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Molecular systematics of the Old World monkey tribe Papionini: analysis of the total available genetic sequences

The phylogenetic relationships among the genera of the tribe Papionini are inferred using a taxonomic congruence approach in which gene trees derived for eight unlinked genetic sequence datasets are compared. Population genetics theory predicts that species relationships will be revealed with greater probability when the topology of gene trees from many unlinked loci are found to be congruent. The theory underlying this approach is described.

Monophyly of the mangabeys is not supported by any of the gene trees; instead, they are polyphyletic with *Cercocebus* found to be the sister taxon to *Mandrillus* in five gene trees (with no conflicting trees), and *Lophocebus* found to be closely related to *Papio* and/or *Theropithecus* in all trees. *Theropithecus* and *Papio* are not strongly supported as sister taxa (present in one or two trees only); *Lophocebus* and *Papio* are supported as sister taxa in the majority of trees. A close relationship between *Mandrillus* and *Papio* is not supported in any of the trees.

The relationships among *Papio*, *Lophocebus*, and *Theropithecus* cannot be resolved by congruence, probably due to the short time interval estimated between their divergences. The mtDNA COII sequences are used to estimate divergence dates within the papionins. The internode between the divergences of these species is estimated to be between 290 ka and 370 ka. Lastly, the evolution of morphological features such as long faces, suborbital facial fossae, and terrestrial skeletal adaptations is discussed.

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Introduction

The Papionini comprise a group of six genera of Old World monkeys which are geographically widespread and ecologically diverse. They can be subdivided into two groups, the exclusively African papionins, including geladas (*Theropithecus*), baboons (*Papio*),¹ mandrills and drills (*Mandrillus*), and the mangabeys (*Cercocebus* and

Lophocebus), as opposed to the largely Asian distributed macaque genus (*Macaca*) (Strasser & Delson, 1987; Disotell, 1992; 1994; Disotell *et al.*, 1992; Morales & Melnick, 1998). As a group, papionins are characterized by facial lengthening, usually some development of facial fossae, increased use of terrestrial substrates, and a diploid karyotype of 42. All known systematic studies of the Old World monkeys, based on either genetic or morphological data, have found the papionin tribe to be a monophyletic group.

The phylogenetic relationships among genera have been studied using essentially two classes of evidence, morphological and

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¹A population of *Papio hamadryas* is known to inhabit coastal regions of Yemen and Saudi Arabia.

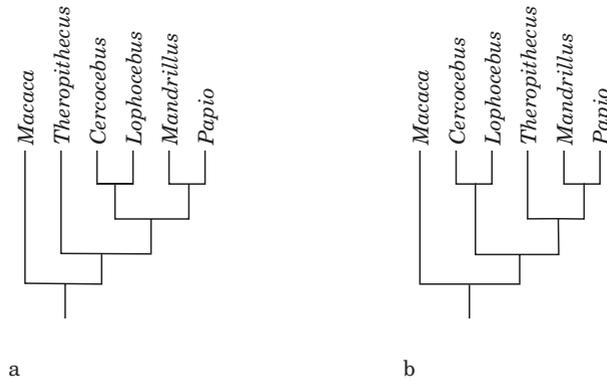


Figure 1. Two morphologically-based trees of papionin phylogeny. Tree (a) was advocated by Kuhn (1967), Szalay and Delson (1979), and Strasser and Delson (1987); tree (b) is after Delson and Dean (1993).

molecular. The various hypotheses for their relationships based on morphology, however, strongly disagree with most molecular phylogenies. This discordance among hypotheses, while strongly apparent between molecular and morphological hypotheses, is not peculiar to this dichotomy and is also found, although to a lesser extent, among molecular hypotheses (as this study describes).

There are two central systematic questions. First, are mangabeys monophyletic as posited by most morphological trees (see Figure 1; Jolly, 1967; Kuhn, 1967; Hill, 1974; Szalay & Delson, 1979; Strasser & Delson, 1987) or polyphyletic as proposed in molecular and chromosomal studies (Cronin & Sarich, 1976; Hewitt-Emmett *et al.*, 1976; Hewitt-Emmett & Cook, 1978; Dutrillaux *et al.*, 1979; Disotell, 1992, 1994; Disotell *et al.*, 1992; Harris & Disotell, 1998) and some morphological studies (Groves, 1978; Fleagle & McGraw, 1989)? Furthermore, if they are polyphyletic how is each mangabey genus related within the papionin group? Second, do the genera *Papio* and *Mandrillus* share a close relationship within the papionins as proposed by all morphologically based hypotheses (see Figure 1), or is *Theropithecus* most closely related to *Papio* as proposed by

molecular trees based on immunology and mtDNA encoded COII sequences (Sarich, 1970; Cronin & Meikle, 1979, 1982; Disotell, 1992, 1994; Disotell *et al.*, 1992)?

There now exist nine datasets of DNA and amino acid sequences for papionin genera, which can be analyzed together to examine these three questions. These sequences derive from genomic regions belonging to different chromosomes or different genomes (i.e., nuclear and mitochondrial) and therefore can be subdivided into separate linkage groups. A linkage group represents a unit of the genome which segregates independently and recombines freely with respect to other such groups.

The tree estimated based on each gene region is properly conceived of as a gene tree in contrast to a species trees (see Hey, 1994). The terminal branches of gene trees bear homologous gene sequences and not organisms or "species". Likewise, the nodes of gene trees represent ancestral DNA sequences and not ancestral organisms or "species". Proceeding back in time from the terminal DNA sequences to the ancestral DNA sequence represents a process known as coalescence.

It is often assumed that gene trees accurately estimate the species tree. However, there are several reasons why this

assumption may be incorrect. First, gene trees may be incorrectly estimated because of sampling bias when trees are estimated from relatively short sequences. Traditionally, the length of homologous DNA sequences compared across species is on the order of several hundred base pairs. Saitou and Nei (1986) show that this problem can be diminished if amply long DNA sequences are compared. Second, natural selection could have constrained variation among lineages resulting in a tree that conflicts with actual phylogenetic relationships. Third, assuming that gene trees have been correctly estimated, incongruence between gene trees and the species tree can be due to random lineage sorting. The theoretical basis of random lineage sorting has been discussed extensively in the population genetics literature (see Hudson, 1983; Nei, 1987; Pamilo & Nei, 1988; Rogers, 1993; Hey, 1994; Moore, 1995, 1997; Avise & Wollenberg, 1997; Hoelzer, 1997; Doyle, 1997; Maddison, 1997) and is briefly described here.

The coalescence time of homologous gene sequences sampled from two sister species will predate the divergence time of the species. When the coalescence of homologous gene sequences occurs in the most recent common ancestral population of two species, the topology of the gene tree will be the same as the species tree. But if the two homologous DNA sequences fail to coalesce in the ancestral population of these two species, instead coalescing in the common ancestral population that these species share with a third species, then the gene tree may not reflect the actual order of divergences among the species. This is because the DNA lineages found in the ancestral population have randomly sorted into the three descendant species lineages. The mismatch between gene trees (from multiple unlinked loci) and the species tree will occur with a probability that can be modeled by population genetics theory and may be considerable under certain conditions, for example

when species divergences have occurred relatively close in time (Nei, 1987; Pamilo & Nei, 1988).

