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RESEARCH ARTICLE

Phylogenetic Relationships Among the Lorisoidea As Indicated by Craniodental Morphology and Mitochondrial Sequence Data

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The phylogeny of the Afro-Asian Lorisoidea is controversial. While postcranial data attest strongly to the monophyly of the Lorisidae, most molecular analyses portray them as paraphyletic and group the Galagidae alternately with the Asian or African lorisids. One of the problems that has bedevilled phylogenetic analysis of the group in the past is the limited number of taxa sampled for both ingroup families. We present the results of a series of phylogenetic analyses based on 635 base pairs (bp) from two mitochondrial genes (12S and 16S rRNA) with and without 36 craniodental characters, for 11 galagid and five lorisid taxa. The outgroup was the gray mouse lemur (*Microcebus murinus*). Analyses of the molecular data included maximum parsimony (MP), neighbor joining (NJ), maximum likelihood (ML), and Bayesian methods. The model-based analyses and the combined ''molecules+morphology'' analyses supported monophyly of the Lorisidae and Galagidae. The lorisids form two geographically defined clades. We find no support for the taxonomy of Galagidae as proposed recently by Groves [*Primate Taxonomy*, Washington, DC: Smithsonian Institution Press. 350 p, 2001]. The taxonomy of Nash et al. [*International Journal of Primatology* 10:57–80, 1989] is supported by the combined ''molecules+morphology'' analysis; however, the model-based analyses suggest that *Galagoides* may be an assemblage of species united by plesiomorphic craniodental characters. Am. J. Primatol. 69:6–15, 2007.

Key words: Galagidae; Lorisidae; phylogeny; molecules; morphology

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INTRODUCTION

The relationships between and within the families Lorisidae (pottos and lorises) and Galagidae (galagos or bushbabies) have long been debated [Masters & Brothers, 2002; Masters et al., 2005; Rasmussen & Nekaris, 1998]. The major points of contention are the following:

1. Monophyly of Lorisidae and Galagidae: Both mitochondrial and nuclear sequences, particularly when analyzed using maximum parsimony (MP), have consistently failed to portray the Lorisidae as a clade that is independent of the Galagidae [Porter et al., 1997; Yoder et al., 2001; Roos et al., 2004; Masters et al., 2005]. These results echo those of early immunological and histological studies [reviewed in Masters et al., 2005], and contradict morphological, paleontological, and retroposon evidence against paraphyly [Masters et al., 2005; Roos et al., 2004; Yoder et al., 2001].
2. Subclades within Lorisidae: Nucleotide sequence data consistently support a geographic subdivision of Lorisidae into African (*Arctocebus*, *Perodicticus*) and Asian (*Loris, Nycticebus*) clades [Masters et al., 2005; Roos et al., 2004], whereas morphological [Masters & Brothers, 2002; Schwartz & Tattersall, 1985; Schwartz, 1992] and karyological [De Boer, 1973] data do not.
3. The number of subclades within Galagidae: Nash et al. [1989] divided the living Galagidae into three genera comprising 11 species: *Galago* (including *elegantulus*, *gallarum*, *matschiei*, *moholi*, and *senegalensis*), *Galagoides* (including *alleni*, *demidoff*, *thomasi*, and *zanzibaricus*), and *Otolemur* (including *crassicaudatus* and *garnettii*). Kingdon [1997] recognized the needle-clawed species (*elegantulus*) as a separate genus (*Euoticus*), and elevated seven subspecies and as-yet-undescribed populations to the species level, bringing the total number of species identified to 18. Groves [2001] supported these decisions, and added some species of his own. His taxonomy lists three genera comprising 23 species, three of which are undescribed.
4. The composition of the genera within Galagidae: The enigmatic species *alleni* has been allocated to either *Galago* [Groves, 2001; Zimmermann, 1990] or *Galagoides* [Masters & Brothers, 2002; Nash et al., 1989; Olson, 1979], while molecular analyses have fairly consistently allied it with the greater galagos (*Otolemur*) [Crovella et al., 1994; DelPero et al., 2000; Masters et al., 1994; Roos et al., 2004]. Similarly, *zanzibaricus* was first classified as a subspecies of *G. senegalensis* [Hill, 1953], and reclassified as a species of *Galagoides* [Nash et al., 1989; Olson, 1979]. Zimmermann's [1990] reconstruction allied the species with *Otolemur*; however, in a molecular analysis [DelPero et al., 2000] it was grouped with no other taxa. The needle-clawed *Galago*/*Euoticus elegantulus* shares many cranial features with other *Galago* species, but it is also highly apomorphic, and some morphological analyses placed it as the sister taxon to all other galagids [Masters & Brothers, 2002]. Some of this variable taxonomy is reflected in Table I.

