The Auk 118(4):849–863, 2001

PHYLOGENY AND SYSTEMATICS OF GROUND ROLLERS (BRACHYPTERACIIDAE) OF MADAGASCAR

JEREMY J. KIRCHMAN,[1,3] SHANNON J. HACKETT,[1] STEVEN M. GOODMAN,[1,2] AND JOHN M. BATES[1]

[1]*Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA; and*
[2]*World Wide Fund for Nature, Boite Postale 738, Antananarivo (101), Madagascar*

ABSTRACT.—We studied relationships of five extant members of the endemic Malagasy family Brachypteraciidae, the ground rollers, using several mitochondrial genes (cytochrome-*b*, NADH dehydrogenase 2, 12S ribosomal RNA, and cytochrome oxidase I). As outgroups, we used other coraciiforms including the Cuckoo Roller (Family Leptosomatidae, *Leptosomus discolor*), several true rollers (Corcaciidae) and a tody (Todidae). Partial sequences of the Long-tailed Ground Roller (*Uratelornis chimaera*) were obtained from toe pad samples taken off museum specimens. For a combined data set of all genes, Kimura two-parameter distances between sequences of the five ground roller species were high, averaging 11% divergence. For several species, samples were available from widely separated geographic regions and intraspecific sequence divergence was low (≤0.8%). Unweighted and weighted parsimony and maximum-likelihood analyses consistently recovered monophyly of the family, a sister relationship between Brachypteraciidae and Coraciidae, and monophyly of one of three currently recognized ground roller genera (*Atelornis*). At the base of the Brachypteraciidae clade, we could not fully resolve relationships between *Uratelornis* and two species currently placed in *Brachypteracias*. Because of the uncertainty of basal nodes in our phylogenetic reconstructions, we recommend returning *B. squamigera* to the monotypic genus *Geobiastes*. High levels of divergence among ground rollers are similar to levels found in other avian groups endemic to Madagascar. However, we suggest that molecular divergences appear far too low to be consistent with mid-Eocene fossils attributed to the family. *Received 3 August 2000, accepted 28 February 2001.*

MADAGASCAR LONG HAS commanded attention of biologists with its high level of endemicity and large number of animal groups reputed to be examples of adaptive radiations. The island last was connected to Africa ~160 Mya and to India ~90 Mya (Krause et al. 1997) resulting in a long period of isolation that almost certainly began prior to the evolution of the vast majority of extant bird groups (Feduccia 1999). Thus, it is assumed that ancestors of the modern Malagasy avifauna arrived on the island by dispersal. Given that their affinities are believed to be primarily African (Moreau 1966, Dorst 1972, Keith 1980), dispersal across the 400–550 km passage of the Mozambique Channel between Africa and Madagascar is the most likely explanation for the island's colonization. Phylogenetic work on Malagasy bird groups (Prum 1993, Houde et al. 1997, Cibois et al. 1999, Fjeldså et al. 1999, Johnson et al. 2000) has begun to produce a clearer picture of the island's avifaunal history, but further phylogenetic analyses are necessary to better understand factors that have shaped Madagascar's extraordinary endemicity.

In recent years, there has been a dramatic increase in number of field researchers conducting ecological studies on Malagasy birds, particularly the endemic radiations. Reconstructing phylogenies and testing monophyly of such groups is critical to understanding their evolutionary history. An example is the ground rollers (Brachypteraciidae), which have been the subject of several ecological studies (Appert 1968, Turner 1984, Rakotoarisoa 1998, 1999; Razafimahaimodison 1995, Thorstrom and Lind 1999). This family long has been allied to the African "true" rollers (Coraciidae), but little is known regarding their phylogeny.