A solution to the problem of gene tree/species tree mismatch lies in the search for congruence among the branching patterns of gene trees that are derived from separate linkage groups (Saitou & Nei, 1986; Pamilo & Nei, 1988; Wu, 1991). This is because population level processes like speciation are expected to produce similar effects across many loci. In contrast, processes that can obfuscate species relationships like random lineage sorting and natural selection are expected to have locus specific effects (Hey, 1994). Following this reasoning, when a majority of gene regions are concordant in supporting trees showing the same branching pattern, the most likely explanation is that this pattern was shaped by the actual species divergences. Congruence among gene trees derived from unlinked loci is therefore a powerful tool for inferring species trees. This general approach has been described as taxonomic congruence (Mickevich, 1978)—the agreement among the supported topologies of different data sets (Miyamoto & Fitch, 1995).

In this paper, a robust phylogenetic tree for all papionin genera is developed using a taxonomic congruence approach in which the total available genetic sequences for papionin genera are analyzed. The central phylogenetic questions presented above are the focus of the study. The pattern of discordance among gene trees is interpreted in terms of population genetics theory and its significance for understanding the evolutionary history of papionins is discussed. Finally, the evolution of morphological features within the papionin group is discussed in light of the molecular phylogeny.

Background

Harris & Disotell (1998) obtained gene trees for five nuclear gene regions including CD4,

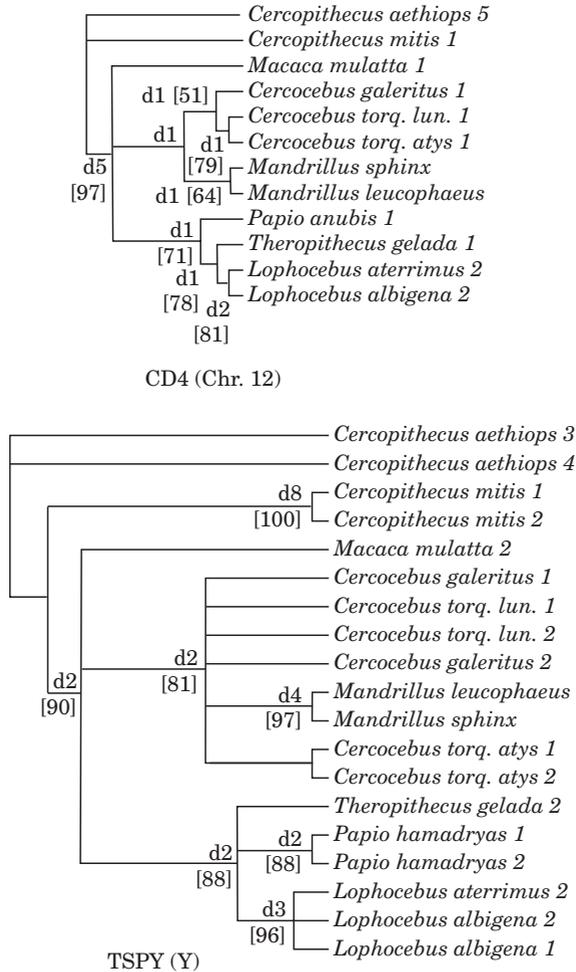
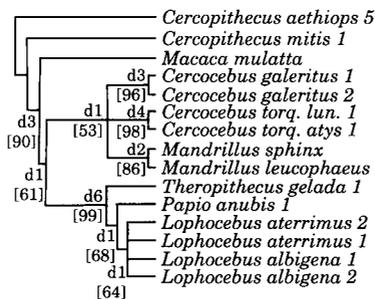


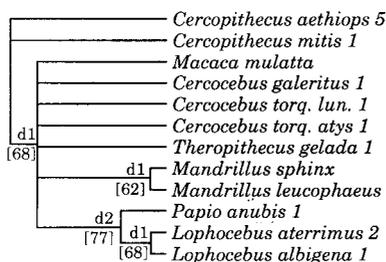
Figure 2. Eight gene trees obtained using maximum parsimony. The CD4, TSPY, α 1,3 GT, and α hemoglobin trees are all strict consensus trees. The *Papio hamadryas* 1 sequence in the TSPY tree is from Kim & Takenaka (1996). The $\psi\beta$ - δ -globin intergenic and COII & 12S rRNA combined mtDNA trees were the single MP trees estimated for these regions. The IRBP tree is the single MP tree obtained using an *a priori* weighting scheme in which transversions were given twice the weight as transitions. The numbers following taxa indicate different individuals sequenced. In the α hemoglobin tree, xa, xb, yc indicate different alleles. The prion protein tree is a 50% majority rule tree. Bootstrap percentages (in brackets) and decay indices (denoted by “d”) are given alongside the branches. A decay index of zero (d0) means this clade was not present in some but not all most parsimonious reconstructions (see Bremer, 1994).

TSPY, the $\psi\beta$ - δ -globin intergenic region, α 1,3 galactosyltransferase (α 1,3 GT), and IRBP (see Figure 2). These regions range in length from 514 to 717 bp and consist of noncoding DNA sequences comprising either intron segments, intergenic regions, or pseudogene sequences. Since the gene

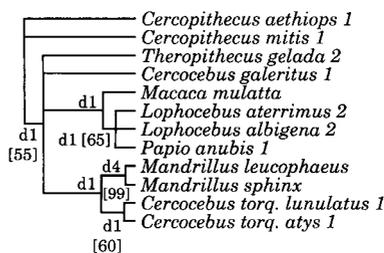
trees for these regions are used in the present analysis they are briefly reviewed here [see Harris & Disotell (1998) for additional details]. The phylogenetic methods used to obtain these trees are identical to the methods employed here (see Materials and methods).



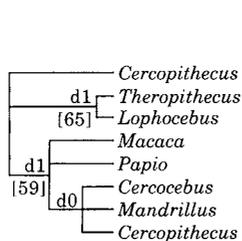
ψβ-δ-globin intergenic (Chr. 11)



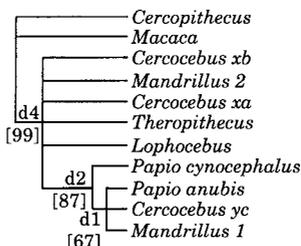
α 1,3 GT (Chr. 9)



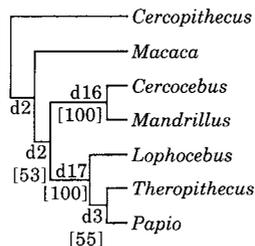
IRBP (Chr. 10)



prion protein (Chr. 20)



α chain hemoglobin (Chr. 16)



combined COII and 12S rRNA

Figure 2. (Continued—legend on facing p. 238.)