In this paper we investigate these persistent problems using mtDNA sequences and craniodental morphology in the largest taxonomic sample of lorisoids analyzed to date.

MATERIALS AND METHODS

Taxa Included in the Analysis

Table I lists the ingroup taxa included in the analysis. The galagids are listed according to two conflicting classifications, i.e., the assignments of Nash et al.

TABLE I. Ingroup Taxa Included in the Analysis*

Taxa		Specimen source
Lorisidae		
Arctocebus aureus		Franceville, *Gabon*
Perodicticus potto		University of Bochum, Germany
Loris lydekkerianus		Duke Univserity Primate Center
Nycticebus coucang		Duke University Primate Center
Nycticebus pygmaeus		Duke University Primate Center
Galagidae		
Galago elegantulus[1]	*Euoticus elegantulus*[2]	Senckenberg Museum, Germany
Galago matschiei[1]	*Galago matschiei*[2]	Kibara National Park, Burundi
Galago moholi[1]	*Galago moholi*[2]	Gauteng, South Africa
Galago s.braccatus[1]	*Galago s.braccatus*[2]	Somalia, locality unknown
Galago s.senegalensis[1]	*Galago senegalensis*[2]	Stuttgart Primate Facility, Germany
Galagoides alleni[1]	*Galago alleni*[2]	Museum d'Histoire Naturelle, France
Galagoides demidoff[1]	*Galago demidoff*[2]	Duke University Primate Center
Galagoides thomasi[1]	*Galago thomasi*[2]	Parc National du Haut Niger, Guinea
Galagoides zanzibaricus[1]	*Galago zanzibaricus*[2]	Zambezia, Mozambique
Otolemur crassicaudatus[1]	*Otolemur crassicaudatus*[2]	Tübingen, Germany
Otolemur garnettii[1]	*Otolemur garnettii*[2]	Tübingen, Germany

*Galagid Taxonomy According to [1]Nash et al. [1989] and [2]Groves [2001].

[1989] and Groves [2001]. *Microcebus murinus* was chosen as the outgroup based on the comparability of its craniodental characters, as well as the fact that cheirogaleids are widely regarded as the least specialized lorisoids [Martin, 1972], and are believed to approximate the ancestral strepsirrhine condition behaviorally and morphologically [Charles-Dominique & Martin, 1970; Yoder, 1994]. Inclusion of additional lemuroid outgroups did not alter sister-group relationships, but resulted in a significant decrease in clade resolution, suggesting that we had reached the limit of phylogenetic applicability for our molecular data set. Although multiple outgroups are usually desirable, it is not necessary to have more than one outgroup [Nixon & Carpenter, 1993], and we report the results of the *Microcebus murinus* analyses below.

Data Sets Included in the Analysis

The combined molecular data set comprises 389 base pairs (bp) of the variable third domain of the 12s rDNA gene, and 246 bp of the highly variable portion of the 16S rDNA gene. In total, 635 bp were analyzed. To test for heterogeneity in phylogenetic signal among the sequences, we performed a partition homogeneity test [Farris et al., 1994] with 100 replicates on the combined data set, using PAUP* (version 4.0b10 [Swofford, 2003]). For the combined ''molecules + morphology'' analysis, we included 36 craniodental characters, which are described in detail elsewhere [Masters & Brothers, 2002; Masters et al., 2005].

Phylogenetic Analyses

Because there is so little agreement regarding the philosophy of phylogenetic reconstruction, we performed a series of analyses using several tree-building methods, both including and excluding the morphological data.

Maximum parsimony (MP) analyses were conducted both by treating all characters as equally weighted, and by applying different weighting schemes to evaluate the effects of the transition/transversion bias present in the data set. Gaps were treated as missing data. MP analyses were conducted using the exhaustive search strategy, and branch supports were evaluated using 1,000 bootstrap replicates.