Ground rollers currently are recognized as a family (Brachypteraciidae, Order Coraciiformes) endemic to Madagascar with five extant species placed in three genera (Wetmore 1960, Sibley and Monroe 1990). All species are forest-dwelling with four forms (*Atelornis crossleyi, A. pittoides, Brachypteracias leptosomus,* and *B. squa-*

[3] E-mail: n8urebug@prodigy.net

migera) occurring in humid forests dominating east and central highlands, and the fifth species (*Uratelornis chimaera*) in the spiny bush of the dry southwest (Langrand 1990). Both Brodkorb (1971) and Olson (1985) noted that there is no known fossil history of ground rollers. However, well-preserved material from the Eocene Messel Formation of Germany was said by Martin (1983) and Feduccia (1999) to contain an example of the Brachypteraciidae. Feduccia also described Eocene material from the North American Green River formation as reminiscent of ground rollers. More recently, subfossil material of the family has been recovered from Holocene deposits on Madagascar (Goodman 2001).

Ground rollers first were considered a distinct family (Atélornithinés) by Chenu and des Murs (1852), who placed them at the beginning of the suboscine passerines on the basis of tarsal and foot characters. The name "Atelornithidae," therefore, has priority over the name "Brachypteraciidae Bonaparte, 1854." However, the latter name has been widely used in ornithological literature, and for the sake of stability we follow Bock's (1994) recommendation that it be maintained. Ground rollers are now universally placed in the Coraciiformes and are considered by some authorities to be a subfamily of the Coraciidae (e.g. Peters 1945). Although ground rollers differ markedly from coraciids in their behavior, plumage, and postcranial skeleton, the two groups are very similar in their cranial osteology (Cracraft 1971) and in elements of the feeding apparatus (Burton 1984).

Early classifications of the family differed primarily with respect to the treatment of *Brachypteracias squamigera*, which also was placed in *Atelornis* (Chenu and des Murs 1852, Hartlaub 1861) and in the monotypic genus *Geobiastes* (Sharpe 1871, Hartlaub 1877). However, taxonomy within the family has been stable since the last extant form, *Uratelornis chimaera*, was described in 1895.

Cracraft (1971) examined cranial and postcranial skeletal anatomy in the families Coraciidae (true rollers), Leptosomatidae (Cuckoo Roller [*Leptosomus discolor*]), and in three species of ground rollers (both species of *Atelornis* and *Brachypteracias leptosomus*). He concluded that the Coraciidae is the sister taxon of ground rollers and that the monotypic Leptosomatidae is the sister of that clade. Although Cracraft's study primarily was concerned with interfamilial relationships, he did include a hypothesis of phylogeny and "adaptive pathways" within the ground roller lineage. He proposed that *Atelornis* "is probably more advanced from the primitive ground roller condition" exemplified by *Brachypteracias*, and that "*Uratelornis* is unmistakedly closer to *Atelornis* than to *Brachypteracias*" (Cracraft 1971:748). Although Cracraft did not examine characters in a cladistic framework, his work is the only modern study to examine relationships within the family. Cracraft's conclusions formed the foundation of higher level relationships among roller families in Maurer and Raikow's (1981) examination of hindlimb myology within Coraciiformes and in Sibley and Ahlquist's (1990) DNA–DNA hybridization work, both of which lacked a representative of ground rollers. The dearth of comparative material in museums, particularly skeletons and tissues, has hampered, until recently, further phylogenetic investigation.

The primary goal of our study was to use DNA sequence data from newly available tissue samples and recently developed "antique" DNA protocols to estimate relationships of extant ground rollers and their roller allies. In addition, we characterize patterns of evolution in four mitochondrial genes increasingly used to reconstruct phylogeny and discuss rates of molecular evolution by comparing our data to the fossil record of rollers. Finally, we present a classification of extant ground rollers.