All three maximum parsimony (MP) trees (length=42; see [Figure 2](#)) for CD4 are identical and support mangabey polyphyly in which *Cercocebus* forms a unique clade with *Mandrillus*, and *Lophocebus* forms a clade with *Theropithecus* and *Papio*. *Lophocebus* mangabeys are supported as the exclusive sister taxon to *Theropithecus*, with *Papio* being the sister taxon to this pair. The position of *Macaca* is left unresolved in relation to the two African papionin clades. *A priori* weighting did not change the results.

The six MP trees (length=51; [Figure 2](#)) for TSPY are essentially identical to the tree for CD4, except that the relationships among *Theropithecus*, *Papio*, and *Lophocebus* are left unresolved in all trees. *A priori* weighting did not affect the results.

The single MP tree for the $\psi\beta\text{-}\delta$ -globin intergenic region, found in both uniform and *a priori* weighted analyses (length=43; [Figure 2](#)), is essentially the same as the previous trees with the exception that *Papio* is supported as the sister taxon to *Lophocebus*.

The strict consensus tree of five MP trees (length=33; [Figure 2](#)) found for the α 1,3 GT region is relatively poorly resolved. The only clade supported is a *Lophocebus*–*Papio* clade. The cladistic positions of all other genera are unresolved at the base of the papionin tree. *A priori* weighting did not change the results.

Analysis of IRBP employing uniform weighting resulted in two MP trees (length=30; [Figure 2](#)). These trees both support mangabey polyphyly with *Cercocebus* in a clade with *Mandrillus*, and *Lophocebus* in a clade with *Papio*. *Theropithecus* is either placed in an unresolved position at the base of the African papionin tree (uniform weighting) or in a clade with *Papio*, and *Lophocebus* (in the single *a priori* weighted tree). However, *Macaca* is anomalously supported as the sister taxon to the *Papio*–*Lophocebus* clade.

Four additional genetic sequence datasets are included in the analyses presented here. These include reanalyses of DNA sequence datasets from the mitochondrially encoded cytochrome oxidase subunit II (COII) gene ([Disotell et al., 1992](#); [Disotell, 1992, 1994](#)); the mitochondrially encoded 12S rRNA gene ([Van der Kuyl et al., 1995a](#)); the nuclear encoded prion protein gene ([Schatzl et al., 1995](#); [Van der Kuyl et al., unpublished manuscript](#); [Krakauer et al., 1996](#)); as well as reanalysis of an amino acid sequence dataset from the nuclear encoded α hemoglobin gene ([Hewett-Emmett et al., 1976](#)).

Materials and methods

In total, eight separate genetic loci are examined in the present paper. The papionin taxa represented by these genetic datasets and used in the current analysis are listed in [Table 1](#). These sequences were either collected by the author (see [Harris & Disotell, 1998](#)) or were downloaded from the GenBank database at the National Center for Biotechnology Information. The outgroup taxa in all analyses consisted of *Cercopithecus aethiops* and/or *C. mitis* (and *C. mona* in the analysis of the prion protein sequences), belonging to the tribe Cercopithecini, the nearest sister group to the Papionini ([Strasser & Delson, 1987](#)).

[Table 2](#) reports the length (in base pairs) and inferred chromosomal position of the gene regions analyzed here along with references to the studies in which these sequences were initially analyzed. The prion protein sequences, comprising approximately 744 bp region of the second exon of the prion protein gene, were collected by [Schatzl et al. \(1995\)](#) and [Van der Kuyl et al. \(unpublished manuscript\)](#). The second exon, encoding the entire prion protein, is expressed at high levels in brain tissue and is believed to be involved in several

Table 1 Genetic sequences available for species within the tribe Papionini and for several outgroup species of *Cercopithecus**

Species name	CD4	TSPY	$\psi\beta$ - δ -globin intergenic region	a1,3GT	IRBP	Prion protein	α hemoglobin amino acid	COII	12SrRNA
<i>Cercopithecus aethiops</i>	+	+	+	+	+	+	+	+	+
<i>Cercopithecus mitis</i>	+	+	+	+	+	+			
<i>Cercopithecus mona</i>						+			
<i>Cercocebus galenitus chrysogaster</i>	+	+	+	+	+			+	+
<i>C. galenitus</i> sp.									
<i>C. torquatus lunulatus</i>	+	+	+	+	+	+	+		+
<i>C. torquatus atys</i>	+	+	+	+	+	+		+	+
<i>Lophocebus aterrimus</i>	+	+	+	+	+	+		+	+
<i>L. albigena albigena</i>	+	+	+	+	+				
<i>L. albigena</i> sp.							+		
<i>Macaca mulatta</i>	+	+	+	+	+	+	+	+	+
<i>Papio cynocephalus</i>							+		
<i>Papio anubis</i>	+	+	+	+	+	+	+	+	+
<i>Papio hamadryas</i>	+	+	+	+	+	+	+	+	+
<i>Theropithecus gelada</i>	+	+	+	+	+	+	+	+	+
<i>Mandrillus sphinx</i>	+	+	+	+	+	+	+	+	+
<i>Mandrillus leucophaeus</i>	+	+	+	+	+	+	+	+	+

*This list is not meant to be comprehensive. It serves to outline which species are represented in the current study.

Table 2 Gene regions analyzed in this study subdivided into separate linkage groups

Gene region	Linkage group*	Size (bp/amino acids)	Human chromosomal location†	Presumed papionin chromosomal location‡	References§
<i>Nuclear genome</i>					
CD4	1	717 bp	12p12-pter	12	1
TSPY	2	692 bp	Ypter-p11·2	Y	1
φη intergenic	3	672 bp	Approx. 11p15·4-15·5	11	1
α1,3 galactosyltransferase	4	514 bp	9q33-q34	14	1
IRBP	5	685 bp	10p12	10	1
Prion protein	6	744 bp	20p12-pter	20	2
α-chain hemoglobin	7	14 a.a.	16	16	3
<i>Mitochondrial genome</i>					
COII	8	697 bp	—	—	4
12S rRNA	8	394 bp	—	—	5

*The numbers assigned to linkage groups are arbitrary. All gene regions belong to different linkage groups except the COII and 12S rRNA genes which belong to a single linkage group.

†Human chromosomal locations were obtained from either literature sources or from any of several computer databases including The Human Genome Database, The Online Inheritance in Man data base, GenBank, or the Human Genome Map. p=short arm; q=long arm; ter=terminal.

‡Locations in papionins were inferred from chromosomal homology studies between humans and the papionin species *Macaca fuscata* (Weinberg *et al.*, 1992).

§1, Harris & Disotell (1998); 2, Van der Kuyl *et al.* (unpublished manuscript); 3, Hewett-Emmett *et al.* (1976); 4, Disotell *et al.* (1992); 5, Van der Kuyl *et al.* (1994).

degenerative neurological diseases in mammals, including primates. The α hemoglobin sequences comprise 141 amino acid residues collected and analyzed initially by Hewett-Emmett *et al.* (1976) and Hewett-Emmett & Cook (1978).

The nuclear gene regions, including those initially analyzed in Harris & Disotell (1998) are each found on different chromosomes in humans and probably in papionins as well (see Table 2). Their inferred chromosomal location in papionins was based on the chromosomal synteny study of Weinberg *et al.* (1992) in which humans were compared with the papionin species *Macaca fuscata*.