A neighbor-joining (NJ) tree was constructed by stepwise clustering of the Tamura-Nei genetic distances [Tamura & Nei, 1993], using the method of Saitou and Nei [1987], which allows for different rates of change.

The most appropriate model of nucleotide evolution for maximum likelihood (ML) and Bayesian analyses was estimated using the likelihood ratio test criterion as implemented in Modeltest 3.06 [Posada & Crandall, 1998] and MrModelTest 2.0 [Nylander, 2004]. Bayesian inferences were performed using MrBayes 3.01 [Huelsenbeck et al., 2001]. Analyses were conducted with four incrementally heated Markov chains (MC3, default heating parameter). Chains were run for 1×10^6 generations, and sampled every 100 generations.

ML and MP analyses were conducted using PAUP* (v.4.0b10 [Swofford, 2003]). NJ trees were obtained using MEGA 3 [Kumar et al., 2004].

RESULTS

The partition homogeneity test revealed no significant conflict between the 12S and 16S rRNA sequences, which were thereafter combined. Of the 635 bp, 396 characters were constant, 69 variable characters were parsimony-uninformative, and 170 were parsimony-informative. For the ML and Bayesian analyses, the best-fitting model of nucleotide evolution was the TrN+γ [Tamura & Nei, 1993] with the following estimated base frequencies: A = 0.39810 C = 0.22960 G = 0.13480 T = 0.23750. Among-site rate heterogeneity followed a gamma distribution (shape parameter $\alpha = 0.2150$).

When all bp were equally weighted, MP yielded a single most parsimonious tree (tree length [tl] = 589, Consistency Index [CI] = 0.5908, Retention Index [RI] = 0.5764, Rescaled Consistency Index [RC] = 0.3406), as illustrated in Fig. 1. The genus *Galago* forms a well-supported clade (83% bootstrap support), within which the needle-clawed ''*Euoticus*'' *elegantulus* is securely nested. *Otolemur* is a valid genus, but *Galagoides* appears to be an assemblage of plesiomorphic species. The monophyly of Lorisidae is lost in this reconstruction. The African pottos appear as the basal divergence to the lorisoid clade, with the Asian lorises as the sister taxon to the Galagidae. Weighting each transversion as equivalent to five transitions removed lorisid paraphyly, but lost resolution higher up the tree. Figure 1b is a consensus of the three most parsimonious trees. While the Lorisidae now form a clade, the relationships between the *Otolemur* and *Galagoides* taxa and the genus *Galago* are unresolved. A weighting scheme of 10:1 once again yielded a single tree, but placed the *G. demidoff–G. thomasi* clade as the sister taxon to the Asian lorisids. Both weighted parsimony searches resulted in lower bootstrap values at all nodes.

NJ (Fig. 2) recovered a galagid clade but failed to find a lorisid clade. As with MP, *Galago* formed a well-supported clade, with *Euoticus* nested within it. The enigmatic *alleni* clustered as the sister taxon to the *Otolemur* species (albeit with low bootstrap support) and *zanzibaricus* was the basal member of this clade.

In contrast, the model-based methods recovered both lorisoid families as monophyletic. In ML, *Euoticus* now formed the most basal divergence of the *Galago* clade (Fig. 3), but in the Bayesian analysis it was in the same position as in