METHODS

Taxa examined.—We compared mtDNA sequences from the following coraciiform species (number of individuals in parentheses): ground rollers *Atelornis pittoides* (5), *A. crossleyi* (3), *Brachypteracias leptosomus* (2), *B. squamigera* (1), *Uratelornis chimaera* (2); the Cuckoo Roller (Family Leptosomatidae), *Leptosomus discolor* (1); the true rollers (Family Coraciidae) *Eurystomus orientalis* (1), *E. glaucurus* (1), *Coracias garrulus* (1); and the Jamaican Tody (Family Todidae), *Todus todus* (1). In this paper, we use the term "rollers" to refer to all members of the Brachypteraciidae, Coraciidae, and Leptosomatidae collectively. For all taxa except *Uratelornis chimaera*, tissue samples were preserved in salt-DMSO buffer (Seutin et al. 1991) or in liquid nitrogen at the time of specimen preparation and later stored in the collection of genetic resources of the Bird Division, Field Museum of Nat-

TABLE 1. Primers used in PCR amplification and sequencing of four mitochondrial genes. H and L refer to primers located on the heavy and light strands of the mitochondrial genome, respectively, and numbers refer to the 3′ base of the primer referenced to the complete mtDNA sequence of the chicken (*Gallus gallus*; Desjardins and Morais 1990).

Cyt *b*	5′ → 3′ sequence	Reference
L-14990	CCATCCAACATCTCAGCATGATGAAA	Modified from Kocher et al. 1989
L-15656	AACCTACTAGGAGACCCAGA	Helm-Bychowski and Cracraft 1993
L-15920	ACATGAGTCGGAAGCCAACC	Helm-Bychowski and Cracraft 1993
L-15311	CTACCATGAGGACAAATATC	Helm-Bychowski and Cracraft 1993
H-15424	GGAGGAAGTGCAGGGCGAAGAATCG	Hackett 1996
H-15712	GGCGTATGCAAATAGGAAGTA	FMNH lab primer[a]
H-16065	GGAAGTCTTCAGTCTCTGGTTTACAAGAC	Helm-Bychowski and Cracraft 1993
ND2		
L-5208	CTAATAAAGCTTTCGGGCCCATAC	FMNH lab primer[b]
L-5562	GCAATTTCAATTAAACTAGG	FMNH lab primer[a]
L-5360	CTAGAAATCAACACCCTMGCCA	FMNH lab primer[c]
H-6315	TTCTACTTAAGGCTTTGAAGGC	FMNH lab primer[b]
H-5804	GAGAATAATGGTTATTCATCC	FMNH lab primer[a]
H-5477	TCTCATTGTCCTGTGTGTCA	FMNH lab primer[c]
H-5363	TGGGATTTTGAGATAAGTGGGAT	FMNH lab primer[c]
12S		
L-1746	GCTTCAAACTGGGATTAGATACC	Modified from Kocher et al. 1989
L-1895	TAATCGATAACCCACGATGC	FMNH lab primer[c]
L-2010	AAGACAGGTCAAGGTATAGC	FMNH lab primer[c]
H-2152	GCAGAGGGTGACGGGCGGTGTGT	Modified from Kocher et al. 1989
H-2020	GAAAATGTAGCCCATTTCTTCC	FMNH lab primer[c]
CO I		
CO I E (H7827)	CCAGAGATTAGAGGGAATCAGTG	Modified from Palumbi 1996
CO I F (L7327)	CCTGCAGGAGGAGGAGAYCC	Modified from Palumbi 1996

[a] Designed by S.J.H. from an alignment of a wide range of avian taxa.
[b] Designed by John Hall from an alignment of vertebrate taxa.
[c] Designed by J.J.K. from an alignment of ground rollers for amplifying small fragments in *Uratelornis*.

ural History. Collection localities and voucher specimen information are listed in the Appendix.

DNA extraction and sequencing.—DNA was extracted from frozen tissues using a Puregene DNA isolation kit (Gentra Systems, Minneapolis, Minnesota) following the manufacturer's animal tissue protocol but with an overnight proteinase K incubation at 55°C and with final dilution of DNA in pure water. For *Uratelornis chimaera,* DNA was obtained from small clippings of toe-pad tissue from museum skins supplied by the American Museum of Natural History, New York, and the Muséum National d'Histoire Naturelle, Paris, using a QIAamp DNA mini kit (Qiagen Inc., Valencia, California) following the manufacturer's tissue protocol and modifications suggested by Mundy et al. (1997) including overnight proteinase K incubation at 55°C and processing of negative extraction controls to highlight potential contamination. Final DNA elution was accomplished by twice adding 100 μL of the kit's elution buffer prewarmed to 70°C and allowing this to sit for 5 min at 70°C before removal.