The mitochondrial gene sequences include both the COII (Disotell *et al.*, 1992) and 12S rRNA (Van der Kuyl *et al.*, 1995a) coding regions. The COII gene codes for cytochrome oxidase subunit II, a mitochondrial electron-transport enzyme functioning

in respiration, and 12S rRNA codes for a ribosomal RNA molecule.

Genes falling on different chromosomes necessarily have a recombination fraction of 50% and therefore segregate independently with respect to each other in the formation of gametes. Such genetic regions constitute distinct linkage groups. Since each nuclear gene region analyzed for the papionins is inferred to fall on a different chromosome, there are a total of seven nuclear linkage groups. The two mtDNA sequence datasets, however, form a single additional linkage group since the mitochondrial genome is inherited independently of the nuclear genome and undergoes no recombination among its constituent genes.

Phylogenetic methods

Phylogenetic analyses were performed on each of the genetic data sets separately following a taxonomic congruence approach

(Mickevich, 1978; Miyamoto and Fitch, 1995). An analysis was also done on a single combined dataset in an analysis of "total" evidence (see Kluge, 1989). As the number of taxa and particular taxa sequenced for each gene region differed, a combined dataset was developed for only those taxa represented in all gene regions. In the cases of *Lophocebus* and *Mandrillus*, sequences from different species within these genera needed to be combined in order to form the "combined" sequence for these genera. Although this author believes that a combined analysis is not well justified theoretically, at least for molecular data drawn from distinct genomic regions, it has been included because the approach has been strongly advocated by some traditional systematists (Kluge, 1989; Ernisse & Kluge, 1993; Kluge & Wolf, 1993) and because the results of a combined analysis in the current study can be used to point out the shortcomings of this approach.

Phylogenetic analyses employed maximum parsimony (MP) using the computer program *PAUP* version 3.1 (Swofford, 1993). All MP analyses employed *PAUP*'s branch and bound search option. Deletions were coded as gaps and treated as a fifth character state. Multiple base deletions were treated as a single event. Bootstrap confidence levels were based on 500 random samplings of the data. Decay indices (DI), representing the difference in tree length between the most parsimonious tree possessing a particular clade and the closest suboptimal tree(s) in which this clade is not present (Bremer, 1994), were calculated using *AutoDecay* version 2.9.6 (Eriksson, 1996). MP tree lengths and homoplasy indices (HI) are described for all trees.

Two different character weighting schemes were used in the maximum parsimony analyses. In the uniform weighting scheme, all nucleotide substitutions were weighted equally. In the *a priori* weighting scheme, nuclear sequences were weighted with a 2:1 transition–transversion ratio,

reflecting empirically observed asymmetries in nucleotide substitutions (see Kimura, 1980; Nei, 1987; Ruvolo, 1997; Harris & Disotell, 1998). *A priori* weighting of the mtDNA sequences used the average of the empirically determined transition/transversion ratios (Tr/Tv) found for the COII and 12S rRNA sequences, respectively. Tr/Tvs were determined by counting the number of transition and transversion changes appearing on the MP trees found for these genes. In the analysis of the α hemoglobin amino acid sequences all substitutions were weighted equally.

Results

The results of all phylogenetic analyses including the trees obtained in Harris & Disotell (1998) are summarized in Table 3. Results from the reanalysis of the previously published genetic sequences from the COII, 12S rRNA, prion protein, and α hemoglobin genes are presented below. Additionally, both a consensus tree of the separate MP gene trees is developed, and a combined tree is derived in an analysis of the genetic sequences from each different region pooled as a single dataset. The COII gene sequences are used to estimate divergence dates for papionin genera.

a hemoglobin

The MP trees originally obtained by Hewett-Emmett *et al.* (1976; Figure 3) for the α hemoglobin amino acid sequences were similar to the strict consensus tree (of seven most parsimonious trees, length=18, HI=0.250; Figure 2) obtained in the reanalysis of their sequences. The consensus tree is largely similar to the previous gene trees described, however, *Lophocebus* is supported as the sister taxon to *Papio* (as in the $\psi\beta$ - δ -globin intergenic region, α 1,3 GT, and IRBP trees) with *Theropithecus* as their sister taxon.

Table 3 Papionin phylogenetic hypotheses and their support in the gene trees derived from unlinked gene regions as well as for all the gene regions combined

Phylogenetic hypotheses	CD4 (12)*	TSPY (Y)	φ1 intergenic (11)	α 1,3 GT (14)	IRBP (10)	COII/12s rRNA (mtDNA)¶	α chain hemoglobin (16)	Prion protein (20)	Combined sequences
Mangabey polyphyly	✓†	✓	✓	UR	✓	✓	✓	✓	✓
Mangabey monophyly	×‡	×	×	×	×	×	×	×	×
<i>Theropithecus-Papio-Lophocebus</i>	✓	✓	✓	UR§	×	✓	✓	×	✓
<i>Cercocebus-Mandrillus</i>	✓	✓	✓	UR	✓	✓	UR	UR	✓
<i>Lophocebus-Papio</i>	×	UR	✓	✓	✓	✓	✓	×	✓
<i>Lophocebus-Theropithecus</i>	✓	UR	×	×	×	×	×	✓	×
<i>Theropithecus-Papio</i>	×	UR	×	×	×	×	×	×	×
<i>Mandrillus-Papio</i>	×	×	×	×	×	×	×	×	×

*Inferred chromosomal location in papionins.

†A check-mark indicates that this relationship is supported by maximum parsimony.

‡An × indicates that this relationship is not supported by maximum parsimony.

§UR indicates that this relationship is unresolved.

¶All mtDNA trees referred to are those in which the 12S rRNA sequences for *Theropithecus* were excluded, and in which an *a priori* weighting scheme was employed (see text for details).

Prion protein

A 50% majority rule consensus tree of four most parsimonious trees (length=16; HI=0.333; Figure 2) for the prion protein gene region is largely anomalous compared with the other gene trees. The genes for *Cercopithecus mona* and *Macaca* group with *Cercocebus*, *Mandrillus* and *Papio*. The genes of *Lophocebus* and *Theropithecus* form a related group. The *a priori* weighted MP tree is unchanged. Schätzl *et al.* (1995), Van der Kuyl *et al.* (unpublished manuscript), and Krakauer *et al.* (1996) similarly found that their analyses of prion protein sequences yielded a number of anomalous groupings within the primates not found in other gene trees for this group.

Combined COII and 12S mtDNA sequences

The combined mtDNA sequences from the COII and 12S rRNA genes (see Disotell *et al.*, 1992 and Van der Kuyl *et al.*, 1995a, respectively) comprise a dataset of 1078 bp. Since analyses of the 12S rRNA gene by itself places the *Theropithecus* sequence anomalously outside the papionins (perhaps being a nuclear copy of the mitochondrial gene; see Van der Kuyl *et al.*, 1995b),² analyses were done with the sequence for *T. gelada* excluded. In the *a priori* weighted analyses, transversions were weighted six times that of transitions using the mean of the Tr/Tv ratios calculated for both the COII and 12S rRNA genes based on their separate MP trees (7.9/1 and 4.8/1, respectively; mean=6.35/1).