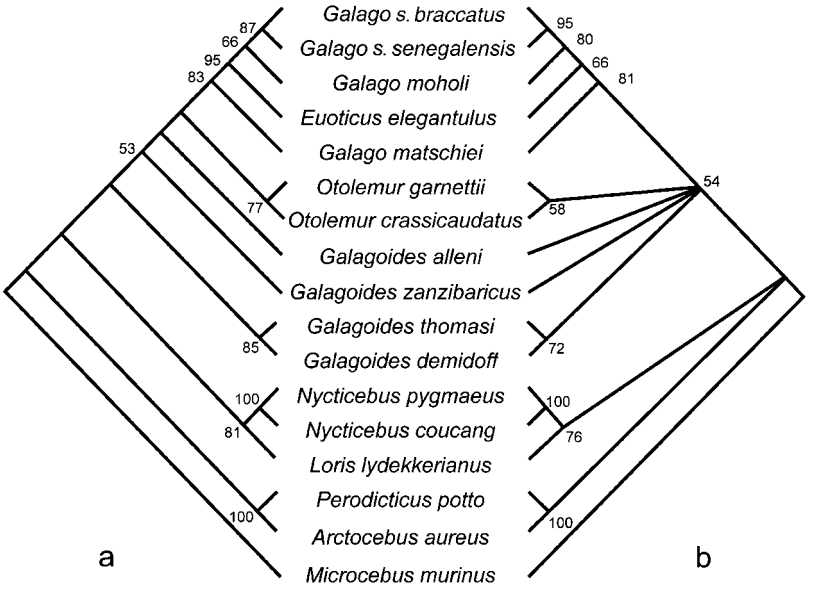

Fig. 1. Trees obtained from the MP analyses of the molecular data sets only. **a**: All characters equally weighted. Tl = 589, CI = 0.59, CI excluding uninformative characters = 0.53, RI = 0.58, RC = 0.34. **b**: Consensus of three trees obtained from MP analysis with a tranversion : transition weighting of 1:5. The numbers represent bootstrap support for the associated node if the values are >50%.

the NJ and MP analyses. The relationships of *alleni* and *zanzibaricus* were the same as for the NJ tree.

The combined ''molecules + morphology'' data set (all characters equally weighted) also recovered two monophyletic families (Fig. 4). The three genera of Nash et al. [1989] can also be justified according to this tree topology.

DISCUSSION

Choosing a Topology

Lack of consensus regarding the most reliable means of reconstructing phylogenies means that our choice of tree topology is heavily influenced by phylogenetic philosophy. There are important (and highly contested) questions that stand to influence that decision:

1. With respect to the molecular data set, which method of phylogenetic inference is preferable: parsimony or likelihood?
2. Should morphological data be included in the primary analysis or not?

We discuss these briefly below:

1. Model-based vs. parsimony-based methods

ML seeks to find the tree topology that confers the highest probability on the observed characteristics of tip species, while MP seeks to find the tree topology that requires the fewest changes in character state to produce the characteristics of those tip species. ML requires the adoption of a model of the evolutionary

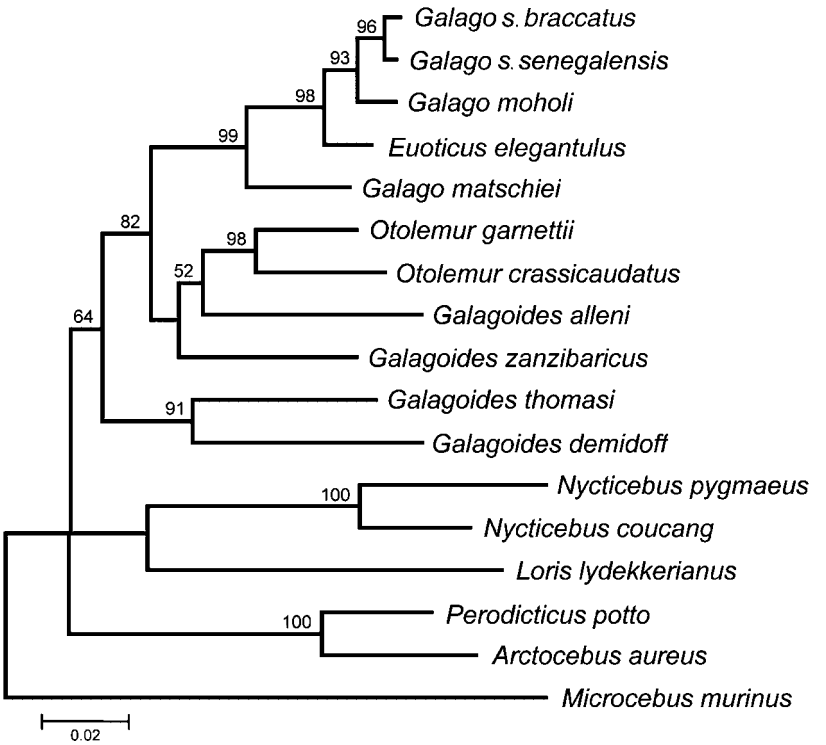

Fig. 2. NJ tree obtained using Tamura-Nei genetic distances. The bootstrap values of internal nodes are indicated if they are $>50\%$.

process that is unlikely to be accurate, whereas the assumptions of MP have been poorly explored [Sober, 2004]. Which is preferable? The answer is far from obvious [Kolaczkowski & Thornton, 2004; Sober 2004; Thornton & Kolaczkowski, 2005].

