey, this taxon was scored and included as an outgroup for all qualitative and non-allometrically influenced quantitative characters.

As described above, I consider *Pp. lothagamensis* to be a separate and more primitive taxon compared with its congeners. Since *Pp. lothagamensis* retains many primitive features seen in *Victoriapithecus*, I consider *Pp. lothagamensis* to be more primitive than *Macaca* as well. For these reasons, *Pp. lothagamensis* is assigned as an outgroup for all analyses. Given that *Macaca* is universally accepted as the sister taxon of the African papionins, it is also assigned as an outgroup for all analyses.

Values for quantitative characters were taken from original fossils, casts of original fossils, and measurements from the literature. Qualitative characters were scored on original fossils and casts. In a small number of cases, published descriptions and photographs of fossil material were used to assess qualitative states.

Each type of character, quantitative and qualitative, requires slightly different rules and techniques for assigning character states. For quantitative characters, a size correction was first applied separately for the two elements of the skull (the cranium and the mandible) because these elements are rarely found associated in the fossil record. Ideally, in the current data set of 62 standard craniometric measurements for each extant specimen,² cranial quantitative characters would be divided by the geometric mean of the 48 cranial measurements for that specimen and mandibular quantitative characters divided by the geometric mean of the 14 mandibular measurements for that specimen. However, for fossil taxa, the same set of measurements used to calculate these geometric means for extant specimens are unlikely to be preserved. To account for this reality, regression analyses of all of the measurements used to calculate the geometric means for each extant specimen were performed separately for extant male and female specimens. The individual cranial measurement and mandibular measurement 1) with the highest correlation coefficient relative to the cranial and mandibular geometric means, and 2) commonly preserved in the fossil record, were then used as size corrections for each extant and fossil cranial and mandibular specimen. For the current analysis, the cranial measurement P2

² The 62 measurements from Collard and Wood (2000, 2001) were used for the calculation of the geometric mean for each taxon (see Gilbert and Rossie [2007]; Gilbert et al. [2009a]).

Table 4
Characters used in this study.

Character	Definition	Character type	Reference
^a C1	Glabella-inion	QN, O	Wood, 1991
^a C2	Bregma-basion	QN, O	Wood, 1991
^a C3	Minimum frontal breadth (minimum chord distance between frontotemporale; i.e., maximum width in the coronal plane)	QN, O	Wood, 1991
^a C4	Biporionic breadth	QN, O	Wood, 1991
^a C5	Glabella-bregma	QN, O	Wood, 1991
^a C6	Postglabellar sulcus-bregma (distance between the deepest point of the postglabellar depression and bregma)	QN, O	Wood, 1991
^a C7	Parietal-sagittal chord (bregma-lambda)	QN, O	Wood, 1991
^a C8	Parietal-lambdoid chord (chord distance along the lambdoid border of the intact parietal)	QN, O	Wood, 1991
C9	Lambda-inion	QN, O	Wood, 1991
C10	Occipital-sagittal length (lambda-opisthion)	QN, O	Wood, 1991
^a C11	Foramen magnum max width	QN, O	Wood, 1991
C12	Occipital condyle max length	QN, O	Wood, 1991
C13	Lambda thickness of parietal	QN, O	Wood, 1991
^a C14	Breadth between carotid canals	QN, O	Chamberlain, 1987
^a C15	Breadth between petrous apices	QN, O	Chamberlain, 1987
C16	Length of tympanic plate (distance from the most lateral point on the inferior surface of the tympanic plate to the carotid canal)	QN, O	Chamberlain, 1987
C17	Adult male sagittal crest position States: 0 = absent, 1 = intermediate, 2 = present only posteriorly, 3 = intermediate, 4 = extends anteriorly. The distinction between states 2 and 4 is determined by whether the anteriormost point of the crest is well anterior to bregma or begins approximately at or posterior to bregma. Crest is defined here as the meeting or contact of the temporal lines.	QL, O	Eck and Jablonski, 1984, 1987
C18	Postorbital sulcus States: 0 = absent, 1 = intermediate, 2 = post-glabbellar depression present, 3 = intermediate, 4 = post-orbital sulcus present, 5 = polymorphic	QL, U	Szalay and Delson, 1979
^a C19	Auditory meatus position Small Taxa States: 0 = medial (inferior margin of the meatus is medial to porion and thus overhung by a supermeatal roof), 1 = intermediate, 2 = Extended laterally relative to the medial state, but still medial to the lateral border of the neurocranium Large Taxa States: 0 = Extended laterally relative to the medial state, but still medial to the lateral border of the neurocranium, 1 = intermediate, 2 = lateral (inferior margin of the meatus is lateral to porion)	QL, O	Groves, 1978, 2000
C20	Anterior temporal line divergence States: 0 = pinched, 1 = intermediate, 2 = slightly divergent, 3 = intermediate, 4 = widely divergent	QL, O	Groves, 2000; McGraw and Fleagle, 2006; Gilbert, 2007a
C21	Nuchal lines in the midline where discernable States: 0 = downturned, 1 = intermediate, 2 = straight, 3 = intermediate, 4 = upturned	QL, O	Gilbert, 2007a
^a C22	Calvarial shape (biporionic length/labella-inion)	QN, O	General
C23	Cranial vault index (basion-bregma/labella-inion)	QN, O	General
^a C24	Postorbital constriction (min frontal breadth/max biorbital breadth)	QN, O	General
^a C25	Compound temporonuchal crest Small Taxa States: 0 = absent, 1 = intermediate, 2 = partial crest confined to the lateral third of bi-asterionic breadth Large Taxa States: 0 = partial crest confined to the lateral third of bi-asterionic breadth, 1 = intermediate, 2 = extensive crest extending almost the entire distance between inion and the lateral margin of the supramastoid crest	QL, O	Strait et al., 1997
C26	Definitive parietal notch States: 0 = parietal/asterionic notch absent, 1 = intermediate, 2 = parietal/asterionic notch present	QL, O	Groves, 2000
^a C27	Position of the tympanic relative to the postglenoid process Small Taxa States: 0 = tympanic fused with postglenoid, 1 = intermediate, 2 = tympanic unfused and separated from the postglenoid process Large Taxa States: 0 = tympanic unfused and separated from the postglenoid process, 1 = intermediate, 2 = tympanic unfused and widely separated from the tympanic	QL, O	Groves, 2000
C28	Postglenoid process height States: 0 = very tall, 1 = intermediate, 2 = normal, 3 = intermediate, 4 = shortened	QL, O	Groves, 2000
C29	EAM tympanic crest States: 0 = present, 1 = intermediate, 2 = absent	QL, O	Groves, 2000
^a C30	Foramen magnum max length (opisthion-basion)	QN, O	General

Table 4 (continued)

Character	Definition	Character type	Reference
C31	Position of the foramen magnum relative to the biporionic line States: 0 = basion is well posterior to the line, 1 = intermediate, 2 = basion approximates the line, 3 = intermediate, 4 = basion is well anterior to the line	QL, O	Dean and Wood, 1981, 1982; Strait et al., 1997
C32	EAM size States: 0 = small, 1 = intermediate, 2 = large	QL, O	Strait and Grine, 2004
^a C33	Opisthion-inion	QN, O	General
^a C34	Bieuryonic breadth	QN, O	General
^a C35	Breadth between infratemporal crests (measured where spheno-temporal suture meets the infratemporal crest)	QN, O	Chamberlain, 1987; Collard and Wood, 2000, 2001
C36	Basioccipital length (basion to sphenoccipital synchondrosis in the midline)	QN, O	Chamberlain, 1987
C37	Anterior basioccipital breadth (measured across the sphenoccipital synchondrosis)	QN, O	Chamberlain, 1987
^a C38	Posterior basioccipital breadth (measured across the anterior edge of the jugular foramina)	QN, O	Chamberlain, 1987
^a C39	Basisphenoid length (measured from the sphenoccipital synchondrosis to the junction with the vomer in the midline)	QN, O	General
C40	Petrous apex ossified beyond spheno-occipital synchondrosis States: 0 = absent, 1 = intermediate, 2 = present	QL, O	Collard and Wood, 2000
^a C41	Shape of the choanal sides Small Taxa States: 0 = divergent anteriorly, 1 = intermediate Large Taxa States: 0 = intermediate, 1 = parallel	QL, O	Groves, 2000
^a C42	Shape at the posterior end of the medial pterygoid plates Small Taxa States: 0 = moderately divergent, 1 = intermediate, 2 = strongly divergent Large Taxa States: 0 = intermediate, 1 = moderately divergent, 2 = intermediate	QL, O	Groves, 2000
C43	Shape at the posterior edge of vomer States: 0 = not incised, 1 = intermediate, 2 = incised	QL, O	Groves, 2000
C44	Vomer-presphenoid junction States: 0 = vomer uninflated, 1 = intermediate, 2 = vomer inflated	QL, O	Groves, 2000
C45	Vomer/Sphenoid/Palatine contact States: 0 = meet at one point, 1 = intermediate, 2 = separated by another bone, 3 = intermediate, 4 = palatine does not reach vomer, 5 = polymorphic	QL, U	General
^a C46	Vomer/sphenoid contact in the midline Small Taxa States: 0 = intermediate, 1 = another bone between Large Taxa States: 0 = clean contact, 1 = intermediate	QL, O	General
C47	Petrous process position States: 0 = medially positioned, 1 = intermediate, 2 = laterally positioned	QL, O	Gilbert, 2007a
C48	Appearance of fossae anterior to the foramen magnum States: 0 = absent or poorly defined, 1 = intermediate, 2 = present and clearly visible, 3 = intermediate, 4 = deeply excavated and sharply defined	QL, O	General
^a F1	Superior facial height (nasion–prosthion)	QN, O	Wood, 1991
F2	Alveolar height (nasospinale–prosthion)	QN, O	Wood, 1991
^a F3	Superior facial breadth (frontomalararetemporale–frontomalararetemporale)	QN, O	Wood, 1991
F4	Bizygomatic breadth (zygion–zygion)	QN, O	Wood, 1991
^a F5	Bimaxillary breadth (zygomaxillare–zygomaxillare)	QN, O	Wood, 1991
F6	Anterior interorbital breadth (maxillofrontale–maxillofrontale)	QN, O	Wood, 1991
^a F7	Orbital height (maxillofrontale–ektoconchion)	QN, O	Wood, 1991
F8	Min malar height (min distance from inferior orbital margin to inferior border of zygomatic process of the maxilla)	QN, O	Wood, 1991
F9	Max nasal aperture width (max width at whatever height it occurs)	QN, O	Wood, 1991
^a F10	Nasal height (nasion–nasospinale)	QN, O	Wood, 1991
^a F11	Sagittal length of nasal bones (nasion–rhinion)	QN, O	Wood, 1991
^a F12	Superior breadth of nasal bones (max chord distance across the paired nasal bones at their proximal end)	QN, O	Wood, 1991
F13	Inferior breadth of nasal bones (maximum chord distance across the paired nasal bones at their distal end)	QN, O	Wood, 1991
F14	Zygomaxillare–porion	QN, O	Wood, 1991
^a F15	Upper facial prognathism (porion–glabella)	QN, O	Chamberlain, 1987
^a F16	Lower facial prognathism (porion–prosthion)	QN, O	Chamberlain, 1987
F17	Lacrimal bone position States: 0 = extends outside the orbit, 1 = intermediate, 2 = within orbit	QL, O	Szalay and Delson, 1979
F18	Medial orbital wall composition States: 0 = vomer contribution (frontal covers ethmoid), 1 = ethmoid contribution	QL, O	Trevor-Jones, 1972
F19	Presence/Absence of maxillary fossae States: 0 = absent, 1 = intermediate, 2 = present	QL, O	Szalay and Delson, 1979

(continued on next page)

Table 4 (continued)