The uniformly weighted MP (length=386, HI=0.377; Figure 2) tree is fully resolved and is largely similar to the previous gene trees (except prion protein). *Lophocebus*, *Papio*, and *Theropithecus* form a clade, as in most of the other gene trees, with *Theropithecus* as the sister taxon to *Papio*, exclusive of *Lophocebus*. *Cercocebus* is supported as the

²Van der Kuyl *et al.* (1995b) found nuclear counterparts of the mtDNA encoded 12S rRNA gene in several Old World monkey species.

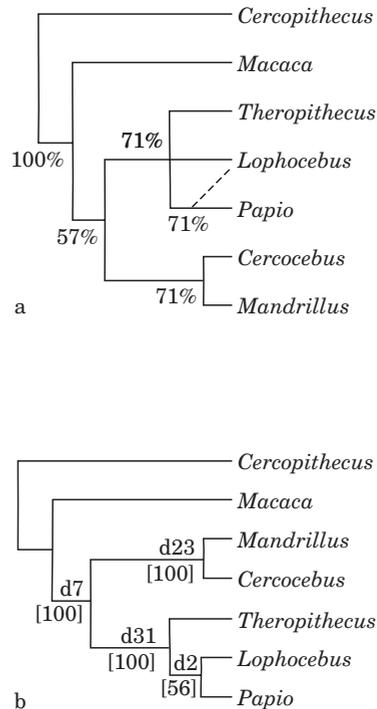


Figure 3. (a) 50% majority rule consensus tree of the seven separate gene trees obtained using maximum parsimony. Percentages indicate the fraction of the total gene trees supporting a particular clade; (b) single MP tree found in an analysis of a single dataset of all seven nuclear gene regions and the two mitochondrial gene regions combined.

sister taxon to *Mandrillus*. *Macaca* is supported as the sister taxon to the African papionins. However, the *a priori* weighted MP tree supports *Lophocebus* rather than *Theropithecus* as the sister taxon to *Papio*.

Consensus tree. A 50% majority rule consensus tree indicating congruent clades amongst seven MP gene trees is given in Figure 3. The consensus tree was derived based on the five gene trees from Harris & Disotell (1998) and two of the gene trees derived in the current study. The actual trees used in the consensus analysis were pruned versions of the trees in Figure 2, in which only a single sequence was selected to represent each papionin genus. The prion

protein gene results were excluded from this analysis because its trees are notably anomalous. Therefore, the tree represents the consensus of seven gene trees.

It is the case that all the gene trees reject monophyly of the mangabeys. Five gene trees (71%) support mangabeys (*Lophocebus* and *Cercocebus*) as falling into two separate clades (CD4, TSPY, $\psi\beta$ - δ -globin intergenic region, IRBP, combined mtDNA). In these trees, *Cercocebus* is supported as the sister taxon to *Mandrillus* and *Lophocebus* in a clade with *Theropithecus* and *Papio*. Within the clade consisting of *Lophocebus*, *Theropithecus*, and *Papio*, five trees show *Papio* and *Lophocebus* as sister taxa exclusive to *Theropithecus*, and two trees show either *Lophocebus* as the exclusive sister taxon to *Theropithecus* (CD4), or these three taxa as an unresolved trichotomy (TSPY). The two trees that do not place each mangabey genus into different clades leave the relationships of at least one of these genera (*Cercocebus*) unresolved at the base of the African papionin tree. These unresolved trees are not incongruent with mangabey polyphyly.

Macaca is supported as the sister taxon to the African papionins in three gene trees ($\psi\beta$ - δ -globin intergenic region, mtDNA, α hemoglobin). Only a single tree (IRBP) conflicts with this position; the remaining trees leave the relationship of this genus unresolved at the base of the papionin tree.

A combined analysis of the "total" sequences

All seven nuclear datasets (including prion protein) were combined with the mtDNA dataset (excluding the 12S rRNA sequence for *T. gelada* as above) to form a single large dataset consisting of 5252 bp of sequence for papionins. The single uniformly weighted tree (length=590, HI=0.188, Figure 3) supports a clade comprised of *Papio*, *Lophocebus*, and *Theropithecus* with these first two genera linked as sister taxa; *Cercocebus* shares a unique clade with *Mandrillus*. All clades, except for the *Papio*-

Lophocebus clade, are strongly supported by decay indices as well as bootstrap measures.

Estimation of divergence dates. Divergence dates were estimated based on the mtDNA COII DNA sequences using distances calculated in MEGA 1.01 (Kumar *et al.*, 1993). Distances are based on third codon positions only, because most substitutions at these positions are synonymous (i.e., cause no amino acid change), and were corrected using Kimura's (1980) two-parameter method since considerably transition-transversion bias occurs. Estimations were restricted to the COII gene since its estimated distances have the smallest associated standard errors (e.g., the mean standard error of the distances is 14%). In contrast, the Kimura corrected distances for the nuclear DNA regions (TSPY, the $\psi\beta$ - δ -globin intergenic region, CD4, α 1,3 GT, and IRBP) have associated standard errors that range from 28.29% (TSPY) to as great as 47.49% (α 1,3 GT) presumably due to relatively low levels of sequence divergence (see Harris and Disotell, 1998), thus giving the COII distances relatively the highest level of confidence. Divergence dates were not estimated for the combined dataset of all gene regions. Doing this ignores the significant problem caused by combining regions having disparate levels of diversity reflecting different rates of evolution. It also ignores the widely different standard errors associated with the distances estimated for these regions.

Separate estimates of the times of species divergences were made using two different calibration points: a divergence between humans and orang-utans at around 13 million years, and a divergence of *Theropithecus* from the African papionins at around 4 million years. These dates are the earliest times at which we find fossils attributable to *Sivapithecus*, an early derivative of the orang-utan lineage (Kappelman *et al.*, 1991) and *Theropithecus* (Eck &

Table 4 Relative rate tests using *Cercopithecus aethiops* as the outgroup species based on the Kimura (1980) two-parameter corrected distances for third codon positions

Ingroup 1	Ingroup 2	Difference between ingroup branch distances (S.E. of difference)	P value
<i>Cercocebus galeritus</i>	<i>Papio anubis</i>	0.049 (0.085)	0.2810
	<i>Theropithecus gelada</i>	0.066 (0.087)	0.2236
	<i>Lophocebus albigena</i>	0.071 (0.083)	0.1949
	<i>Mandrillus leucophaeus</i>	0.017 (0.064)	0.3936
	<i>Macaca mulatta</i>	0.124 (0.092)	0.0901
<i>Mandrillus leucophaeus</i>	<i>Papio anubis</i>	0.066 (0.089)	0.2266
	<i>Theropithecus gelada</i>	0.084 (0.092)	0.1814
	<i>Lophocebus albigena</i>	0.088 (0.086)	0.1515
	<i>Macaca mulatta</i>	0.141 (0.093)	0.0643
<i>Theropithecus gelada</i>	<i>Papio anubis</i>	0.017 (0.080)	0.4129
	<i>Lophocebus</i>	0.005 (0.080)	0.4761
	<i>Macaca mulatta</i>	0.058 (0.101)	0.2843
<i>Macaca</i>	<i>Papio anubis</i>	0.075 (0.102)	0.2327
	<i>Lophocebus albigena</i>	0.053 (0.098)	0.2946

Jablonski, 1984; Szalay & Delson, 1979), though Delson & Dean (1993) note that the earliest *Theropithecus* may be slightly more recent, and they provide minimum estimates of the divergence times for these species. Dates were calculated assuming a uniform substitution rate and were based on the mean of the successive distances between a taxon and each in-group taxon. For example, for the divergence between *Macaca* and the African papionins, the distances between the genus and *Papio*, *Theropithecus*, *Lophocebus*, *Cercocebus* and *Mandrillus* were averaged and used in the date calculations.