In our analyses, equally weighted MP analysis of the molecular data set did not recover the lorisid clade, while ML and Bayesian analysis did. An extensive suite of postcranial characters [Masters et al., 2005; Yoder et al., 2001] and retroposon integrations [Roos et al., 2004] afford strong support for this clade. In defense of parsimony methods, the sequences used in our study are short and rapidly evolving. Longer, more evolutionarily stable sequences could yield a different result, although studies to date indicate that mtDNA sequences are unlikely to do so.

2. Should morphological characters be included?

Scotland et al. [2003] argued against the primary inclusion of morphological characters in phylogenetic reconstruction on the grounds that they represent too few unambiguous characters to construct robust phylogenies, and that homologues may be difficult to identify with accuracy. Additionally, those homologues that are readily identified may diagnose nonmonophyletic groups, as, for example, in the case of plesiomorphies.

This suggestion has been vigorously contested by Jenner [2004] and Wiens [2004] as being built on mistaken premises and bound to fail. Morphological data

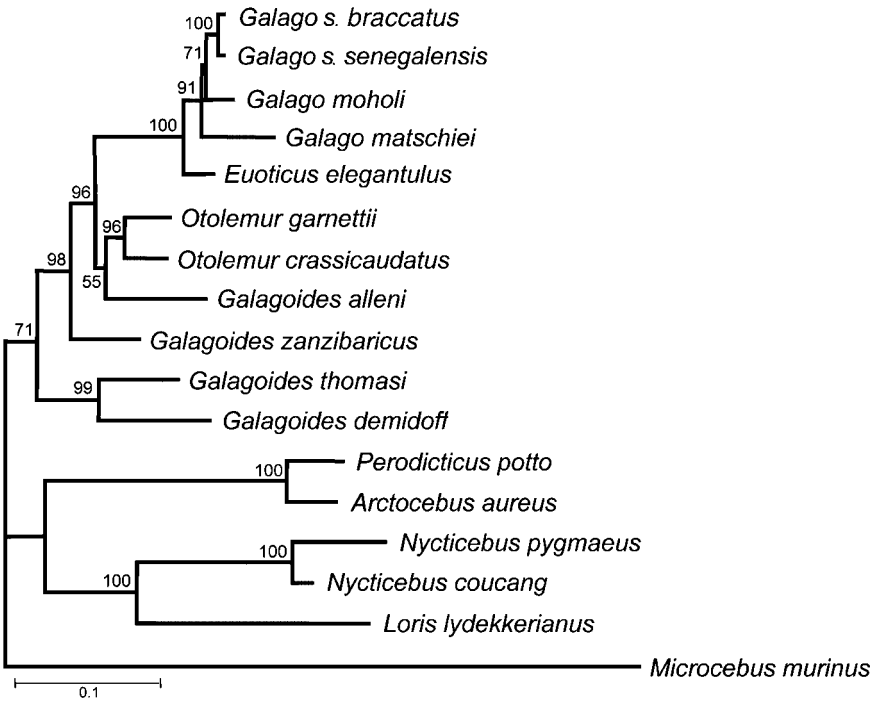

Fig. 3. ML tree (-ln $L = 3375.54350$) obtained for the combined molecular data set. The bootstrap values of internal nodes are indicated if they are $>50\%$.

are crucial for correct identification of specimens, for comprehensive sampling that includes rare taxa, for realistic estimates of macroevolutionary rates and timing, and for the inclusion of fossil information into phylogeny reconstruction. Furthermore, unlike DNA sequences, they provide phylogenetic signal at many phylogenetic levels simultaneously [Jenner, 2004].