Character	Definition	Character type	Reference
^a F20	Development of maxillary fossae Given present in F19, Small Taxa States: 0 = very shallow, not clearly defined, 1 = intermediate, 2 = extend up to the infraorbital plate, 3 = intermediate, 4 = invades infraorbital plate, 5 = intermediate, 6 = deeply invades the infraorbital plate Given present in F19, Large Taxa States: 0 = very shallow, not clearly defined, 1 = intermediate, 2 = superior to alveolus only, 3 = intermediate, 4 = extend up to the infraorbital plate, 5 = intermediate, 6 = invades infraorbital plate	QL, O	Gilbert, 2007a,b
F21	Maxillary ridge in males States: 0 = absent, 1 = intermediate, 2 = present	QL, O	General
F22	Male maxillary ridge orientation States: 0 = medial towards incisors, 1 = intermediate, 2 = lateral towards canines	QL, O	McGraw and Fleagle, 2006
F23	Muzzle dorsum outline States: 0 = rounded, 1 = intermediate, 2 = peaked, 3 = intermediate, 4 = flat, 5 = polymorphic between states 0 and 4, 6 = polymorphic between states 0, 2, and 4	QL, U	General
F24	Contact of maxillary frontal processes States: 0 = frontal processes of maxillae do not meet in the midline, 1 = intermediate, 2 = frontal processes of maxillae meet in the midline	QL, O	General
F25	Frontal/premaxilla contact States: 0 = absent, 1 = intermediate, 2 = present	QL, O	General
F26	Maxillary sinus States: 0 = absent, 1 = present	QL, O	Rae and Koppe, 2003; Rae, 2008
F27	Positioning of the zygomatic foramina States: 0 = no foramina observable, 1 = intermediate, 2 = at or below plane of orbital rim, 3 = intermediate, 4 = foramina above and below the plane of the orbital rim, 5 = intermediate, 6 = above plane of orbital rim, 7 = polymorphic	QL, U	General
F28	Projection of nasal bones States: 0 = nasal bones do not project above the frontal/maxillary suture, 1 = intermediate, 2 = nasal bones project above the frontal/maxillary suture	QL, O	General
F29	Glabella prominence States: 0 = glabella not prominent, 1 = intermediate, 2 = glabella prominent	QL, O	General
F30	General facial profile in lateral view States: 0 = straight, 1 = intermediate, 2 = concave	QL, O	General
F31	Nasal bone orientation in lateral view States: 0 = straight (after anteorbital drop, if present), 1 = intermediate, 2 = slightly upturned, 3 = intermediate, 4 = upturned	QL, O	Gilbert, 2007a,b
F32	Nasal bone extension over nasal aperture States: 0 = no extension, 1 = intermediate, 2 = slight extension, 3 = intermediate, 4 = significant extension, 5 = polymorphic	QL, O	Gilbert, 2007a,b
F33	Anteorbital drop States: 0 = absent, 1 = intermediate, 2 = present	QL, O	General
F34	Piriform profile States: 0 = no anteorbital drop, distinct point at rhinion, 1 = intermediate, 2 = anteorbital drop, distinct point at rhinion, 3 = intermediate, 4 = anteorbital drop, no distinct point at rhinion	QL, O	General
^a F35	Relative nasal length (nasion–rhinion/nasion–prosthion)	QN, O	Szalay and Delson, 1979; Groves, 1989
F36	Max nasal aperture height (rhinion–nasospinale)	QN, O	General
^a P1	Maxillo-alveolar length (prosthion to a point where the line joining the posterior borders of the maxillary tuberosities crosses the median plane)	QN, O	Wood, 1991
^a P2	Maxillo-alveolar breadth (ectomolare–ectomolare)	QN, O	Wood, 1991
^a P3	Incisive canal-palatomaxillary suture (distance between the posterior edge of the incisive canal and the palatomaxillary suture)	QN, O	Wood, 1991
P4	Upper incisor alveolar length (distance between prosthion and the midpoint of the interalveolar septum between I ² and C ¹)	QN, O	Wood, 1991
P5	Palatal height at M ¹ (height in the midline between an imaginary line joining the alveolar process at the midpoint of M ¹ and the roof of the palate)	QN, O	Wood, 1991
P6	Upper premolar alveolar length (min distance between the midpoints of the interalveolar septa between C ¹ /P ³ and P ⁴ /M ¹)	QN, O	Wood, 1991
P7	Upper molar length (min distance between the midpoint of the P ⁴ /M ¹ interalveolar septum and the most posterior of the walls of the M ³ alveoli)	QN, O	Wood, 1991
P8	Canine interalveolar distance (min distance between the upper canine alveoli)	QN, O	Wood, 1991
P9	Last premolar interalveolar distance (min distance between the palatal walls of the P ⁴ alveoli)	QN, O	Wood, 1991
^a P10	Second molar interalveolar distance (min distance between the palatal walls of the M ² alveoli)	QN, O	Wood, 1991

Table 4 (continued)

Character	Definition	Character type	Reference
^a P11	I ¹ MD crown diameter (max crown diameter parallel to the cervical line)	QN, O	Wood, 1991
^a P12	I ¹ BL crown diameter (max crown diameter perpendicular to the basal part of the labial enamel surface)	QN, O	Wood, 1991
P13	C ¹ MD crown diameter (max diameter of crown perpendicular to the labiolingual axis of the tooth)	QN, O	Wood, 1991
P14	C ¹ BL crown diameter (max diameter of the crown in the labiolingual axis of the tooth)	QN, O	Wood, 1991
^a P15	M ³ interalveolar distance (min distance between the inner aspect of the alveolar process at the midpoint of M ³)	QN, O	Wood, 1991
P16	Palate depth at incisive fossa (the most inferior point on the posterior margin of the incisive fossa in the midline to the line between the centers of the alveolar margin on the lingual sides of C ¹ s)	QN, O	Chamberlain, 1987
P17	Upper premolar ratio (P ⁴ crown area/M ¹ crown area)	QN, O	Fleagle and McGraw, 1999, 2002
P18	Mesial compressed sulcus on upper male canine States: 0 = present on the crown only, 1 = present and extends onto root	QL, O	Szalay and Delson, 1979; Strasser and Delson, 1987
P19	Premaxilla length (premaxillary suture at level of alveoli to prosthion)	QN, O	General
P20	Bilophodont molars States: 0 = incomplete bilophodonty, 1 = intermediate, 2 = complete bilophodonty	QL, O	General
P21	P ³ protocone relative to paracone States: 0 = protocone strongly reduced or absent, 1 = protocone present and significantly shorter than paracone, 2 = paracone present and nearly equal in height to the paracone	QL, O	Szalay and Delson, 1979
P22	M ³ distal loph reduction (BL width of M ³ mesial loph/BL width of M ³ distal loph)	QN, O	Szalay and Delson, 1979
P23	Upper I ¹ shape States: 0 = rhomboidal, 1 = spatulate (defined as lingually cupped with flare, not flare by itself)	QL, O	Szalay and Delson, 1979; Strasser and Delson, 1987
P24	Upper I ² shape States: 0 = caniniform, 1 = apically and mesially inclined	QL, O	Szalay and Delson, 1979; Strasser and Delson, 1987
P25	Female C ¹ shape States = 0 = 'masculine', 1 = intermediate, 2 = conical, 3 = intermediate, 4 = incisoriform	QL, U	Szalay and Delson, 1979; Napier, 1981, 1985
P26	Size of I ¹ relative to I ² States: 0 = I ¹ ~ I ² , 1 = intermediate, 2 = I ¹ > I ²	QL, O	General
^a P27	Canine size (canine crown area)	QN, O	General
^a P28	Canine size dimorphism (male relative canine crown area/female relative canine crown area)	QN, O	General
P29	Upper molariform crown shape (M ² max BL width/M ² max MD length)	QN, O	Szalay and Delson, 1979
P30	Molar flare States: 0 = low level of flare, 1 = intermediate level of flare, 2 = high level of flare	QL, O	Szalay and Delson, 1979; Frost, 2001a, b
P31	M ¹ shape (BL width of mesial loph/BL width of distal loph)	QN, O	Szalay and Delson, 1979
P32	M ² shape (BL width of mesial loph/BL width of distal loph)	QN, O	Szalay and Delson, 1979
^a M1	Symphyseal height (min distance between the base of the symphysis and infradentale)	QN, O	Wood, 1991
^a M2	Max symphyseal depth (max depth, at right angles to symphyseal height)	QN, O	Wood, 1991
M3	Corpus height at M ₁	QN, O	Wood, 1991
M4	Corpus width at M ₁ (max width at right angles to corpus height at M ₁ , taken at the midpoint of M ₁)	QN, O	Wood, 1991
M5	Corpus height at M ₃	QN, O	Wood, 1991
M6	Corpus width at M ₃ (max width at right angles to corpus height at M ₃ , taken at the midpoint of M ₃)	QN, O	Wood, 1991
^a M7	Lower premolar alveolar length (min distance between the midpoints of the interalveolar septa between C ₁ /P ₃ and P ₄ /M ₁)	QN, O	Wood, 1991
M8	Lower molar alveolar length (min distance between the midpoints of the interalveolar septa between P ₄ /M ₁ and the most posterior of the walls of the M ₃ alveolus)	QN, O	Wood, 1991
M9	P ₄ max MD crown diameter	QN, O	Wood, 1991
M10	P ₄ max BL crown diameter	QN, O	Wood, 1991
M11	M ₁ max MD crown diameter	QN, O	Wood, 1991
M12	M ₁ max BL crown diameter	QN, O	Wood, 1991
M13	M ₂ max MD crown diameter	QN, O	Wood, 1991
M14	M ₂ max BL crown diameter	QN, O	Wood, 1991
M15	Lower premolar ratio (P ₄ crown area/M ₁ crown area)	QN, O	Fleagle and McGraw, 1999, 2002
M16	P ₃ distal cingulum States: 0 = absent, 1 = present	QL, O	Szalay and Delson, 1979
M17	Buccal face of P ₄ crown States: 0 = straight as seen in occlusal view, 1 = intermediate, 2 = inflated as seen in occlusal view	QL, O	Szalay and Delson, 1979
M18	P ₄ orientation States: 0 = oblique, 1 = straight	QL, O	Benefit, 1993; Leakey et al., 2003

(continued on next page)

Table 4 (continued)

Character	Definition	Character type	Reference
M19	P ₄ mesiobuccal flange, an extension of the enamel cap down onto the root States: 0 = absent, 1 = present	QL, O	Szalay and Delson, 1979
M20	Lower molar hypoconulid States: 0 = hypoconulid present in all lower molariform teeth, 1 = intermediate, 2 = hypoconulid absent in all lower molariform teeth except M ₃ , 3 = intermediate, 4 = hypoconulid absent in all lower molariform teeth	QL, O	Szalay and Delson, 1979
M21	M ₃ tuberculum sextum States: 0 = absent, 1 = intermediate, 2 = present	QL, O	General
M22	Enamel folding States: 0 = non-elevated, 1 = elevated	QL, O	Szalay and Delson, 1979
M23	Lophid orientation relative to the mandibular corpus States: 0 = transverse, 1 = intermediate, 2 = oblique	QL, O	Szalay and Delson, 1979
M24	Accessory cuspsules in lower molar notches States: 0 = absent, 1 = intermediate, 2 = present	QL, O	Szalay and Delson, 1979
M25	Lower incisor lingual enamel States: 0 = absent, 1 = present	QL, O	Szalay and Delson, 1979
M26	Shape of lower I ₂ distal surface States: 0 = straight, 1 = intermediate, 2 = bulge, 3 = intermediate, 4 = distinct prong	QL, O	Szalay and Delson, 1979
M27	Mandibular ramus angle States: 0 = inclined, 1 = intermediate, 2 = vertical	QL, O	Jolly, 1972; Szalay and Delson, 1979
M28	Gonial region expansion on mandibular ramus States: 0 = absent, 1 = intermediate, 2 = present	QL, O	General
M29	Inferior mandibular symphysis length as scored to a specific tooth in occlusal view States: 0 = P ₃ , 1 = intermediate, 2 = P ₃ –P ₄ , 3 = intermediate, 4 = P ₄ , 5 = intermediate, 6 = P ₄ –M ₁ , 7 = intermediate, 8 = M ₁ , 9 = polymorphic	QL, U	General
M30	Median mental foramen States: 0 = absent, 1 = present	QL, O	Szalay and Delson, 1979
M31	Mental ridges on the symphysis in males States: 0 = absent, 1 = intermediate, 2 = present	QL, O	Szalay and Delson, 1979
M32	Development of mandibular corpus fossae States: 0 = absent, 1 = intermediate, 2 = present	QL, O	Gilbert, 2007a,b
M33	Width of the extramolar sulcus States: 0 = narrow, 1 = intermediate, 2 = moderate, 3 = intermediate, 4 = wide	QL, O	General
M34	Lingual mental foramina positioning States: 0 = present-single, 1 = intermediate, 2 = present-horizontally positioned, 3 = intermediate, 4 = present-vertically positioned, 5 = intermediate, 6 = present-variably positioned, 7 = polymorphic	QL, U	Gilbert, 2007a,b
^a M35	P ₄ crown shape (P ₄ max BL width/P ₄ max MD length)	QN, O	General
M36	M ₁ crown shape (M ₁ max BL width/M ₁ max MD length)	QN, O	General
^a M37	M ₂ crown shape (M ₂ max BL width/M ₂ max MD length)	QN, O	General
M38	P ₃ lingual 'bulge', i.e., P ₃ crown obliquity States: 0 = lingual bulge absent (not oblique), 1 = lingual bulge is present (oblique)	QL, O	General
M39	Lower molariform tooth shape (M ₁ mesial lophid/M ₁ distal lophid)	QN, O	Szalay and Delson, 1979
^a M40	Mandibular profile (corpus height at M ₁ /corpus height at M ₃)	QN, O	Szalay and Delson, 1979
M41	Curve of Spee shape States: 0 = normal, 1 = intermediate, 2 = reversed	QL, O	Eck and Jablonski, 1984; Delson and Dean, 1993
M42	Symphyseal sloping States: 0 = absent, 1 = intermediate, 2 = present (sloping), 3 = intermediate, 4 = present, extremely sloping	QL, O	Frost, 2001b
BS1	Body size (cranial size) 0 = small, 1 = large, 2 = very large	QL, O	Smith and Jungers, 1997; Fleagle, 1999; Delson et al., 2000

Notes: "Intermediate" character states refer to polymorphic conditions as detailed in the Materials and Methods section. Following Collard and Wood (2000, 2001), variables are classified by cranial region as follows: C = Cranial vault and base; F = Face; P = Palate and Upper Dentition; M = Mandible and lower dentition. Max = Maximum; Min = Minimum; BL = Buccolingual; MD = Mediodistal; QN = Quantitative character; QL = Qualitative character; O = Ordered; U = Unordered.

^a Character determined to be influenced by allometry.

Table 5

Extant taxa and sample sizes for characters used in this study.