Relative rate tests of lineages within the Papionini, using *Cercopithecus aethiops* as an outgroup, did not show any of the rates to be significantly different (Table 4). However, observation of the differences between distances does indicate a considerable rate decrease between *Cercocebus* and *Mandrillus* when compared with *Macaca*, a finding made previously by Disotell (1992). Therefore, the estimated time of divergence of a *Cercocebus/Mandrillus* lineage as well as the

divergence of these genera from each other may tend to be underestimated. When the divergence date for the *Macaca* lineage was estimated, in which the distances to *Mandrillus* and *Cercocebus* were averaged with the distances to the remaining genera, it was found to differ only slightly from the estimated date when the distances to these genera were excluded (Table 5).

Additionally, since one of the calibration points falls outside the papionins (and within the hominoids), it is important to calculate the relative rates between this group and the papionins. With respect to this, Adkins *et al.* (1996) found that the rates in these two groups are homogeneous when comparing synonymous substitutions but heterogeneous for nonsynonymous substitutions. This justifies the use here of distances restricted to third codon positions, sites at which substitutions are largely synonymous.

The estimated dates are given in Table 5. It is important to bear in mind that since the fossil calibration points represent minimum dates of divergence, estimated dates based

Table 5 Estimated divergence dates (in millions of years) within the Papionini based on Kimura (1980) two-parameter corrected distances for the mtDNA COII sequences using third codon positions only

Divergence	Estimated date (calibrated on <i>Pongo/Homo</i> divergence)*	Range	Estimated date (calibrated on <i>Theropithecus</i> divergence)†	Range
<i>Macaca</i> vs. African papionins	11.88 (12.49)‡	10.49–14.68	9.27 (9.74)	8.18–11.45
<i>Mandrillus/Cercocebus</i> vs. other papionins	11.48	8.47–14.33	8.95	6.61–11.2
<i>Mandrillus/Cercocebus</i> divergence	4.12	—	3.21	—
<i>Theropithecus/Papio</i> vs. <i>Lophocebus</i>	4.76	4.55–4.97	3.71	3.55–3.88
<i>Theropithecus/Papio</i> divergence	5.13	—	4.0§	—

*The *Pongo/Homo* divergence was inferred to be 13.0 m.y.a. based on the earliest occurrence of fossils attributable to *Sivapithecus* (after Kappelman *et al.*, 1991).

†The *Theropithecus* divergence was inferred to be 4.0 m.y.a. based on the earliest occurrence of fossils attributable to this genus (after Eck & Jablonski, 1984; Szalay & Delson, 1979).

‡Dates in parentheses are estimations in which the distances to *Cercocebus* and *Mandrillus* were excluded because the branches leading to these genera show a rate slowdown relative to other papionin branches.

§This data is the calibration point within the papionin group.

on these calibrations are likely to be underestimated. Equally important to remember, however, is that these dates are based on the divergences between DNA sequences and not the divergence between species. Since gene copies have coalescences that predate the species divergences, these dates tend to be overestimates of the species divergence, though presumably these different factors will act to balance each other to some extent. Because it is difficult to take these variables into account, the dates of divergence presented here are only intended to be rough estimates. Nevertheless, the dates based on either calibration point are generally consistent with the inferred ages of papionin lineages for which a good fossil record is known (see Szalay & Delson, 1979). In light of an incomplete fossil record these estimated dates provide important information concerning the relative times between species divergences within the papionins.

Considering the times between species divergences, two are found to be relatively short. The time between the successive divergences of *Theropithecus*, *Lophocebus*, and *Papio* is estimated to be in the range of

290 ka to 370 ka, and that between *Macaca* and the African papionins is estimated to be in the range of 320 ka to 400 ka. The short times estimated between these divergences (i.e., their internodal branches) are also indicated by the maximum likelihood estimated branch lengths. In the maximum likelihood tree for the combined mtDNA dataset (tree not shown), in which all branch lengths are significantly positive as measured by Felsenstein's (1993) criteria, these two internodes are approximately 31% and 33% of the average branch lengths in the tree, respectively.

Discussion

Gene trees, species trees, and population genetics theory

As discussed earlier, several factors may contribute to discordances among gene trees and species trees. First, gene trees may be incorrectly estimated because of random sampling error (Saitou & Nei, 1986), or because high substitution rates cause homoplasy to bias the tree. Second, natural selection can produce conflicting gene trees. Among the eight gene trees for the

papionins, only the prion protein gene tree, which is notably anomalous, is suspected to be incorrectly estimated, likely as a result of selection pressures on the prion protein. For instance, Van der Kuyl *et al.* (unpublished manuscript) suggest that the relatively low rates of substitutions at nonsynonymous sites (i.e., amino acid changing sites) compared to the much higher rates at synonymous sites (i.e., that cause no amino acid change) indicate strong functional constraint possibly acting to prevent incorrect folding of the PrP protein known to cause disease (see Pan *et al.*, 1993).

Error due to high substitution rates is probably unlikely, since most gene regions showed relatively low diversity (less than 10% variability across papionin species for nuclear regions sequenced by Harris & Disotell (1998). Nucleotide variability is significantly greater in the COII and 12S rRNA genes (Disotell *et al.*, 1992; Van der Kuyl *et al.*, 1995a). However, error is minimized in the analysis of these data by employing a weighting scheme in which the relatively fast changing transitions were downweighted compared to the more conservative transversion changes. The error due to random sampling which occurs in the analysis of relatively short regions of DNA is always difficult to rule out. Saitou & Nei (1986) have estimated that relatively longer DNA sequences (than those usually appearing in phylogenetic analyses) are needed to estimate the correct gene tree with 95% probability. While this concern needs to be balanced in light of the practical limitations to collecting large datasets in the laboratory, these same authors (Saitou & Nei, 1986) point out that the same high probability can be achieved by sequencing multiple independent genes and searching for congruence across their separately estimated gene trees.