In interpreting our results we gave the major weight to the degree of support underlying the various nodes. At deep phylogenetic levels (i.e., the family level in this analysis), the molecular signal became equivocal, while the morphological signal was very strong. At shallower phylogenetic depths, the morphological signal was weak, while the molecular signal became stronger. Applying all of this information to our original questions, we draw the following conclusions:

1. Monophyly of the Lorisidae and Galagidae

According to the molecular data presented here, there is no pressing reason to abandon the Lorisidae and Galagidae clades, which are so strongly supported by morphological characters [Masters et al., 2005; Yoder et al., 2001] and retroposon integrations [Roos et al., 2004], since both of the model-based methods support their monophyly. The combined ''molecules + morphology'' analysis also supports this arrangement.

2. Subclades within Lorisidae

The molecular data are unambiguous in grouping the Lorisidae into two geographically defined subclades–an African and an Asian subclade–as reported previously [Masters et al., 2005; Roos et al., 2004].

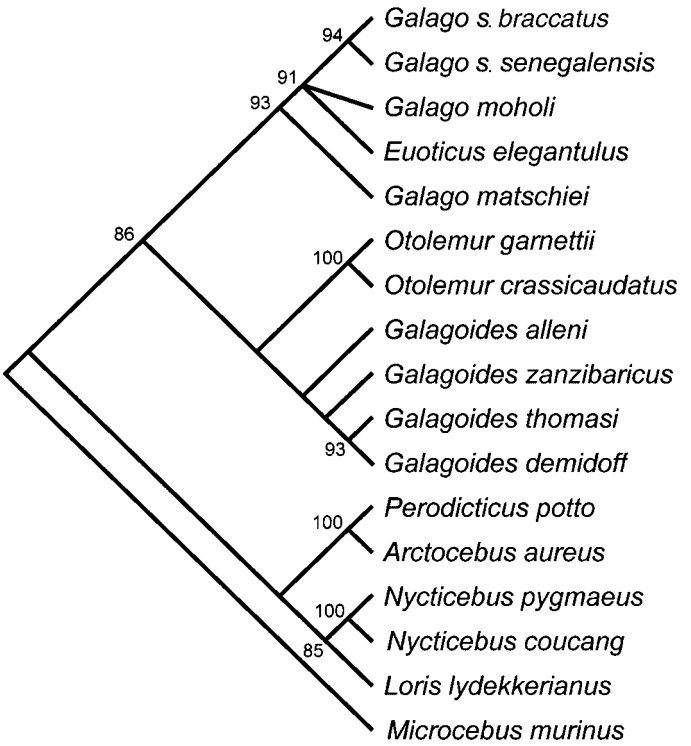

Fig. 4. Consensus of the two most parsimonious trees from the MP analysis of the combined "molecules + morphology" data set. All characters were equally weighted. Tl = 690, CI = 0.57, CI excluding uninformative characters = 0.51, RI = 0.59, RC = 0.33. Bootstrap values >50% are indicated.

3. Number of subclades within Galagidae

The strongest clade supported throughout the study is the genus *Galago*, including *Euoticus*. *Otolemur* is also well supported. *Galagoides* only has coherence when morphological data are included. Even then, the support levels for the nodes are low. Whether this situation will change when more slowly evolving sequences are included remains to be seen. It is also possible that the morphological characters grouping these taxa are plesiomorphic for galagids [Scotland et al., 2003].

4. Composition of the genera within Galagidae

Our analysis indicates with some consistency that *Euoticus* should be downgraded to a subgenus of *Galago*. The composition of this genus should be restricted to the lesser galagos, sensu stricto: *G. elegantulus, G. gallarum, G. matschiei, G. moholi*, and *G. senegalensis*. This is in accordance with the taxonomy of Nash et al. [1989], and in contrast to that of Groves [2001] (see Table I), for which our topologies offer little support. *Galagoides* remains a problem. The large genetic distances between the *G. demidoff–G. thomasi* clade and the remaining taxa suggest to us that this may be a plesiomorphic grouping [DelPero et al., 2000]. If this is true, then *G. alleni* and *G. zanzibaricus* deserve different generic designations. The name given by Gray [1872] to *G. alleni*

(*Sciurocheirus*) is available for this taxon, but there is no name for *G. zanzibaricus*. A new generic diagnosis is therefore required.

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