Taxon	Sample size (males, females)	Characters	Sources
<i>Cercocebus</i>	(20, 20)	C1–C16, C22–C23, F1–F16, F35, P1–P16, P27–P28, M1–M14, M35–M37, M40	Chamberlain, 1987; Collard and Wood, 2000, 2001
	(13, 7)	P17	Fleagle and McGraw, 2002
	(12, 7)	M15	Fleagle and McGraw, 2002
	(11, 11)	C33–C39, F36	This study
	(6, 8)	P19	This study
	(6, 2)	P22	Swindler, 2002
	(10, 8)	P29, P33	Swindler, 2002
	(14, 10)	P32	Swindler, 2002
	(13, 10)	M39	Swindler, 2002
<i>C. torquatus</i>	(33, 16)	Qualitative characters (except C47 and C48)	This study
<i>C. agilis</i>	(17, 11)		
<i>C. atys</i>	(3, 4)		
<i>C. torquatus</i>	(9, 7)	C47	This study
<i>C. agilis</i>	(7, 7)		
<i>C. atys</i>	(2, 2)		
<i>C. torquatus</i>	(25, 14)	C48	This study
<i>C. agilis</i>	(5, 4)		
<i>C. atys</i>	(2, 2)		
<i>Lophocebus</i>	(20, 20)	C1–C16, C22–C23, F1–F16, F35, P1–P16, P27–P28, M1–M14, M35–M37, M40	Chamberlain, 1987; Collard and Wood, 2000, 2001
	(15, 7)	P17, M15	Fleagle and McGraw, 2002
	(11, 9)	C33–C39, F36	This study
	(6, 6)	P19	This study
	(18, 18)	P22	Swindler, 2002
	(29, 27)	P29	Swindler, 2002
	(30, 28)	P32	Swindler, 2002
	(29, 25)	P33	Swindler, 2002
	(30, 27)	M39	Swindler, 2002
<i>L. albigena</i>	(35, 36)	Qualitative characters (except C47 and C48)	This study
<i>L. aterrimus</i>	(29, 22)		
<i>L. albigena</i>	(7, 8)	C47	This study
<i>L. aterrimus</i>	(25, 18)		
<i>L. albigena</i>	(7, 9)	C48	This study
<i>L. aterrimus</i>	(25, 18)		
<i>Macaca</i>	(20, 20)	C1–C16, C22–C23, F1–F16, F35, P1–P16, P27–P28, M1–M14, M35–M37, M40	Chamberlain, 1987; Collard and Wood, 2000, 2001
	(9, 13)	P17, M15	Fleagle and McGraw, 2002; Gilbert, 2007a,b
	(10, 10)	C33–C39, F36	This study
	(6, 6)	P19	This study
	(44, 29)	P22	Swindler, 2002
	(57, 46)	P29	Swindler, 2002
	(64, 49)	P32	Swindler, 2002
	(56, 47)	P33	Swindler, 2002
	(58, 52)	M39	Swindler, 2002
<i>M. fascicularis</i>	(29, 18)	Qualitative characters (except C47 and C48)	This study
<i>M. nemestrina</i>	(23, 14)		
<i>M. mulatta</i>	(22, 31)		
<i>M. sylvanus</i>	(8, 12)		
<i>M. fascicularis</i>	(8, 9)	C47	This study
<i>M. nemestrina</i>	(6, 4)		
<i>M. sylvanus</i>	(5, 7)		
<i>M. nemestrina</i>	(6, 4)	C48	This study
<i>M. sylvanus</i>	(4, 5)		
<i>Mandrillus</i>	(42, 20)	C1–C16, C22–C23, F1–F16, F35, P1–P16, P27–P28, M1–M14, M35–M37, M40	Chamberlain, 1987; Collard and Wood, 2000, 2001
	(13, 6)	P17	Fleagle and McGraw, 2002
	(14, 6)	M15	Fleagle and McGraw, 2002
	(10, 6)	C33–C39, F36	This study
	(6, 6)	P19	This study
	(6, 4)	P22, P29, P32, P33, M39	This study
<i>M. sphinx</i>	(18, 9)	Qualitative characters (except C47 and C48)	This study
<i>M. leucophaeus</i>	(18, 20)		
<i>M. sphinx</i>	(7, 5)	C47	This study
<i>M. leucophaeus</i>	(3, 2)		
<i>M. sphinx</i>	(5, 2)	C48	This study
<i>M. leucophaeus</i>	(7, 14)		
<i>Papio</i>	(20, 19)	C1–C16, C22–C23, F1–F16, F35, P1–P16, P27–P28, M1–M14, M35–M37, M40	Chamberlain, 1987; Collard and Wood, 2000, 2001
	(14, 7)	P17	Fleagle and McGraw, 2002
	(8, 5)	M15	This study
	(15, 5)	C33–C39, F36	This study

(continued on next page)

Table 5 (continued)

Taxon	Sample size (males, females)	Characters	Sources
	(24, 20)	P19	Swindler, 2002
	(37, 31)	P22	Swindler, 2002
	(38, 36)	P29, P33	Swindler, 2002
	(36, 29)	P32	Swindler, 2002
	(37, 36)	M39	Swindler, 2002
<i>P. h. ursinus</i>	(36, 11)	Qualitative characters (except C47 and C48)	This study
<i>P. h. cynocephalus</i>	(15, 6)		
<i>P. h. kindae</i>	(14, 17)		
<i>P. h. anubis</i>	(39, 17)		
<i>P. h. hamadryas</i>	(14, 2)		
<i>P. h. papio</i>	(10, 1)		
<i>P. h. ursinus</i>	(7, 4)	C47	This study
<i>P. h. cynocephalus</i>	(5, 4)		
<i>P. h. kindae</i>	(9, 4)		
<i>P. h. anubis</i>	(X, 3)		
<i>P. h. hamadryas</i>	(4, X)		
<i>P. h. papio</i>	(7, 1)		
<i>P. h. ursinus</i>	(3, 3)	C48	This study
<i>P. h. cynocephalus</i>	(5, 3)		
<i>P. h. anubis</i>	(X, 3)		
<i>P. h. hamadryas</i>	(6, X)		
<i>P. h. papio</i>	(7, 1)		
<i>Theropithecus</i>	(22, 22)	C1–C16, C22–C23, F1–F16, F35, P1–P16, P27–P28, M1–M14, M35–M37, M40	Chamberlain, 1987; Collard and Wood, 2000, 2001 Fleagle and McGraw, 2002
	(5, 2)	P17	This study
	(8, 3)	M15	This study
	(4, 2)	C33–C39, F36	This study
	(37, 20)	P19	Swindler, 2002
	(18, 9)	P22	Swindler, 2002
	(14, 15)	P29, P33	Swindler, 2002
	(22, 19)	P32	Swindler, 2002
	(12, 11)	M39	Swindler, 2002
	(17, 6)	Qualitative characters (except C47 and C48)	This study
	(11, 5)	C47	This study
	(15, 6)	C48	This study

Notes: For qualitative characters, approximate sample sizes for individual species and subspecies are given. Sample sizes listed for qualitative characters represent maxima; sample sizes for individual characters vary depending on the preservation of the specimens examined.

(see Table 4, maxillo-alveolar breadth defined as biectomolare, $r = 0.948$) and the mandibular measurement M11 (M_1 max mesiodistal crown diameter, $r = 0.935$) were used for male specimens and the measurements P2 ($r = 0.921$) and M12 (M_1 max buccolingual crown diameter, $r = 0.936$) were used as size corrections for female specimens. Regression analyses of the P2 (males and females) and M11 (males) measurements determined that these features were positively allometric. This suggests that using these measurements as size-adjustments results in a slight over-adjustment at large body sizes. However, a slight systematic over-adjustment at large body size was deemed preferable to using different measurements with much lower correlation coefficients and much lower rates of preservation in the fossil record.

After these size corrections, the resulting values for each character represented some aspect of 'shape' (sensu Mosimann, 1970; also see Darroch and Mosimann, 1985). By definition, allometrically influenced characters are those whose shape is significantly correlated with size (Mosimann and James, 1979). Quantitative characters determined to be allometrically influenced have been identified in previous analyses of extant taxa (Gilbert and Rossie, 2007; Gilbert et al., 2009a), and these same characters were considered to be allometrically influenced in this analysis as well (see Table 4 for the complete list of allometrically influenced characters); a new set of correlation analyses to determine allometrically influenced characters including the P2 and M12/M11 size estimates were not employed for a couple of reasons. First, in many cases, multiple characters of interest are not preserved in all fossil specimens and inclusion of some fossil taxa and not others simply due to sampling bias may unfairly influence correlations. In other words, small

sample sizes and spotty character preservation among fossil taxa necessarily introduce some degree of error or uncertainty into the correlation analyses. Second, the P2 and M12/M11 estimates are demonstrably less sensitive to detecting allometric relationships and, therefore, should not be relied upon to do so in a new set of correlation analyses. Using the P2 size estimate, for example, results in the recognition of 24 allometrically influenced characters among the extant papionin taxa while the original correlation analyses using a 62-measurement geometric mean detected 44 allometrically influenced characters. Thus, the size estimates used in this study, while desirable in their wide applicability and high correlation to the geometric mean among extant papionin taxa, are likely to recognize just over half of the characters that have been previously demonstrated to be allometrically influenced. While it is true that, by excluding fossil taxa, the extant only analysis may incorrectly identify a few characters as being allometrically influenced (or not), the potential error incurred is judged here to be much less than the error incurred by relying on size estimates other than a robust geometric mean. Thus, among closely related taxonomic groups such as Tribes, I consider it most reasonable to assume that if a character is allometrically influenced among extant taxa, it is likely to be allometrically influenced among fossil taxa as well.

Due to their correlation with body size, allometrically influenced characters are not independent, and they are not suitable for phylogenetic analysis without some sort of character correction. Recently, two allometric coding methods have been described: the narrow allometric coding method (Gilbert and Rossie, 2007; Gilbert et al., 2009a) and the general allometric coding method (Gilbert et al., 2009a). Because the narrow allometric coding method

Figure 6. Heuristic comparison of general allometric coding and conventional coding of size-adjusted data for hypothetical character 'relative snout length'. The study group exhibits positive allometry for the character 'relative snout length', and taxa within the group are spread across a wide range of sizes. Conventional conversion of craniometric data into phylogenetic characters (depicted in dashed lines and numbers on the Y-axis) would divide the entire range of relative snout lengths (the Y-axis) into segments horizontally, in this case producing five states. General allometric coding plots a regression line-of-best fit (indicated by the red line) and then assigns character states (depicted by the red numbers) on the basis of positive or negative residuals such that the shortest-snouted species across the size-range are coded as 'short', and the longest-snouted species across the size-range are coded as 'long'. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) From Gilbert et al. (2009a).

depends on obvious and discrete body size groups of multiple taxa among OTUs in order to evaluate narrow allometries, it is unsuitable in many cases where such discrete body size groups are not easily discernable (Gilbert et al., 2009a). In these cases where the body size distribution among taxa is more or less continuous over a large range, the general allometric coding method is a better option because it attempts to identify broadly homologous morphologies across all body size distributions (see Gilbert et al., 2009a). In the case of the extant African papionins, taxa fall neatly into two discrete body size groups and either coding method may be used, with the narrow allometric coding method perhaps even preferred (Gilbert and Rossie, 2007; Gilbert et al., 2009a). In the case of the extant and fossil African papionins, the body size distribution is nearly continuous over a range of approximately 5–50 kg, depending on the size estimates for some fossil taxa (e.g., see Delson et al., 2000). In this situation, the narrow allometric coding method is less than ideal and the general allometric coding method is the more appropriate choice to help identify homologous character states among allometrically influenced characters. Therefore, in this analysis, for any quantitative character determined to be allometrically influenced, the general allometric coding method was applied (but see Gilbert [2008] for an analysis including fossil African papionins using the narrow allometric coding method).

After identifying those characters that are allometrically influenced (see Table 4), any such characters are then adjusted through regression analysis. Using the general allometric method, coding is determined for allometrically influenced characters by a positive (character state = '1') or negative residual relative to the regression line (character state = '0'). For all other quantitative characters, gap-weighted coding was used (Thiele, 1993), dividing the variation into three ordered character states (see also Gilbert and Rossie, 2007; Gilbert et al., 2009a, 2011b). Gap-weighted coding is preferable to other methods of quantitative character coding because it

Figure 7. Flow chart outlining the difference between traditional coding methods and the general allometric coding procedure for allometrically influenced characters. Using the example character C7 (distance from bregma to lambda), average values for each taxon are arranged in ascending order. Traditional gap-weighted coding with three character states would assign character states among all taxa treated as one group (left-hand column). The general allometric coding method assigns character states on the basis of positive or negative residuals from a regression line-of-best-fit (right column). Note the difference between the character states assigned to each taxon using the different methods; the general allometric coding method results in a more accurate reflection of homologous character states. From Gilbert et al. (2009a).

Figure 8. Flow chart outlining the general allometric coding procedure for quantitative characters. From Gilbert et al. (2009a).

maintains the integrity of large morphological gaps and, in general, is a more faithful attempt at approximating the continuous nature of quantitative characters (e.g., see discussion in Wiens, 2001). For a visual representation of the general allometric coding method for quantitative characters, see Figs. 6–8.