Portions of the cytochrome-*b* (hereafter cyt *b*), NADH dehydrogenase 2 (ND2), 12S ribosomal RNA, and cytochrome oxidase I (CO I) genes were isolated and amplified by polymerase chain reaction (PCR) using the primers in Table 1. PCR products were electrophoresed in 1.5% agarose gels, stained with ethidium bromide, and visualized under UV light. Reactions containing a single band of the desired size were purified and concentrated in Microcon 100 (Amicon Inc., Beverly, Massachusetts) spin-columns. Purified PCR products were sequenced directly using a cycle-sequencing protocol and Big Dye (PE-Biosystems, Forest City, California) chemistry and were resolved on an automated sequencer (PE-Biosystems ABI 377, Forest City, California). For each gene, nucleotide sequences were determined for both DNA strands. Overlapping sequences were assembled into a verified consensus for each individual using the program SEQUENCHER (version 3.1, Gene Codes Corp., Ann Arbor, Michigan). Alignments of homologous nucleotides for all genes were constructed using Clustal W 1.5 (Thompson et al. 1994) and were verified by visual comparison to the published mitochondrial genome for the chicken (*Gallus gallus*; Desjardins and Morais 1990). Alignment of the 12S gene also was verified by comparison with a secondary structure model proposed for *Falco peregrinus* (Mindell et al. 1997).

Sequence analyses.—We used the computer program PAUP* (beta version 4.0b4; Swofford 1998) to calculate base frequencies, site variation, pairwise genetic distances (uncorrected *P,* Tamura-Nei, and

TABLE 2. Percent nucleotide composition, nucleotide variability at 1st, 2nd, and 3rd codon position (protein-coding genes) and in loops and stems (rRNA gene), and amino acid variability for all taxa in the Appendix.

					Nucleotides			Amino acids		
	A	C	G	T	Total	Variable	Informative	Total	Variable	Informative
CO I	25.8	29.1	17.1	28.0	510	155	111	169	9	1
1st	24.3	19.9	31.9	23.9	170	16	5			
2nd	18.8	22.8	16.0	42.4	170	1	0			
3rd	34.3	44.5	3.5	17.7	170	138	106			
Cyt *b*	27.1	35.8	12.3	24.8	1045	392	236	348	76	36
1st	25.6	30.4	21.2	22.8	348	76	43			
2nd	20.1	25.8	13.6	40.5	348	35	12			
3rd	35.6	51.2	2.1	11.1	349	281	181			
ND2	30.8	36.0	10.0	23.2	1038	479	341	346	129	76
1st	35.4	30.7	15.4	18.5	346	128	81			
2nd	17.1	35.6	9.2	38.1	346	53	30			
3rd	39.9	41.7	5.3	13.1	346	298	230			
12S	31.3	29.5	21.2	18.0	397	125	76			
Stems	24.1	28.8	26.4	20.7	234	62	32			
Loops	42.3	29.2	14.7	13.8	163	63	44			

Kimura two-parameter), and likelihood ratio tests of clock-like evolution. We also used PAUP* to compute partition homogeneity tests (500 replicates with uninformative characters removed) to determine if data from different genes suggested different phylogenetic signals. Phylogenetic trees and tree statistics (Consistency Index, Homoplasy Index, and Retention Index) were generated in PAUP* using branch-and-bound searches under criteria of maximum parsimony (MP) and maximum likelihood (ML). Support for nodes was assessed by bootstrapping (100 replicates). We used the program MODELTEST (version 3.0 beta2; Posada and Crandall 1998) to evaluate models of DNA sequence evolution for input into ML analyses. MODELTEST performs likelihood ratio tests on nested models of DNA substitution. Evaluation begins with the simplest model of substitution (Jukes and Cantor 1969); parameters are subsequently added (increasing complexity of the substitution matrix, and including estimating invariant sites and a gamma distribution of rates for variable sites), and likelihood-ratio tests performed after each added parameter. The model of DNA sequence evolution that minimized parameters without significantly improving likelihood scores was input into detailed maximum-likelihood tree searches.