As discussed earlier, the third phenomenon that can cause discordances among gene trees (and between gene trees and the

actual species tree) is the random sorting of ancestral DNA sequences into descendant lineages. For example, considering just three species, the probability that a gene tree has the same topology as the species tree is given by

$$P = 1 - 2/3e^{-T/2N_e}$$

where T is the time between successive species divergences, and N_e is the effective population size (of gene copies) (Pamilo & Nei, 1988). For any particular gene tree, two factors will tend to reduce the probability that it matches the species tree, when T is small, and/or when N_e is large. This is because random genetic drift is less efficient at fixing polymorphic DNA sequences within a population over relatively short periods of time or when effective population sizes are large. Under these circumstances the random sorting of ancestral DNA lineages into descendant species lineages can produce a gene tree different from the species tree. Examining the influence solely of time, Pamilo & Nei (1988) found that when the interval between successive divergences among species is only several hundred thousand years, or roughly 20,000 to 30,000 generations (assuming a generation of ten years), the probability of mismatch between gene and species tree may be considerable.

Under these circumstances, increasing the number of unlinked loci can considerably increase the probability of obtaining the actual species tree (Saitou & Nei, 1986; Pamilo & Nei, 1988). Congruence in the pattern of species relationships across multiple separate gene trees can greatly increase the probability that real phylogenetic associations are identified (above the level at which these associations will occur by chance alone). Using the eight unlinked loci analyzed here, this approach has been applied to the investigation of the central questions in papionin systematics outlined earlier.

Systematic questions

Are mangabeys monophyletic? Mangabey monophyly is not supported by any of the eight gene trees. The question is, then, to which papionin genera is each mangabey genus most closely related? For *Cercocebus*, a sister group relationship with *Mandrillus* is well supported by five gene trees (CD4, TSPY, $\psi\beta$ - δ -globin intergenic region, IRBP, mtDNA) while the remaining gene trees (α 1,3 GT and α hemoglobin) are not incongruent with such a clade. The genus *Lophocebus* is well supported as closely related to *Papio* and/or *Theropithecus* in all of the gene trees, making the close relationship among these three genera strongly corroborated. However, resolving the detailed relationships among these taxa is more problematic since there is considerable conflict among the gene trees for these taxa (see discussion below). A recent analysis of DNA sequences for two different genes (gamma 1 and 2) within the β -globin cluster (chromosome 11) supports the close relationship between *Papio* and *Theropithecus* to the exclusion of *Lophocebus* (Page *et al.*, 1999).

Are Papio and Mandrillus sister taxa? The hypothesized sister group relationship between *Papio* and *Mandrillus* (in morphological studies) is not supported in any of the eight gene trees, thus strongly rejecting it. In fact, at least five gene trees place these genera in two distinct clades. Again, recent analyses of two genes within the β -globin cluster (gamma 1 and 2) also do not support a close relationship between these genera (Page *et al.*, 1999). These sequences may in fact be linked with the $\psi\beta$ - δ -globin intergenic sequences analyzed in this paper. Therefore, they may not provide independent evidence concerning the relationships of these genera. However, they do increase the reliability of the gene tree based on this genetic locus.

How are Lophocebus, Papio, and Theropithecus related? It is clear that the major

area of incongruence among the gene trees concerns the order of divergence of *Lophocebus*, *Papio* and *Theropithecus*. For three taxa, there are three possible alternative bifurcating rooted trees, [(*Lophocebus*, *Papio*), *Theropithecus*], [(*Lophocebus*, *Theropithecus*), *Papio*], and [*Lophocebus*, (*Papio*, *Theropithecus*)], all of which have been found in the gene trees analyzed. The distribution of gene trees supporting the alternative pairings of these taxa can be obtained. TSPY yields an unresolved tree for these taxa and is excluded. As discussed earlier, prion protein is excluded since its gene trees are anomalous. The distribution is: 4 (α 1,3 GT, $\psi\beta$ - δ -globin intergenic region, IRBP, α hemoglobin), 1 (CD4), and 1 (mtDNA MP tree; uniform weighting), respectively. The distribution would change slightly to 5, 1, and 0 if the mtDNA MP *a priori* weighted tree is adopted which supports a *Lophocebus/Papio* clade.

A likelihood ratio test for multiple loci developed by Wu (1991) can be used to evaluate whether such a distribution permits the selection of one particular tree as the actual species tree. In the case of six gene trees, Wu's test requires that all of these trees support the same branching pattern in order to reject the null hypothesis, that the three genera form a trichotomy, or that one of the less frequent alternative trees may in fact represent the actual species tree (see Wu, 1991). For the present distributions, statistical rejection of the null hypothesis is not possible. The acceptance of any single pairing among these three taxa as representative of the actual species tree (on the basis of Wu's 1991 test) may require further data from unlinked genetic loci. Indeed, Ruvolo's (1997) recent application of the multi-locus test towards resolving the relationships among the three "African" hominoids was able to find statistical support for a *Pan-Homo* pairing on the basis of a total of 14 unlinked loci. Moreover, Moore (1995) has estimated that as many as 16 nuclear loci

may be required to reach statistical confidence in a species tree, particularly when species' divergences have occurred close in time. Despite such findings, there may be reason to suggest that a sister taxon relationship between *Lophocebus* and *Papio* is the favored phylogenetic hypothesis at present (if we insist on a bifurcating tree), since this relationship is most frequently supported amongst the available gene trees.

Nevertheless, the discordances among gene trees for these three genera presumably indicate that their divergences with respect to each other took place over a relatively short time interval. This is supported by the relatively short time between their divergences estimated based on the COII sequences (ranging from 290 ka to 370 ka), as well as the relatively short internodal branch lengths (estimated by maximum likelihood) between their divergences. A parallel example of this phenomenon is the case of the hominoid "trichotomy" where various gene trees support alternative pairings amongst *Homo*, *Pan* and *Gorilla* with the time between their divergences estimated to be perhaps as short as several hundred thousand years (Rogers, 1993; Ruvolo, 1997), though some estimates are considerably greater (see Ruvolo, 1997).

Given the similar situation for the papionin genera, we might ask the following questions. Why did *Papio*, *Theropithecus*, and *Lophocebus* speciate so relatively close in time around 5 m.y.a. or so? Are there common causal factors underlying the rough coincidence in the divergences among the papionin genera and the slightly earlier divergences among the large "African" hominoids? What were the speciation processes involved in the divergence of these species?

Separate versus combined analysis of multiple gene regions

One approach to resolving the region of incongruence in the papionin tree is to fol-

low a "total" evidence approach and adopt the combined tree as the actual phylogenetic relationships of papionin genera. The goal of this approach is to maximize the informativeness and explanatory power of the data (Kluge, 1989; Ernisse & Kluge, 1993; Kluge & Wolf, 1993). However, in the analysis of unlinked genetic regions such an approach makes little theoretical sense. Unlinked genetic regions can have different biological properties (e.g., in gene function, levels of diversity, base composition, transition/transversion ratios) as well as different evolutionary properties (e.g., in gene coalescence, biparental versus uniparental inheritance, variation shaped by natural selection) which make it unnatural to combine them in a single dataset (Miyamoto and Fitch, 1995). In the present study, the combined analysis yielded a single bifurcating tree in which *Lophocebus* is supported as the sister taxon to *Papio* to the exclusion of *Theropithecus*. However, adopting this tree would limit insight into the evolutionary history of the papionins especially the rapid-fire divergence of *Lophocebus*, *Papio*, and *Theropithecus* gained by examination of the pattern of incongruence among separate gene trees.