Qualitative characters were scored according to the character state criteria listed in Table 4. To better encompass variation, polymorphic character states were employed. Including polymorphic characters generally increases accuracy in phylogenetic analyses (e.g., see Wiens, 2000), and the methodology used here and in previous analyses (Gilbert et al., 2009a, 2011b) is similar to the 'scaled' and 'unscaled' approaches discussed by Wiens (2000) and advocated by Campbell and Frost (1993) as well as Wiens (2000). Where polymorphisms are observed, characters are ordered and it is assumed that the polymorphism lies between the two 'fixed' traits on either side (e.g., it is 'intermediate', see Table 4). Due to small sample sizes, an intermediate (polymorphic) state was assigned to any fossil taxon that exhibited more than one character state among its specimens. An extant species was considered polymorphic for a given character if two or more character states were observed in more than 20% of specimens examined. For characters with more than two discrete character states, an intermediate (polymorphic) state was assigned if two adjacent character states combined totaled $\geq 80\%$ of all observations. For example, if a character has three discrete states (0, 2, and 4), and a taxon displays states 0 or 2 combined for $\geq 80\%$ of all observations, an intermediate (polymorphic) state (1) was assigned for this particular taxon. If no two adjacent character states combined totaled $\geq 80\%$ of all observations, or if a fossil taxon displayed more than two adjacent character states, an additional polymorphic state was added and the character was considered unordered. In the case of multistate characters where more than two pairs of adjacent states totaled 80%, the average of the two possible intermediate states was used. For example, if states 0 + 2 total 80% (intermediate state 1) but states 2 + 4 also total 80% (intermediate state 3), the average of the intermediate states, in this case $(1 + 3)/2 = 2$, was assigned.

Unless otherwise noted, qualitative characters were considered ordered. If no polymorphism is observed, the character is not

necessarily assumed to have passed through an intermediate/polymorphic state, unless there is good reason to believe otherwise. Polymorphic characters were considered unordered if there was good evidence that the polymorphisms did not represent 'intermediate' states on an obvious continuum (e.g., lingual mental foramina position, character M34 in Table 4). For a full description of characters, character states, and character types, see Table 4. Where certain characters were not preserved or were inapplicable, qualitative or quantitative, the missing data ('?') code was used. In an effort to reduce the amount of missing data in the analysis, any

Figure 9. Hypothesized phylogeny of the African papionins combining results from previous morphological (Gilbert and Rossie, 2007; Gilbert et al., 2009a, 2011b) and molecular studies (Disotell et al., 1992; Disotell, 1994, 2000; Harris and Disotell, 1998; Harris, 2000; Tosi et al., 2003; Davenport et al., 2006; Olson et al., 2008; Burrell et al., 2009; Zinner et al., 2009; Roberts et al., 2010). Drawings courtesy of Stephen Nash.

Figure 10. Summary of the four MPTs recovered from Analysis 1. Tree length = 1303, CI = 0.396, RI = 0.463, RC = 0.183, HI = 0.604. (a) Strict consensus tree of the extant and fossil Papionini. Decay indices are provided above each branch on the tree. (b) Majority-rule consensus tree of the extant and fossil Papionini. Bootstrap values are provided above each branch on the tree. (c) Majority-rule consensus tree of all trees within 1% of the length of the most parsimonious tree. Percentage of trees within 1% of the MPT found supporting a given clade are provided above each branch on the tree.

qualitative character state that was constant between male and female specimens of extant taxa was also assumed to be constant between male and female specimens of fossil taxa where the morphology of both sexes was not preserved.

Three separate phylogenetic analyses were performed. The first analysis included all of the taxa listed in Table 1. The second analysis included the newly discovered extant papionin genus *Rungwecebus*, using adult character states estimated from two juvenile male specimens as detailed in Gilbert et al. (2011b). Finally, the third

analysis considered *P. angusticeps* to be a subspecies of the extant *P. hamadryas*, as suggested by Delson (1988).

The resulting character matrices were then subjected to a parsimony analysis using PAUP 4.0b10 (Swofford, 2001), and character transformations were mapped using Mesquite 2.74 (Maddison and Maddison, 2010). A 10,000 replication, random addition sequence heuristic search was used to find the most parsimonious trees. To assess the stability of reconstructed clades, three measures were employed. First, decay indices were calculated

for the strict consensus tree. Second, a 1000 replication bootstrap analysis with replacement was performed. Finally, a majority-rule consensus tree of all trees within 1% of the length of the most parsimonious tree was constructed (Strait et al., 1997).

Results

For comparison, the hypothesized phylogeny of extant papionin taxa is given in Fig. 9.

Analysis 1

Four most parsimonious trees (MPTs) were recovered in the first phylogenetic analysis, and these trees differ in three main areas: the placement of *Dinopithecus ingens* among crown papionins, the placement of *P. angusticeps* among crown African papionins, and the placement of *Theropithecus* among crown African papionins (SOM Figs. 1–4). The majority-rule and strict consensus of these four trees are presented in Fig. 10 (Fig. 10a and b; see SOM Figs. 1–4 for each individual tree). Decay indices, bootstrap support values, and the majority-rule consensus of the trees within 1% of the length of the shortest tree are also provided in Fig. 10a–b.

The most parsimonious trees summarized in Fig. 10 suggest that the basal African papionin taxon is *Parapapio*, represented by *Pp. ado*, *Pp. whitei*, *Pp. jonesi*, and *Pp. broomi* (see Fig. 10a–c). These taxa form successive groups at the bottom of the African papionin tree, with the East African *Pp. ado* found at the base of the tree and the three traditional South African taxa (*Pp. jonesi*, *Pp. broomi*, and *Pp. whitei*) reconstructed as the next clade to branch off. Within the South African *Parapapio* clade, *Pp. broomi* and *Pp. whitei* are hypothesized as sister taxa. The *Parapapio* taxa are followed successively by *Pliopapio alemui* and then *P. izodi*. Taken together, these six taxa (*Parapapio* sp., *Pl. alemui*, and *P. izodi*) all represent stem African papionins in this analysis.

Among the crown African papionin taxa in the most parsimonious trees, it is interesting to note that the inclusion of fossil taxa results in the reconstruction of *Theropithecus* as the basal crown African papionin taxon rather than a member of a clade also containing *Lophocebus* and *Papio* in half of the MPTs (see Fig. 10a and b). In the other two MPTs, the clade containing *Theropithecus* is reconstructed as the sister to the clade containing *Lophocebus* and *Papio*, similar to the relationships suggested on the basis of extant morphological and molecular data alone. *T. baringensis* is strongly supported as the basal member of the *Theropithecus* clade, confirming its taxonomic status in the genus *Theropithecus*. While the trees recovered in this analysis suggest that *T. baringensis* is a basal member of the genus *Theropithecus*, they do not necessarily support a special relationship between *T. baringensis* and *T. brumpti* as hypothesized by Eck and Jablonski (1984, 1987). Taken literally, the trees here suggest that *T. baringensis* should be viewed as broadly ancestral to *T. brumpti* and *Theropithecus gelada* + *T. o. darti*. Since *T. baringensis* is still unknown in many details of its morphology compared with the other *Theropithecus* taxa (e.g., the male neurocranium, male basicranium, female cranium, postcrania, etc.), it is possible that additional fossils will document a closer relationship to *T. brumpti* than is currently apparent. As hypothesized by previous authors (Eck and Jablonski, 1987; Delson, 1993), among *Theropithecus* taxa, the *T. oswaldi* and *T. gelada* lineages are reconstructed as sisters among the most parsimonious trees recovered here, and this pair represents the best-supported sister group in the entire African papionin tree (Fig. 10a–c).

Two fossil taxa appear relatively unstable in the analysis and are thus found in multiple positions among the crown African papionin taxa: *D. ingens* and *P. angusticeps* (Fig. 10, SOM Figs. 1–4). In one of the MPTs, *D. ingens* is regarded as the ancestor/sister to

Theropithecus, in another, *P. angusticeps* and *D. ingens* are regarded as successive ancestors to *Theropithecus*. The other two MPTs place *Theropithecus* at the base of the crown African papionin clade and place *D. ingens* as a basal non-*Theropithecus* crown African papionin (preceded by *P. angusticeps*) or as the sister to a *Soromandrillus*/*Mandrillus*/*Procercocebus*/*Cercocebus* clade. Among the four MPTs, *P. angusticeps* is placed as the ancestor/sister to *Papio*/*Gorgopithecus*/*Lophocebus* half of the time. In the other two MPTs, *P. angusticeps* is considered either the ancestor/sister to the *Dinopithecus* + *Theropithecus* clade or the ancestor/sister to the non-*Theropithecus* African papionins.

The two remaining clades found in all of the most parsimonious trees (see Fig. 10a, SOM Figs. 1–4) contain the extant *Cercocebus*/*Mandrillus* group on the one hand and the *Papio*/*Lophocebus* group on the other. Within the *Papio*/*Lophocebus* clade, the ~2 Ma *Lophocebus* cf. *albigena* from Koobi Fora is predictably reconstructed as the sister taxon to the extant genus *Lophocebus*. The other close relative of *Papio* and *Lophocebus* is the fossil taxon *Gorgopithecus major*, which is reconstructed specifically as the sister to *Lophocebus*. The extant *P. hamadryas* is viewed as the sister to this *Gorgopithecus* + *Lophocebus* group. Finally, within the broader *Cercocebus*/*Mandrillus* clade, the most parsimonious trees in this analysis suggest that *Procercocebus antiquus* is indeed the sister taxon to *Cercocebus*, as hypothesized by Gilbert (2007a). In fact, a clade containing *Cercocebus* and *Procercocebus* is one of the most strongly supported clades and has the highest decay index among non-*Theropithecus* clades (Fig. 10a–c). The four MPTs also suggest that *S. quadratiostris* is equally likely to be either the basal taxon to a *Mandrillus*/*Procercocebus*/*Cercocebus* clade or the sister taxon to *Mandrillus* (Fig. 10a). However, an examination of bootstrap support values (Fig. 10b) and trees within 1% of the length of the MPTs (Fig. 10c) perhaps indicates that *S. quadratiostris* is more likely to be the sister taxon to *Mandrillus*, as hypothesized in the Introduction. In either case, *Soromandrillus* appears to be an appropriate and valid genus closely related to extant mandrills, drills and *Cercocebus* mangabeys.

Analysis 2

The second phylogenetic analysis differs from the first in that it includes the newly discovered and little known extant genus *Rungwecebus* (the kipunji). Because *Rungwecebus* is only known morphologically from two juvenile male specimens, many characters could not be scored for this taxon, including almost the entire female morphotype. Perhaps predictably, then, adding *Rungwecebus* to the analysis increased the number of missing data cells in the matrix substantially, resulting in additional phylogenetic uncertainty (see also Discussion section). In the second analysis, sixteen MPTs were recovered, differing from the first analysis in the various placements of *P. hamadryas*, *Rungwecebus*, *P. angusticeps*, and *Dinopithecus*. The second analysis is summarized by the majority-rule and strict consensus trees presented in Fig. 11 (Fig. 11a and b; see SOM Figs. 5–20 for each individual tree). Decay indices, bootstrap support values, and the majority-rule consensus of the trees within 1% of the length of the shortest tree are also provided in Fig. 11a–c.

Overall, the MPTs in the second analysis are similar in structure to the first analysis and they only differ in the various positions of the four taxa mentioned above. The stem papionins *Parapapio* sp., *P. izodi*, and *Pliopapio*, are reconstructed in exactly the same position as in Analysis 1. *Rungwecebus* is always reconstructed as the sister taxon to either the extant *Lophocebus* or the fossil *Lophocebus* cf. *albigena*. Similar to Analysis 1, a clade containing *Theropithecus* (*T. baringensis*/*T. brumpti*/*T. darti*/*T. gelada*) is alternatively regarded as either the basal crown African papionin clade (10 MPTs) or a member of the sister clade to *Papio*/*Gorgopithecus*/*Lophocebus*/

Figure 11. Summary of the 16 MPTs recovered from Analysis 2. Tree length = 1322, CI = 0.392, RI = 0.465, RC = 0.182, HI = 0.608. (a) Strict consensus tree of the extant and fossil Papionini. Decay indices are provided above each branch on the tree. (b) Majority-rule consensus tree of the extant and fossil Papionini. Bootstrap values are provided above each branch on the tree. (c) Majority-rule consensus tree of all trees within 1% of the length of the most parsimonious tree. Percentage of trees within 1% of the MPT found supporting a given clade are provided above each branch on the tree.

Rungwecebus (six MPTs) (see SOM Figs. 5–20). In 14 of the 16 MPTs, *P. hamadryas* is regarded as a member of a clade including *Lophocebus*/*Rungwecebus*/*Gorgopithecus*, just as in the first analysis (SOM Figs. 5–20). In the other two MPTs, *P. angusticeps* and *P. hamadryas* are considered successive ancestors of a *Gorgopithecus*/*Lophocebus*/*Rungwecebus* clade plus a *Dinopithecus*/*Soromandrillus*/*Mandrillus*/*Cercocebus*/*Procercopithecus* clade (SOM Figs. 5–20). Otherwise, the various positions of *Dinopithecus* and *P. angusticeps* are the same as

described in Analysis 1, only in combination with the various alternative arrangements of *Rungwecebus* and *P. hamadryas*. In two of the MPTs, *P. angusticeps* and *Dinopithecus* are considered sister taxa ancestral to the rest of the non-*Theropithecus* crown African papionin taxa. Finally, the 16 MPTs suggest that *S. quadratiostris* is again likely to be either the basal taxon to a *Mandrillus*/*Procercopithecus*/*Cercocebus* clade (10 MPTs) or the sister taxon to *Mandrillus* (six MPTs) (SOM Figs. 5–20).

Figure 12. Summary of the five MPTs recovered from Analysis 3. Tree length = 1261, CI = 0.409, RI = 0.466, RC = 0.191, HI = 0.591. (a) Strict consensus tree of the extant and fossil Papionini. Decay indices are provided above each branch on the tree. (b) Majority-rule consensus tree of the extant and fossil Papionini. Bootstrap values are provided above each branch on the tree. (c) Majority-rule consensus tree of all trees within 1% of the length of the most parsimonious tree. Percentage of trees within 1% of the MPT found supporting a given clade are provided above each branch on the tree.

Analysis 3

The third phylogenetic analysis considered *P. angusticeps* as a member of the extant *P. hamadryas* group and resulted in five MPTs. Analysis 3 is summarized by the majority-rule and strict consensus presented in Fig. 12 (Fig. 12a and b; see SOM Figs. 21–25 for each individual tree). Decay indices, bootstrap support values, and the majority-rule consensus of the trees

within 1% of the length of the shortest tree are also provided in Fig. 12a–c.

Consistent with the first two analyses, *Dinopithecus* is again an unstable taxon occupying multiple positions in all of the MPTs. Stem African papionin taxa remain the same as in the first two analyses, with the only exception being that *Dinopithecus* is included as a stem African papionin branching off between *Pliopapio* and *P. izodi* (*Dinopithecus*(*P. izodi* + crown African

papionins)) in two of the MPTs (SOM Figs. 21–25). In the other three MPTs, *Dinopithecus* is either reconstructed as the sister to the *Soromandrillus*/*Mandrillus*/*Cercocebus*/*Procercocebus* clade or the sister to all of the non-*Theropithecus* crown African papionins (SOM Figs. 21–25).

Similar to the first two analyses, *Theropithecus* (*T. baringensis*/*T. brumpti*/*T. darti*/*T. gelada*) is either regarded as the basal crown African papionin clade (three MPTs) or as the sister to the *Papio*/*Lophocebus*/*Gorgopithecus* clade (two MPTs). *S. quadratiostris* is again reconstructed as either the basal taxon to a *Mandrillus*/*Procercocebus*/*Cercocebus* clade (three MPTs) or the sister taxon to *Mandrillus* (two MPTs) (SOM Figs. 21–25).

Discussion

The results of the above analyses may offer some insight into the evolution of the highly successful cercopithecine monkey tribe Papionini. It has long been a frustrating irony that the African papionins represent one of the best documented primate radiations in the fossil record, with many specimens of nearly complete crania, and yet the relationships of these fossil taxa to the extant African papionin taxa as well to each other have remained unresolved. The increased confidence in the ability of craniodental data to accurately reflect papionin phylogenetic relationships (Gilbert and Rossie, 2007; Gilbert et al., 2009a) and, more specifically, the high confidence in the phylogenetic utility of the current data set (Gilbert et al., 2009a), lends weight to the phylogenetic hypotheses presented in Figs. 10–12. Some of the clades reconstructed in these

phylogenetic trees support previous suggestions of phylogenetic relationships and some hypothesized relationships are contrary to previous views, including relationships that have not previously been recognized.

Supported phylogenetic hypotheses

Parapapio and Pliopapio *Parapapio* has long been recognized as a stem African papionin, if not the basal African papionin taxon (e.g., Szalay and Delson, 1979; Frost, 2001b; Jablonski, 2002). The results of this phylogenetic analysis support that view. Taken literally, the MPTs generated here also suggest that *Parapapio* may be paraphyletic, with the East African *Pp. ado* representing a more primitive taxon than the other *Parapapio* taxa. In fact, the high decay indices required to place *Pp. ado* in the same clade as the other *Parapapio* taxa may suggest that *Pp. ado* is best recognized as a separate genus. Given that *Pp. ado* is much less completely known than other *Parapapio* species, represented cranially by only a few fragments rather than partial and complete crania, it is probably best to continue to refer to *Pp. ado* as a species of *Parapapio* until more information becomes available. The differences documented by Frost (2001b) and Harrison (2011) in mandibular symphyseal morphology, however, are noteworthy.

Frost (2001b) suggested that *Pliopapio* represented either a stem African papionin or a stem member of the *Papio*/*Lophocebus*/*Theropithecus* clade. The trees recovered in this study support the former hypothesis.

Figure 13. Comparison of *Procercopithecus* with extant *Cercopithecus*. Top: *Pr. antiquus* male (TP9, left) compared with *C. torquatus* male (right). Bottom: *Pr. antiquus* female (TP8, left) compared with *C. agilis* female (right). From Gilbert (2007a).

?T. baringensis *?T. baringensis* is reconstructed in this analysis as a primitive member of the *Theropithecus* lineage (as initially suggested by Eck and Jablonski, 1984). This phylogenetic position for *T. baringensis* is strongly supported (Figs. 10–12), although a close relationship to *T. brumpti* is uncertain. Therefore, the results of this study suggest that the question mark should be removed from the nomen for this taxon and its status as a member of *Theropithecus* should be formally and universally recognized.

Procercocebus The results of this phylogenetic analysis support the suggestion that *Procercocebus* is a member of the crown African papionin clade containing *Cercocebus* and *Mandrillus* (Gilbert, 2007a; see also Fig. 13). Furthermore, a sister relationship between *Procercocebus* and *Cercocebus* is one of the most stable groupings in this study (Figs. 10–12). Relative to other clades in the MPTs, it is supported by high bootstrap values and the highest decay indices outside of the genus *Theropithecus*. Meanwhile, a tree placing *Procercocebus* within a clade containing all of the *Parapapio* taxa is 20 steps longer (1.5% longer) in the first analysis, 18 steps longer (1.4% longer) in the second analysis, and 19 steps longer (1.5% longer) in the third analysis. A tree placing *Procercocebus* within a clade containing the South African *Parapapio* taxa is 12 steps longer (0.9% longer), 12 steps longer (0.9% longer), and 11 steps longer (0.9% longer), respectively. In any of these hypothetical cases, *Cercocebus* is reconstructed as the sister of a *Procercocebus* + *Parapapio* clade (*Cercocebus*(*Procercocebus* (*Parapapio*))), with the *Cercocebus*/*Procercocebus*/*Parapapio* clade placed at or near the base of the entire African papionin tree. I consider this arrangement highly unlikely and it represents a phylogenetic hypothesis that no current researcher supports.

Soromandrillus The validity of the newly named genus *Soromandrillus* is supported by the results of the analyses presented here. In all MPTs, *Soromandrillus* is reconstructed as a member of a clade including *Mandrillus*, *Cercocebus*, and *Procercocebus*. While seemingly a member of this broader group, it is still unclear from the current set of analyses whether *Soromandrillus* represents the sister taxon to *Mandrillus* or a more basal taxon broadly ancestral to *Mandrillus*/*Cercocebus*/*Procercocebus*.

Contrary and/or newly recognized phylogenetic positions

P. izodi *P. izodi* is reconstructed here as the last stem African papionin to branch off before the evolution of the crown African papionin taxa. Consequently, this taxon is never placed in the same clade as extant *P. hamadryas* or extant *P. hamadryas* + *P. angusticeps*. This phylogenetic position, if true, calls into question its taxonomic placement in the genus *Papio*.

While perhaps initially surprising, a closer look at the characters used to link *P. izodi* within the modern genus *Papio* are not exclusive to the genus *Papio* at all. For example, an anteorbital drop, moderately-to-well-developed supraorbital tori, relatively small-to-moderately sized premolars, and a relatively long snout are not unique features found only in the extant genus *Papio* among extant and fossil African papionin taxa. In fact, it is quite possible that historical reasons are more responsible for many of the South African fossil papionin taxa retaining a *Papio* or *Parapapio* taxonomic classification rather than a more detailed consideration of morphology.

When Haughton (1925) and Gear (1926) first described fossil papionin specimens from Taung, two taxa were recognized and both placed in the genus *Papio* as *P. antiquus* and *P. izodi*. In large part, these assignments reflected the perception that the fossil specimens were ‘baboons’ in the general sense and that they must somehow be related to the living true baboons of the genus *Papio* that are common throughout South Africa today (*Papio hamadryas ursinus*). This view was also biased by the fact that all of the

Figure 14. Comparison of *P. izodi* with extant *P. hamadryas kindae*. *P. h. kindae* is used in comparisons because it is similar in size to *P. izodi*, therefore controlling for allometric shape changes in larger *Papio* subspecies. (a) Top: *P. izodi* in lateral (left) and frontal (right) views; Bottom: *P. h. kindae* in lateral (left) and frontal (right) views. (b) *P. izodi* (left) and *P. h. kindae* (right) in basicranial view. (c) *P. izodi* (left) and *P. h. kindae* (right) in dorsal view. Note the weak to absent maxillary fossae, weak to absent maxillary ridges, relatively shorter and broader snout, and relatively larger orbits exhibited in *P. izodi*. Specimens in each panel are approximately to scale.

comparisons made in the study of these new fossil specimens used an extant sample composed of ~100 skulls of extant *P. hamadryas* (overwhelmingly *P. h. ursinus*) and did not include any other extant papionin genera (e.g., Gear, 1926, 1958; Jones, 1937; Freedman, 1957). The genus *Parapapio* was erected by Jones in 1937 to accommodate a number of new papionin specimens from Sterkfontein (Jones, 1937), and Broom (1948) suggested that both species from Taung were members of *Parapapio* rather than *Papio*. Interestingly, Jones (1937) felt that *P. antiquus* was clearly a species of the modern genus *Papio* while *P. izodi* was most likely a separate genus.

In his landmark monograph, Freedman (1957) argued just the opposite; that *P. antiquus* was clearly a species of *Parapapio*, but *P. izodi* was a species of *Papio*. Freedman (1957) largely distinguished the genus *Papio* and *Parapapio* on the basis of a few easily observable features: the presence or absence of an anteorbital drop, the presence or absence of a prominent supraorbital region, and the presence or absence of well-developed maxillary ridges in males. Among these, the anteorbital drop and supraorbital region was relied on most heavily in the assignment of *P. izodi* to the genus *Papio*, in part because no male specimens were known at the time (Freedman, 1957). This situation, where generalized South African fossil papionin specimens were either placed in the genus *Papio* or *Parapapio* largely on the basis of the presence or absence of an anteorbital drop, persisted more or less unchanged until a few years ago. In many craniodental characters, the traditionally recognized *Parapapio* taxa and *P. izodi* overlap extensively, including the development of the maxillary fossae (generally less in *Parapapio* taxa, but not always), the development of the maxillary ridges (again, generally less in *Parapapio*, but with overlap), overall

cranial size, and the indistinguishable morphology of most of the dentition, so much so that it is often difficult to distinguish among *P. izodi* and *Parapapio* specimens in the absence of fairly complete crania (e.g., Delson, 1988; Delson et al., 2000).

More recently, this system of referring generalized African papionin specimens to either *Parapapio* or *Papio* was brought into question by the inclusion of a much larger extant comparative sample and the observation that previously recognized *Parapapio* taxa, specifically *Pp. antiquus*, share derived character states with extant mandrills, drills, and *Cercocebus mangabeyi* (Gilbert, 2007a; see Results section and discussion of *Procercocebus* above). These events coincide with the greater understanding of extant African papionin phylogeny over the past 20 years, with the recognition of six distinct genera (rather than two or three genera, as recognized for most of the 20th century) and two distinct clades: *Cercocebus/Mandrillus* and *Rungwecebus/Papio/Lophocebus/Theropithecus* (discussed in more detail below). Given these recent events in combination with the results of the current study, perhaps it is also time to reevaluate the taxonomic placement of *P. izodi* within the genus *Papio*.

P. izodi has previously been noted to be distinguishable from the other fossil *Papio* taxa, both the large taxon *P. h. robinsoni* and the small taxon *P. angusticeps* (e.g., Freedman, 1957; Szalay and Delson, 1979; Delson, 1988; McKee, 1993; Jablonski, 2002; Jablonski and Frost, 2010). In addition, new male specimens of *P. izodi* (see Heaton, 2006 and Table 1) bring much more of the morphology of this taxon into the light and further highlight differences between *P. izodi* and the other extant and fossil *Papio* taxa, for example, the slight development of maxillary fossae, the absent-to-slight development of maxillary ridges in males, absence of a posteriorly-placed sagittal crest in males, more rounded-to-peaked muzzle dorsum, relatively broader and shorter muzzle, relatively larger orbits, relatively shorter cranial height, and relatively larger teeth (e.g., Delson, 1988; McKee, 1993; see Fig. 14). In fact, a tree including *P. izodi*, *P. angusticeps*, and *P. hamadryas* (or just *P. izodi* and *P. hamadryas* in Analysis 3) as a clade is 33 steps longer (2.5% longer, Templeton test $p = 0.03$, Winning Sites Test $p = 0.02$) in Analysis 1, 28 steps longer (2.1% longer, Templeton test $p = 0.09$, Winning Sites Test $p = 0.03$) in Analysis 2, and 34 steps longer (2.7% longer, Templeton test $p = 0.1$, Winning Sites Test $p = 0.1$) in Analysis 3, making this a significantly less probable phylogenetic possibility in half of the analyses. Therefore, as originally suggested by Jones over 70 years ago (Jones, 1937), it is quite possible that *P. izodi* should be reassigned into a new genus to reflect its more primitive morphology than other members currently recognized within the genus *Papio*. Since new and important material representing *P. izodi*, including specimens from Sterkfontein Member 2, is still awaiting formal publication (e.g., see Heaton, 2006), I will leave this taxonomic decision for future studies to consider. While *P. izodi* is generalized enough to be a potential ancestor for the modern forms of *Papio*, the analyses presented here suggest that it is less probable that *P. izodi* shares a more recent ancestor with *Papio* to the exclusion of other crown African papionin taxa.