Implications for morphological evolution within the Papionins. The strong support for mangabey polyphyly found here is in disagreement with traditional phylogenies of the mangabeys based on morphological evidence which suggest their monophyletic grouping. The overall close morphological resemblance between the two mangabey genera therefore requires explanation. In contrast to the other papionin genera, both mangabey genera share moderately prognathic faces, deep suborbital maxillary fossae, a medium body size, and arboreal to semiterrestrial skeletal adaptations. At least two interpretations of the evolution of these features are possible under the present view of their relationships. Either they evolved

in parallel in the two separate mangabey lineages, or they are retained characters from the common ancestor of the African papionins. For the cluster of characters, they indeed may represent a mixture of primitive and independently evolved characters.

Outgroup comparisons with *Macaca* suggest that many of these characters are primitive for the African papionins, such as moderate prognathism, arboreal to semi-terrestrial skeletal adaptations, and medium body size, all of which are variably found in macaque species. However, the fact that *Macaca* lacks even shallow suborbital fossae (Szalay & Delson, 1979) may suggest that the fossae are independently evolved in each mangabey genus.

Despite an overall resemblance between mangabey skulls, Groves (1978) documented a series of minor morphological differences in the crania between *Lophocebus* and *Cercocebus* mangabeys in cranial dimensions, nasal bones, zygomatic arches, suborbital fossae, tubular auditory meati, mandibular morphology, cranial vault sutures, molar wear, central incisor morphology, number and position of the malar and mental foramina, and the morphology of the lachrymal fossae. More recently, differences in the postcranial skeletons of these two genera have been documented (Nakatsukasa, 1994, 1996) which are functionally associated with a basic arboreal/semi-terrestrial-terrestrial ecological division between them. *Lophocebus* is reported to be strictly arboreal, preferring the main canopy of the forest; whereas *Cercocebus* is semi-terrestrial to terrestrial and frequently inhabits the forest's understory and floor (Waser, 1984; Jones & Sabater Pi, 1968; Homewood, 1978).

Fleagle & McGraw (1989) found a number of osteological characters which support the genetic findings of mangabey polyphyly and which link *Cercocebus* with *Mandrillus* in a clade distinct from a *Lophocebus*, *Papio*, and *Theropithecus* clade. They

share a deep scapula; a humerus with a very broad deltoid plane, a proximally extended supinator crest, a broad brachialis flange, and a narrow olecranon fossa with a deep lateral ridge; an ulna with a narrow coronoid process and a relatively large radial notch; a radius and ulna with marked interosseous lines; a robust ilium, reduced gluteal tuberosity on the femur, subequal and sharp borders of the patellar groove, and a tibia with a more rounded midshaft; and in the dentition, relatively large and rounded P4s in the upper and lower jaws. This suite of characters is interpreted to be functionally associated with a general ecological specialization in the *Cercocebus/Mandrillus* clade for foraging for insects, hard nuts, and seeds on the forest floor (Fleagle & McGraw, 1989), a lifestyle which they suggest may be primitive for the papionin tribe. If the late Miocene to Pliocene genus *Parapapio*, often suggested to be an "archetypal" ancestor of either the entire tribe or just the African papionins (Simons & Delson, 1978; Leakey & Delson, 1987), is found to display such a suite of characters this idea would be further supported. However, the frequent fossil presence of *Parapapio* at relatively dry savannah or wooded savannah sites in East Africa such as at Laetoli, Tanzania (Leakey & Delson, 1987) and the relatively dry and open habitats at South African sites such as Sterkfontein, Makapansgat, Bolt's Farm and Taung (Simons & Delson, 1978; Delson, 1975) (does not seem to support) this suggestion. It is possible, however, that if the ancestral papionin species was found in more densely forested habitats like those inhabited by species of *Cercocebus* and *Mandrillus* today (in western and central Africa) than taphonomic conditions may not have been favorable for its fossil preservation.

The strongly supported hypothesis that *Papio* and *Mandrillus* belong to two unrelated lineages within the papionins calls for re-evaluation of morphological

characters traditionally posited as linking them as sister taxa. The long faces shared by these genera apparently either evolved independently in these two genera, or are retained from their common African papionin ancestor. This first interpretation would seem to be supported by the general allometric trend exhibited by the large-bodied papionins in which disproportionate lengthening of the face is correlated with increasing body size (see Freedman, 1962; Jolly, 1970). Lengthening of the face is associated with large body size in a number of living and extinct Old World monkeys including *Macaca nigra*, *Gorgopithecus*, *Dinopithecus*, *Paracolobus*, and *Rhinocolobus* (Szalay & Delson, 1979). It is probable that the trend towards disproportionate facial lengthening (and development of large canine teeth) within this group is also related to a general social system in which there is strong sexual dimorphism with intense intermale competition.

However, the alternative interpretation, that long faces may be primitive for the African Papionini, is also tenable. This view has been suggested by Groves (1978) and more recently by Kingdon (1997) in light of the emerging findings from molecular systematics. According to such an interpretation, the close resemblance in the long faces of *Papio* and *Mandrillus* is a result of their retaining the putative long face of the African papionin common ancestor. Thus, the suborbital maxillary fossae possessed by mangabeys are explained as evolving independently in each genus as a result of independent shortening of their faces as they became phylogenetically smaller from the putatively long-faced African papionin ancestor (see Kingdon, 1997).

Kingdon (1997:42) suggests a structural basis for the development of the fossae as "the result of buckling in the plane of junction [between face and cranium]" whereas Groves (1978) emphasizes their functional basis in preserving a complex facial musculature.

Obviously, these explanations are not exclusive, and the causal relationship between a decrease in body size (and facial length) can be examined in comparative ontogenetic and morphological studies of facial morphology in mangabeys and other papionin genera. Nevertheless, the hypothesis that a large body size and long face characterized the last common ancestor of the African papionins might be better supported if additional mangabey features, common to both genera and functionally uncorrelated with the face (e.g., features of the postcranium such as size of articular surface areas, and diaphyseal cross sectional areas), were shown to reveal a phyletic decrease in their overall size.

Another finding of the current study is that *Theropithecus* may not be the sister taxon to *Papio*, as suggested in immunological and mtDNA COII studies (Sarich, 1970; Disotell *et al.*, 1992). This may indicate that the morphological features shared by these genera—terrestrially adapted postcrania, large body size, and long (although differently shaped) faces—may also be independent acquisitions. Of course, as discussed before, the alternative explanation that they are primitive for the group is also possible.

Clearly, further investigation of the polarity of morphological evolution in papionins is needed. Particular focus might be on comparing the ontogeny of faces within the papionins (e.g. see Delson & Dean, 1993; Shah & Leigh, 1995), as well as investigating the structural and functional attributes of facial fossae, specifically the deep suborbital fossae in the mangabeys. A well supported molecular phylogeny will provide a useful template upon which morphological contrasts between genera and species can be studied.

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