Dinopithecus The overall uncertain placement of *Dinopithecus* is contrary to most authors' previous hypotheses suggesting that it is a very large 'baboon,' closely related to extant *Papio* (e.g., Freedman, 1957; Szalay and Delson, 1979; Delson and Dean, 1993; Frost, 2001a). Among the MPTs, *Dinopithecus* is sometimes placed at the base of the non-*Theropithecus* crown African papionin radiation (occasionally with *P. angusticeps*), sometimes placed as the ancestor/sister of the *S. quadratiostris*/*Mandrillus*/*Cercocebus*/*Procercocebus* clade, sometimes placed as the ancestor/sister of the *Theropithecus* clade (see SOM), and sometimes placed as a stem African papionin (Analysis 3 only). The second arrangement is broadly compatible with Delson and Dean's (1993) view that

Figure 15. Comparison of *D. ingens* (top) and *S. quadratiostris* (bottom) basicrania focusing on the orientation of the external auditory meatus (EAM). Note that in *D. ingens*, the EAM is oriented at a 90-degree angle, with the biporionic line roughly approximating basion. In *S. quadratiostris*, the EAM is oriented posteriorly at a 45-degree angle, making the biporionic line well posterior to basion. The condition seen in *S. quadratiostris* is common among extant large African papionins as well. Note: photos not to scale.

Figure 16. *Dinopithecus ingens* male (SK599, left) and female (SK553, right). Note the incompleteness of the male specimen and the lack of definitive maxillary fossae in both specimens. Scale in each panel = 1 cm.

D. ingens is morphologically similar to *S. quadratiostris*, but [Delson and Dean \(1993\)](#) also viewed *Dinopithecus* and *Mandrillus* as subgenera of *Papio*, further demonstrating the difficulty of separating these taxa in the absence of more complete male cranial material. I find very few convincing synapomorphies to link *D. ingens* with the broader clade including *Soromandrillus*, *Mandrillus*, *Cercocebus* and *Procercocebus*. In particular, from what can be discerned of the male *D. ingens* cranium, the temporal lines of *D. ingens* are clearly pinched like modern large *Papio* males rather than *Mandrillus* or *S. quadratiostris* and the external auditory meatus (EAM) is oriented such that the biporion chord approximates basion rather than being posterior to basion, as in *S. quadratiostris*, *Mandrillus*, and most other large African papionin taxa (Figs. 15 and 16). Other than very large body size, I also find very few, if any, obvious synapomorphies linking

D. ingens with later *Theropithecus* taxa. *Dinopithecus* displays none of the dental specializations of *Theropithecus*, and the grouping here with *Theropithecus* most likely reflects the retention of a number of primitive crown African papionin characters among the two genera along with the fact that much of the *D. ingens* male cranium remains unknown.

The uncertain phylogenetic placement of *D. ingens* is probably to be expected given the large amount of missing data for this taxon, especially in the case of the male cranium (Fig. 16). As males are often more phylogenetically informative among papionin taxa (see [Gilbert and Rossie, 2007](#); [Gilbert, 2007a](#); [Gilbert et al., 2009a](#)), in the case of *Dinopithecus* the analyses rely heavily on the less distinctive female morphologies and aspects of the male and female dentition. In addition, the highly variable extant population of *Papio* results in this taxon being coded with many intermediate

Figure 17. Development of the maxillary/suborbital fossae in the hypothesized clade including extant taxa *Papio* and *Lophocebus* as well as the fossil taxon *Gorgopithecus*. Top: *Gorgopithecus major* male (KA192, left) and female (KA153, right). Bottom: *L. albigena* female (left), *P. hamadryas kindae* female (middle), *P. h. ursinus* female (right). Note the deep and extensive maxillary/suborbital fossae found in all taxa. The results of this analysis suggest that the extensive maxillary/suborbital fossae are a defining feature of this group. Note: photos not to scale.

(polymorphic) states. Because only one or two incomplete male and female *D. ingens* cranial specimens exist, very few characters were coded with the intermediate/polymorphic state, perhaps masking shared character states that would be evident with a larger sample size (see also further discussion below). Another potential issue is that the size-adjustment used in this analysis slightly over-adjusts at large body sizes, particularly for male crania. Since *Dinopithecus* is the largest taxon included in this study, it is possible that the size-adjustment employed here slightly misrepresents certain *Dinopithecus* cranial features.

One final reason for the uncertain placement of *D. ingens* seems closely tied to the presence/absence of facial fossae (Figs. 16 and 17). The presence of well-developed facial fossae is reconstructed as a synapomorphy of crown African papionins in this analysis with one exception: *Dinopithecus*. I have argued previously that the development of facial fossae is allometrically influenced (Gilbert, 2007a; also note, for example, that the very large specimens in the *T. oswaldi* lineage also lack definitive maxillary fossae), and so it is possible that *D. ingens* lacks facial fossae due to its very large size and that the allometric coding corrections used here were too crude to interpret the morphology of *D. ingens* correctly. Regardless of these caveats, the most likely interpretation of *D. ingens* craniodental morphology, as represented by this data set, is that *D. ingens* is a very large crown African papionin.

Papio angusticeps Similar to the situation with *Dinopithecus* (see below), the phylogenetic placement of *P. angusticeps* appears uncertain if *P. angusticeps* is treated as a separate taxon from the extant *P. hamadryas* (e.g., Analysis 1 and 2). Among the MPTs generated in the first two analyses, *P. angusticeps* is regarded most often as either the most primitive member of a clade containing *Papio*, *Lophocebus* and *Gorgopithecus* or as a primitive crown African papionin (along with *Dinopithecus*); a phylogenetic hypothesis placing *P. angusticeps* as the sister taxon of extant *Papio* is between five (Analysis 1) and four (Analysis 2) steps longer than the MPTs. However, similar to the situation with *Dinopithecus*, there is a potential problem with low

sample size affecting the ability of *P. angusticeps* to share polymorphic character states with the larger *P. hamadryas* sample. To test this possibility, I conducted a post-hoc experiment replacing *P. angusticeps* with a small sample of the similarly-sized *P. hamadryas* subspecies, *Papio hamadryas kindae* (one male and one female). The resulting three MPTs placed *Papio kindae* as the sister taxon to *Papio*/*Gorgopithecus*/*Lophocebus*, which is the same phylogenetic position as *P. angusticeps* in a number of MPTs (see SOM Figs. 26 and 27 for consensus trees from this experimental analysis). Thus, since low sample sizes representing living subspecies of *P. hamadryas* are placed in the same phylogenetic position as *P. angusticeps*, it is quite possible that *P. angusticeps* does indeed represent a fossil subspecies of *P. hamadryas*, as suggested by Delson (1988). If one subscribes to this view, then Analysis 3 provides the most meaningful MPTs recovered in this study.

Theropithecus In just under half of the MPTs, *Theropithecus* is placed in the sister clade to *Papio*/*Lophocebus*/*Gorgopithecus*, a phylogenetic position congruent with the consensus molecular and morphological trees based on extant data alone. However, in slightly over half of the MPTs, the analyses above appear to contradict molecular and morphological analyses of extant taxa in that they reconstruct *Theropithecus* as the most primitive crown African papionin taxon rather than as a member of a larger clade containing *Papio* and *Lophocebus*. Thus, while the results of the current analyses are inconclusive on the phylogenetic position of *Theropithecus*, it is interesting to consider that a basal position among crown African papionins might indeed be correct; *Theropithecus* has been previously hypothesized in this phylogenetic position (e.g., Jolly, 1972; Szalay and Delson, 1979; Strasser and Delson, 1987) as it displays a number of primitive and autapomorphic features not seen in other crown African papionin taxa.

Among extant taxa for which large amounts of data are available (i.e., excluding *Rungwecebus*), molecular and morphological data cannot resolve the relationships among *Papio*, *Lophocebus*, and

Table 6
Selected synapomorphies suggested by character transformation analyses.

	Reconstructed synapomorphies	Character reference
CLADE 1: African papionins	Vomer invariably incised^b, Invariable projection of the nasal bones above the frontal-maxillary suture, Relatively tall nasal aperture^b, Shallow anterior palate^b , Relatively wide nasal aperture in males ^b , Relatively deep mandibular corpus at the level of the M ₁ in males	C43, F28, F36, P16 , F9 (M), M3 (M)
CLADE 2: Crown African papionins	Relatively wide neurocranium (biporion) in males, Relatively long occipital (opisthion-inion) in males, Relatively tall malar height in males ^a , Relatively long zygomaxillare-porion in males ^a , Well-developed maxillary fossae present in males, Well-developed maxillary ridges in males, Mandibular corpus fossae definitively present in males	C4 (M), C33 (M), F8 (M), F14 (M), F20 (M), F21 (M), M32 (M)
CLADE 3: <i>Theropithecus</i>	Small incisors, Low degree of molar flare^a, Increased level of enamel folding in mandibular molars , Temporal lines meet to form sagittal crest well anterior to bregma in males, Deeply excavated fossae anterior to foramen magnum in males, Mandibular corpus shallows posteriorly in males ^a	P26, P30, M22 , C17 (M), C48 (M), M40 (M)
CLADE 4: <i>Papio/Lophocebus</i> / <i>Theropithecus/Gorgopithecus</i> / (<i>Rungwecebus</i>)	Relatively long cranium from glabella to inion^a, Increased upper facial prognathism^a , Relatively long distance from glabella to bregma in males ^a , Relatively long distance from bregma to lambda in males ^a , Wide posterior basioccipital breadth in males, Relatively short orbits in males ^a , Relatively broad superior nasal breadth in males ^a , Relatively wide posterior interalveolar distance in males ^a , Mandibular corpus fossae definitively present in females	C1, F15 , C5 (M), C7 (M), C38 (M), F7 (M), F12 (M), P15 (M), M32 (F)
CLADE 5: <i>Papio/Lophocebus</i> / <i>Gorgopithecus</i> (<i>Rungwecebus</i>)	Wide posterior basioccipital breadth^a, Deep/Extensive maxillary fossae^a , Relatively broad frontal in males ^a , Long occipital condyles in males ^a , Thin parietals in males, Relatively short alveolar process in females ^a , Long premaxilla in females, Relatively deep mandibular symphysis in females ^a	C38, F20 , C3 (M), C12 (M), C13 (M), F2 (F), P19 (F), M2 (F)
CLADE 6: <i>Lophocebus</i> / <i>Gorgopithecus</i> / <i>Rungwecebus</i>	Deepest/Most extensive maxillary fossae , Anteriorly placed EAM relative to basion in males ^a , Relatively short sagittal nasal length in males (nasion–rhinion) ^a , Relatively short nasal prognathism in males (nasion–rhinion/nasion/prosthion) ^a , Wide interalveolar distance at level of P ⁴	F20 , C31 (M), F11 (M), F35 (M), P9 (M)
CLADE 7: <i>Lophocebus</i> / <i>Gorgopithecus</i>	Deepest/Most extensive maxillary fossae, Extension of the nasal bones over the nasal aperture^a , Anteriorly placed EAM relative to basion in males ^a , Relatively short sagittal nasal length in males (nasion–rhinion) ^a , Relatively short nasal prognathism in males (nasion–rhinion/nasion/prosthion) ^a , Wide interalveolar distance at level of P ⁴	F20, F32 , C31 (M), F11 (M), F35 (M), P9 (M)
CLADE 8: <i>Lophocebus</i> / <i>Rungwecebus</i>	Short postglenoid process in males ^a , Short M ₂ MD length in males ^a	C28 (M), M13 (M)
CLADE 9: <i>Soromandrillus</i> / <i>Mandrillus/Cercocebus</i> / <i>Procercocebus</i>	Widely divergent temporal lines, Upturned nuchal crests across the midline, Medially positioned inferior petrous process, Relatively straight nasal bones in lateral view^a, Relatively large maxillary premolars, Relatively large mandibular premolars^a, Horizontally positioned lingual mental foramina^a , Thick parietals in males, Medially oriented maxillary ridges in males, Relatively deep mandibular symphysis in males ^a , Moderately divergent medial pterygoid plates in females	C20, C21, C47, F31, P17, M15, M34 , C13 (M), F22 (M), M2 (M), C42 (F)

Notes: Listed characters represent those suggesting a character state transition at the corresponding node and display few to no reversals as they are traced up the tree. Characters in bold are recognized as synapomorphies in both males and females. *Rungwecebus* is listed in parentheses when reconstructed as a member of a larger clade also found in Analyses 1 and 3.

^a Also found in other taxa.

^b Uncertain synapomorphy due to absence of preservation in *Pp. ado*. See Figs. 10–12 for trees with corresponding clades.

Theropithecus. The analyses including fossil taxa suggest that *Papio* and *Lophocebus* are more closely related to the exclusion of *Theropithecus* (see also recent molecular analyses by Perelman et al., 2011; Guevara and Steiper, in revision). Because fossil data provide important information regarding character polarities that are unavailable from extant data alone (e.g., breaking down long branches), perhaps a similar phylogenetic result would be obtained if molecular data from these fossil taxa could be included as well. In any case, the placement of *Theropithecus* outside a grouping of *Papio* + *Lophocebus* in all of the MPTs recovered here suggests that our current inability to resolve the *Papio/Lophocebus/Theropithecus* trichotomy among extant taxa may simply be a problem of incomplete taxon sampling and data shortage. It is interesting to note, for instance, the earliest hypothesized appearances of *Papio* (either *P. angusticeps* or *P. hamadryas* ssp.) and *Lophocebus* in the fossil record occur much later than the first appearance of *Theropithecus* ~3.97 Ma at Koobi Fora (Jablonski et al., 2008; Leakey et al., 2008): *P. h. robinsoni* first appearance at Swartkrans or Sterkfontein, ~2.6–2.1 Ma (Herries, 2003; Partridge, 2005; Herries et al., 2010), *P. angusticeps* first appearance at Gladysvale or Kromdraai ~2.4–2.0 Ma (Curnoe, 1999; Thackeray et al., 2002;

Berger et al., 2003; Herries et al., 2009, 2010), *L. cf. albigena* at Koobi Fora ~2.0 Ma (Jablonski et al., 2008; Jablonski and Frost, 2010). Therefore, the geochronological evidence also hints at a later divergence between *Lophocebus* and *Papio* among the *Papio/Lophocebus/Theropithecus* group. While *Lophocebus* and *Papio* both appear in the fossil record around the same time (~2.5–2.0 Ma), the first specimens attributable to *Theropithecus* are found almost ~1.5–2.0 million years earlier.

Since *Theropithecus* is reconstructed as the basal crown African papionin taxon in some of the MPTs, yet found in the sister clade to *Papio/Gorgopithecus/Lophocebus* in others, it is probably prudent to regard the choice between these two alternatives as equivocal for now. Additional resolution will most likely depend on additional information regarding the morphology of the unstable taxa *Dinopithecus* and *P. angusticeps* (if considered a distinct species of *Papio*), whose instability affect not only their own phylogenetic position but the placement of *Theropithecus* as well.

Gorgopithecus The phylogenetic position of the enigmatic *Gorgopithecus* has always been uncertain, however, no previous author has suggested that *G. major* and *Lophocebus* are sister taxa. While the placement of *G. major* as a relative of extant *Papio* and *Lophocebus*

seems a reasonable hypothesis, the hypothesis that *Gorgopithecus* may be more closely related to *Lophocebus* than to *P. hamadryas* is indeed surprising. Similar to the case with *Dinopithecus*, this reconstruction may be due to missing data, as the one good male *Gorgopithecus* cranium is squashed and *Gorgopithecus* female craniodental morphology remains mostly unknown. Regardless, the *Gorgopithecus*/*Lophocebus* clade is relatively well-supported by decay indices and bootstrap values in the consensus trees, and character transformation analyses identify a number of character states linking *Lophocebus* and *Gorgopithecus* to the exclusion of *P. hamadryas* such as short nasal bones in males, an anteriorly oriented EAM in males (shared also with *Dinopithecus*, see Fig. 15), frequent nasal bone extension over the nasal aperture in males and females, a reduction in the development of the maxillary ridges in males, and the most extensive development of the maxillary fossae seen among African papionins (males and females; see Fig. 17).

Larger sample sizes of *Gorgopithecus* specimens with additional morphological regions preserved will no doubt be necessary to help resolve its phylogenetic position. The fact that the best preserved male specimen of *Gorgopithecus* is a heavily distorted cranium casts doubt on at least some of the quantitative male character states derived from this specimen. Thus, more specimens are necessary to accurately represent *Gorgopithecus* craniodental morphology and to confirm the *Lophocebus*/*Gorgopithecus* synapomorphies proposed here.

Rungwecebus The recently discovered and described extant papionin genus *Rungwecebus* (the kipunji) was included in Analysis 2. Contrary to extant molecular analyses that hypothesize a closer relationship between *Papio* and *Rungwecebus* than *Lophocebus* and *Rungwecebus* (i.e., Davenport et al., 2006; Olson et al., 2008; Burrell et al., 2009; Zinner et al., 2009; Roberts et al., 2010), the trees recovered in the second analysis are similar to those of previous morphological assessments in hypothesizing *Lophocebus* and *Rungwecebus* as most similar (e.g., Jones et al., 2005; Singleton et al., 2010; Gilbert et al., 2011b). However, because this taxon is known morphologically from only two subadult male specimens, it is impossible to be certain about many adult male and female *Rungwecebus* morphologies, making any assessment of its phylogenetic position preliminary and still uncertain at this time (see also Gilbert et al., 2011b). Because adult *Rungwecebus* morphology is poorly known (more poorly known than some fossil taxa), adding *Rungwecebus* to the matrices used in this study also had the effect of introducing uncertainty to the resulting phylogenetic analyses, resulting in the recovery of many more phylogenetic hypotheses (MPTs) and lower bootstrap and decay index values.

Character evolution

As the low CI values in the most parsimonious trees imply, there is considerable morphological homoplasy in the African papionin radiation. This makes craniodental synapomorphies difficult to identify for many higher level clades, particularly across the three separate analyses. However, there are a few characters that can be identified in the transformation analyses as particularly distinctive during the evolutionary transition to certain clades. Because of the large amount of uncertainty associated with some of the trees, Table 6 highlights the most distinctive synapomorphies at selected nodes across all three analyses.

African papionins There are only a few features identified as synapomorphies setting African papionin taxa apart from macaques and other early papionins, and almost none of them is immune to later reversals in the African papionin tree (exception: mandibular corpus height in males). Thus, compared to the ancestral papionin

condition, the character transformation analyses suggest that the last common ancestor of African papionins exhibited an invariably incised vomer (with later reversal back to polymorphism in *Lophocebus*), invariable projection of the nasal bones above the frontal-maxillary suture (with later reversals back to polymorphism), a relatively tall nasal aperture (with later reversals), a relatively shallow anterior palate (with later reversal to a deep palate in *Mandrillus*), a relatively wide interorbital distance (also seen in *Victoriapithecus*), a relatively wide nasal aperture in males (reversals in *Cercocebus* and *T. brumpti*), and a relatively deep mandibular corpus at the level of the M₁ in males. Some of these features are not obvious and some of them are either not preserved or not observable in early African papionin taxa such as *Pp. ado*, highlighting the difficulty of recognizing stem African papionins apart from macaques outside of their geographic distribution. This situation is perhaps to be expected if African papionins evolved from an ancestral macaque-like population.

Crown African papionins All of the cranial synapomorphies found at the evolutionary transition from stem to crown African papionins are observed most clearly in males. The presence of well-developed maxillary fossae (particularly in males), well-developed male mandibular corpus fossae, and well-developed male maxillary ridges are the most obvious of these, but crown African papionin males also display a relatively wide neurocranium, a relatively long occipital, a relatively tall malar region, and a relatively long zygomaxillare-porion chord. Another character state found only among the crown African papionin taxa is very large body size, particularly seen in *Dinopithecus*, *Gorgopithecus*, *S. quadratiostris*, and *Theropithecus* sp. Similar to the situation with African papionins, some crown African papionin taxa exhibit reversals in these characters, illustrating that occasional homoplasies are an evolutionary fact of life among the African papionins (and other primate groups; Lockwood and Fleagle, 1999).

Papio/*Lophocebus*/*Theropithecus*/*Gorgopithecus*/(*Rungwecebus*)

The morphological transition that took place at the origin of the *P/L/T/G/(R)* clade includes the evolution of a relatively long cranium and an increase in upper facial prognathism. In addition, males exhibit relatively long anterior and posterior neurocrania, relatively wide posterior basioccipitals, relatively short orbits, relatively broad nasals, and relatively wide posterior palates. Females within this clade distinctively exhibit definitive mandibular corpus fossae. Within more restricted clades among the African papionins, such as *P/L/T/G* (and *Rungwecebus* when included), unique character states not found among other groups begin to appear. Definitive female mandibular corpus fossae and wide male posterior basioccipitals are features not found elsewhere among papionin taxa.

Theropithecus Many previous characters identified as synapomorphies of *Theropithecus* were confirmed in this study. The most distinctive (and in many cases, unique) characters recognized during the evolution of the genus *Theropithecus* include small incisors, a low degree of molar flare, increased enamel infoldings on the premolars and molars, temporal lines that meet anteriorly in males, deeply excavated fossae anterior to the foramen magnum (for longus capitis), more obliquely oriented lophids on the lower molars (except in *T. baringensis*), and a reversed curve of Spee for the tooth row (except in *T. baringensis*).

***Papio*/*Lophocebus*/*Gorgopithecus*/(*Rungwecebus*)** *Papio*, *Lophocebus* and *Gorgopithecus* (and *Rungwecebus*, when included) are recognized apart from other African papionins by the extreme development of maxillary fossae. While *Cercocebus* and *T. gelada* also display well-excavated maxillary fossae in parallel, the *P/L/G/(R)* group appears to have evolved deeply excavated fossae at their origin and the group includes taxa with the deepest and most extensive

fossae among all papionin taxa. Other unique character states found at the origin of the *P/L/G/(R)* clade include thin parietals in males and a relatively long premaxilla in females. The origin of the *P/L/G/(R)* clade is also defined by the evolution of a wide posterior basioccipital, a broad frontal in males, long occipital condyles in males, a short alveolar process in females, and a relatively deep mandibular symphysis in females, but these character states are also seen elsewhere in the African papionin tree.

Lophocebus/Gorgopithecus/Rungwecebus The *Lophocebus/Gorgopithecus/Rungwecebus* clade is characterized at its origins by the evolution of the deepest and most extensive maxillary fossae among the African papionins. In addition, the group displays an anteriorly placed EAM relative to basion in males (also found in *Dinopithecus*), relatively short nasal bones (also found in some other taxa), and a wide palate at the level of the P⁴.

Lophocebus/Gorgopithecus In the analyses excluding *Rungwecebus*, *Lophocebus* and *Gorgopithecus* are united at their origin by all of the features listed above for *L/G/R* as well as the extension of the nasal bones over the nasal aperture (also found in some *Parapapio* taxa).

Lophocebus/Rungwecebus In addition to the synapomorphies noted for *L/G/R*, the analyses including *Rungwecebus* suggest that the common ancestor of *Lophocebus* and *Rungwecebus* also displayed short postglenoid processes and a short M₂ length in males (both character states are also found in other taxa).

Soromandrillus/Mandrillus/Cercocebus/Procercocebus A series of characters can be identified as synapomorphies defining the *S/M/C/P* clade at its origin. These taxa are all united by the unique appearance of widely divergent temporal lines (especially in males), upturned nuchal crests (especially in males), medially positioned inferior petrous processes, thick parietals in males, and moderately divergent medial pterygoid plates in females. There is also a tendency to develop very large premolars relative to the molars among the *S/M/C/P* clade. Depending on whether *S. quadratiostris* is regarded as a direct ancestor to *Mandrillus* or *Mandrillus* + *Procercocebus/Cercocebus*, this last feature may have developed in parallel at least twice, once in *S. quadratiostris* and at least once among *Mandrillus*, *Cercocebus*, and *Procercocebus*. Finally, *S/M/C/P* are also characterized by relatively straight nasal bones in lateral view (also seen in *Parapapio* taxa), medially oriented maxillary ridges in males (occasionally seen in *Pp. broomi* when maxillary ridges exist), and less extensive development of the maxillary fossae compared with most other crown African papionin taxa.

Radiation of the African papionins

With a better understanding of the synapomorphies that characterize the origin of the different papionin clades, it is possible to speculate about their adaptive significance during the Plio-Pleistocene radiation of these monkeys. From the phylogenetic hypotheses presented here, it is likely that the earliest and most primitive African papionins were macaque-like in appearance, lacking maxillary and mandibular corpus fossae, and having a generalized bilophodont dentition with relatively small-to-intermediately sized premolars. Similar to macaques, *Parapapio* species came in a variety of sizes, and probably partitioned niche space in the Plio-Pleistocene by differentiation in body size, locomotor pattern, and diet (e.g., Ciochon, 1993; Elton, 2001; Fourie et al., 2008).

In contrast to *Parapapio* and *Pliopapio*, the common ancestor of all crown African papionins evolved definitive maxillary ridges, well-developed maxillary fossae, and well-developed mandibular corpus fossae (at least in males). The adaptive significance as well as the underlying anatomical causes of these osteological features are unclear, however, given that they are most obviously expressed

in males, sexual selection is one potential hypothesis. In any case, it seems that there is an allometric component associated with the development and extent of maxillary fossae among taxa that possess them (Gilbert, 2007a). Thus, as body size and skull size decrease, the depth and extent of the maxillary fossae generally increases and extends into the infraorbital plate (*Gorgopithecus* is a notable large-bodied exception). Among the papionin radiation, extremely large body size is only seen among crown African papionin taxa (e.g., *D. ingens*, *Gorgopithecus*, *Soromandrillus*, and *T. oswaldi*) and it seems most likely that the ancestral crown African papionin was a large animal. The hypothesized distribution of body size also suggests that the extant mangabeys, *Lophocebus* and *Cercocebus*, are secondarily derived in their smaller size and associated cranial morphologies, as suggested by Singleton (2002). Thus, *Lophocebus* and *Cercocebus/Procercocebus* independently evolved smaller body size, and this reduction in body size and its allometric consequences most likely resulted in the reduction in snout length, loss of an anteorbital drop, and the extension of maxillary fossae into the suborbital region of the skull.

As previously noted, (e.g., Jolly, 1970, 1972; Szalay and Delson, 1979; Eck and Jablonski, 1984, 1987; Jablonski, 1993, 2002), later members of the genus *Theropithecus* are easily identified by a number of dental synapomorphies clearly associated with adaptations to a heavily herbaceous and gummivorous diet. While early members of the genus *Theropithecus*, as characterized by *T. baringensis*, do not possess all of the derived dental features seen in later *Theropithecus* taxa, they can be identified by the anterior union of the temporal lines (Fig. 18), increased enamel infoldings on the premolars and/or molars, (not as developed as later *Theropithecus* taxa, but more so than other papionins), columnar cusps, and deeply excavated longus capitis fossae anterior to the foramen magnum. The anterior position of the temporal lines seems related to the increased size of the temporalis musculature as well as the optimal placement of the temporalis in order to increase occlusal forces on the molar battery (Jolly, 1970; see Fig. 18). This increase in musculature and chewing emphasis probably also helped to drive selection for even further increased enamel infoldings, a delayed eruption pattern, and reversed curve of Spee to lengthen the life of the molars in later *Theropithecus* taxa. The reversed curve of Spee, associated with the delayed eruption pattern, functions to keep the posterior molar row from full occlusion as long as possible, thereby extending the life of the most posterior teeth. The adaptive and functional significance of the deeply excavated longus capitis fossae anterior to the foramen magnum are unclear, although one may speculate that they are related to the orientation of the neck and skull, which may be linked in modern geladas to their unique posture while foraging.

While the *Theropithecus* lineage is, in part, linked to adaptations associated with increasing the emphasis of chewing onto the posterior dentition, the *Soromandrillus/Mandrillus/Cercocebus/Procercocebus* clade is defined in large part by a shift of chewing-muscle forces onto the premolars. This anterior shift most likely provides selective pressure for larger premolars. In extant *Cercocebus* and *Mandrillus*, large premolars are suggested to be adaptations for processing hard-object food items acquired while foraging on the forest floor (Fleagle and McGraw, 1999, 2002). If both *Cercocebus* and *Mandrillus* have experienced co-evolution along with these hard-object food items and the plants that produce them, a 'Red-Queen'-type of situation could be invoked to potentially explain the apparent evolution of very large premolars in parallel.

A similar ecological situation probably existed in the Plio-Pleistocene *S. quadratiostris* lineage. In East Africa, the reconstructed environment of the Usno Formation includes riverine forests and woodlands (Reed, 1997). The Shungura Members E

Figure 18. Comparison of the four *Theropithecus* taxa recognized in this analysis. Note the anterior union of the temporal lines well anterior to bregma, a defining feature of *Theropithecus* linked here to an increase in the size of temporalis as well as the optimal placement of temporalis in order to increase occlusal forces on the molar battery. Note: photos not to scale.

through G are also often noted as including a forest or woodland component (Eck and Jablonski, 1984, 1987; Ciochon, 1993; Reed, 1997), and a transition from well-watered riparian forests/woodlands to a river with slightly more open woodlands is documented through time (Reed, 1997). Forests and woodlands are the same types of environment that *Cercocebus* and *Mandrillus* occupy today. Therefore, similar dietary selection pressures on early members of this clade were likely, and premolar size increases through time among *S. quadratiostris* specimens in the Omo Shungura section (Table 4).

The reconstructed environment of the Angolan Humpata Plateau also includes more forested environments (Pickford et al., 1994), which is again consistent with the preferred habitat of extant members of this group. In the case of East Africa, a shift to a hard-object niche may have helped to avoid direct competition with the contemporaneous and forest-adapted *T. brumpti* (Eck and Jablonski, 1984, 1987). Overall, the available evidence indicates that the *Soromandrillus*/*Mandrillus*/*Cercocebus*/*Procercocebus* clade has always been a forest-adapted lineage, which may have avoided competition with the expanding savannah-adapted *Papio* lineage. In addition, a shift to a hard-object feeding niche may have helped to avoid competition with other forest-living cercopithecines such as guenons, *Lophocebus* mangabeys, and *T. brumpti*.

The remaining crown African papionin taxa (*P. hamadryas*, *Lophocebus*, *Gorgopithecus*, *Dinopithecus*, *Rungwecebus*, and *P. angusticeps*) are not obviously grouped in any adaptively cohesive way. In fact, it seems that this group of monkeys is better defined as being unspecialized generalists than being committed to any specific type of lifestyle. The defining synapomorphy of the *Papio*/*Lophocebus*/*Gorgopithecus*/(*Rungwecebus*) group (whether *P. angusticeps* is included or excluded) is the possession of the deepest and most extensive maxillary fossae among crown African papionins, taken to the extreme in *Lophocebus*/*Gorgopithecus* (Fig. 17). However, as previously discussed, the adaptive significance of this feature is unclear, and deep maxillary fossae also appear in *Cercocebus* and *T. gelada*. As is the case with most fossil papionin taxa, postcrania cannot be assigned to *Gorgopithecus*, so it is not possible to definitively assess whether or not *Lophocebus* is the only arboreal taxon among this group, although it seems likely given the available evidence.

Finally, it is currently difficult to understand the evolution of *D. ingens* on the basis of the available evidence. In some of the MPTs, *D. ingens* is regarded as the ancestor to the broader clade containing *Soromandrillus*, *Mandrillus*, *Cercocebus*, and *Procercocebus*, mostly on the basis of reduced maxillary fossae development and other shared primitive morphologies. As discussed above, the lack of definitive facial fossae in *Dinopithecus* may be allometrically related to its extremely large body size; in any case, *D. ingens* is reconstructed as either losing definitive fossae from a common ancestor or, alternatively, definitive maxillary fossae developed multiple times among crown African papionin taxa. In other trees, *D. ingens* is reconstructed as the ancestor to *Theropithecus*, although derived morphological features uniting these two genera are also not obvious, and again, this would potentially imply that *Theropithecus* and the other crown African papionin taxa evolved facial fossae independently. Finally, *D. ingens* is often reconstructed at the base of the non-*Theropithecus* African papionins. Given the current evidence, a position near the base of the crown African papionin group makes the most intuitive sense phylogenetically, as there are no convincing morphological synapomorphies or adaptations yet known to push *D. ingens* definitively into one crown clade or the other.

Timing of the African papionin radiation

One final aspect of the phylogenetic hypotheses presented in this study concerns the time of divergence of specific clades. Molecular studies suggest that the basic division between *Mandrillus*/*Cercocebus* and *Papio*/*Lophocebus*/*Theropithecus* took place between 6 and 10 Ma (Disotell and Raaum, 2002; Tosi et al., 2003, 2005). The separation of *Papio*, *Lophocebus*, and *Theropithecus* has been estimated to be around 4–5 Ma (Disotell and Raaum, 2002; Tosi et al., 2005). This date accords well with the phylogeny presented here, as no taxon reconstructed as diverging after *Theropithecus* is present in the fossil record before 3.4 Ma. It does, however, suggest that there was a very quick radiation of crown African papionins, as *Cercocebus* and *Mandrillus* are estimated to have diverged between 3.6 and 4.1 Ma, and *P. quadratiostris*, by virtue of its earlier hypothesized branching event in some of the trees, is reconstructed to have possibly diverged sometime before that. This rapid radiation of crown African papionins at the beginning of the Pliocene may help to explain why molecular data cannot resolve the relationship between taxa such as *Papio*, *Lophocebus* and *Theropithecus*. In summary, the phylogenetic hypotheses presented here are in general agreement with previous estimates of papionin divergence dates. However, the identification of new taxa related to the *Cercocebus*/*Mandrillus* clade provides further evidence of minimum divergence dates that may be used in future molecular studies and which may slightly alter molecular divergence estimates moving forward.

Remaining issues

The analyses presented here represent a current and comprehensive view of African papionin systematics, including as much craniodental information as possible from both extant and fossil specimens. However, like any study, there are limitations to the data set and these may have affected the resulting phylogenetic hypotheses. I will now briefly consider the most obvious limitations and their potential effects.

The first issue, discussed throughout the above text, is that of missing data from incomplete specimens and underrepresented taxa in the fossil record. Missing data is an obvious limitation when including fossil taxa, but the downside is largely if not entirely outweighed by the critical information on character polarities contained within the data that is actually preserved. Still, missing data adds uncertainty to the analysis, and it is almost certainly responsible for the instability of taxa such as *P. angusticeps* and *D. ingens* in addition to lowering bootstrap values and negatively affecting other confidence measures. Missing data may also be responsible for the appearance of a paraphyletic *Parapapio*. *Pp. ado* is not well represented cranially and additional specimens preserving the cranium will most likely be required to ascertain its true phylogenetic and taxonomic position with more certainty.

A second issue, related to the first but also a by-product of the methodology used in this study, is that of sample size among fossil taxa. Because polymorphic character states were used to code qualitative characters in this study, small sample sizes in many cases make it difficult to observe polymorphisms in fossil taxa, if they existed. The result is that extant taxa, which have large sample sizes, may be coded with a different character state than a close fossil relative only because sample sizes in the fossil taxon were not large enough to detect the same polymorphisms. In addition to the missing data problem, small sample sizes for certain characters and a lack of observed polymorphisms may be responsible for the uncertain or unorthodox placement of taxa such as *P. angusticeps*, *D. ingens*, and *P. izodi*. Small sample sizes are a problem with quantitative characters as well because the coding of these characters relies on average values for taxa. For instance, a recent study by Gilbert and Grine (2010) demonstrated that a sample size of five to ten individuals is necessary to be confident that a fossil sample is within 5–10% of the true population mean, and a sample size of 15 is preferable to be confident of sampling within 3% of the true population mean. Unfortunately, sample sizes among fossil taxa rarely reach these levels for many characters, and therefore it is possible that some of the quantitative character states coded on the basis of single specimens will change with additional information (and change the character states of other taxa as well).

A final issue or consideration concerning the analyses presented here has to do with the allometric coding methodology. As mentioned earlier, the size correction proxies used here may slightly overcorrect at large body sizes, and this phenomenon could have affected the interpretation of some of the quantitative character states among the largest taxa included in the analysis. While the narrow allometric coding method might have been preferred for quantitative characters, the current study includes many fossil taxa that span a more or less continuous and wide range of body sizes, making the assignment of taxa into discrete body size categories a much more difficult and arbitrary task compared with the two obvious body size categories among extant taxa. Therefore, the narrow allometric coding method was not appropriate for this particular data set, and the general allometric character coding was applied instead. The general allometric coding method is no doubt a blunt instrument, but it has nonetheless proven effective and

more widely applicable than the narrow allometric coding method (Gilbert et al., 2009a), and those two factors dictate and justify its use here. The development of new coding methods in the future may help improve our understanding of African papionin phylogenetic history.

Like any working hypothesis, I expect the phylogenies presented here to change slightly as more information becomes available and added to future analyses. Although I believe the basic relationships recovered in this study offer a framework for understanding African papionin evolution moving forward, by no means do the hypotheses presented here, or in any phylogenetic study, represent the final word on the subject. Minor changes, clarifications, and reshufflings in the African papionin tree are likely, but I consider the broad relationships recovered in this study as likely to be accurate and, in particular, I would argue that the well-supported clades should be viewed as secure. Perhaps the most informative summary trees are found in Figs. 10a, 11a and 12b, which to my mind, offer the most reasonable and well-supported summaries of extant and fossil African papionin phylogeny given the available evidence. Our knowledge and understanding will no doubt increase as new data, larger sample sizes, and improved phylogenetic methods become available.

Conclusions

A large set of qualitative and quantitative craniodental characters for extant and fossil members of the cercopithecine monkey subtribe Papionina was subjected to phylogenetic analysis using parsimony. In order to account for the well-documented influence of allometry on the craniodental morphology of this group, the general allometric coding method was employed (Gilbert and Rossie, 2007). The resulting phylogenetic hypotheses reconstruct *Parapapio*, *Pliopapio* and *P. izodi* as stem African papionins.

The origin of crown African papionins is defined, at least in part, by the appearance of definitive facial fossae and maxillary ridges, particularly in males. Among crown African papionins, *Theropithecus* is sometimes reconstructed as the basal crown African papionin taxon and the status of *T. baringensis* as a member of the genus *Theropithecus* is strongly supported. The adaptive origins of the genus *Theropithecus* are associated, in part, with dietary adaptations requiring an increase in temporalis musculature and chewing emphasis onto the molars (Jolly, 1970). *Gorgopithecus* is reconstructed as having been closely related to *Papio* and (perhaps especially) *Lophocebus*, and this group is characterized by the deepest and most extensive maxillary fossae among all crown African papionins. *Lophocebus* is possibly a secondarily arboreal taxon.

P. quadratiostris, as defined by Delson and Dean (1993) to include the Usno cranium, later Omo Shungura material, and some of the material from the Angolan Humpata Plateau, is reassigned to a new genus, *Soromandrillus*, and reconstructed as either the sister taxon to *Cercocebus*, *Procercocobus*, and *Mandrillus*, or as the sister taxon to *Mandrillus*. This clade appears largely restricted to forested environments, and it is characterized by the tendency to evolve adaptations for hard-object food items, which has possibly happened in parallel. Morphological features that define this group and are linked to this ecological focus include widely divergent temporal lines that shift chewing-muscle forces towards the anterior dentition, and the consequent enlargement of the premolars.

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Appendix A. Supplementary material

Supplementary material related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2013.01.013>.

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