RESULTS

We obtained partial sequences from cyt *b*, ND2, CO I, and 12S resulting in a total alignment (12S alignments are deposited in The Field Museum Archives and are available from the authors on request) of 3,007 nucleotides for 13 individual ground rollers and 5 outgroup taxa (see Appendix). From the dried foot tissue of *Uratelornis*, we obtained 337 bases of cyt *b* (MNHN specimen only), 414 (MNHN) and 255 (AMNH) bases of 12S, and 359 (MNHN) and 219 (AMNH) bases of ND2. All sequences were deposited in GenBank as accessions AF407420–AF407487. Sequences for protein-coding genes contained no insertions, deletions, or stop codons; 12S sequences closely matched known avian secondary structure (Mindell et al. 1997). Two regions of 12S totaling 15 bases could not be aligned unambiguously and were not considered further in phylogenetic analyses. The total number of aligned bases analyzed for each gene as well as base frequencies are listed in Table 2.

Sequences of the cyt *b* gene of two individuals were found to be anomalous and were not included in phylogenetic analyses. Sequence chromatograms were consistently unreadable from single specimens of *Brachypteracias leptosomus* (FMNH 384731) and *Atelornis crossleyi* (FMNH 384704) despite the fact that PCR reactions contained a single band of the expected size. To determine the reason for lack of sequence resolution, we cloned PCR products from both individuals. We ligated unpurified PCR products into Bluescript (Stratagene, La Jolla, California) plasmid vector cut with EcoR V using T4 ligase (Promega, Madison, Wisconsin). Colonies of plasmid-transformed competent cells were grown on selective medium. We extracted DNA from as many as 10 colonies and cycle-sequenced cyt *b* from them as de-

scribed above. Sequences from multiple clones revealed presence of multiple versions of cyt *b* in PCR products from each sample, and we did not include cyt *b* sequences from those individuals in any analysis (see below).

Base compositional biases were observed for ground rollers and allies that are typical for mitochondrial protein-coding genes. Cytosine greatly outnumbered guanine at all codon positions in cyt *b*, ND2 and in 2nd and 3rd positions of CO I (Table 2). That bias was greatest at 3rd positions in all three genes. ND2 exhibited highest overall compositional bias (G = 10.0%), but at 3rd positions cyt *b* had the highest skew (G = 2.1%). Proportion of variable sites in protein-coding genes (including all outgroups) ranged from 30.4 (CO I) and 37.5 (cyt *b*) to 46.1% (ND2). Patterns of variability among codon positions matched those found in other vertebrates in that 3rd positions were most variable followed by 1st positions and then 2nd positions. That differential variability was greatest for CO I in which 89% of variable sites were 3rd positions compared to only 0.6% for 2nd positions (Table 2). Comparisons between structural components of 12S indicated that reciprocally pairing stems and single-stranded loops are equally variable, but that loops are more compositionally biased. Protein-coding genes demonstrated a range of variability in amino acid substitutions, with ND2 exhibiting the most variability and CO I the least (Table 2).

Pairwise genetic distances calculated using correction for back mutations of Tamura and Nei (1993) had means of 0.3% (range = 0.1–0.8) for comparisons among individuals of the same species, 11.0% (8.8–13.9) among species of ground rollers, and 19.1% (18.8–24.8) for comparisons among ground rollers and other coraciiforms. Mean divergence among all rollers and *T. todus* was 21.8%. That trend can be seen in discrete gaps along the abscissa of the plots in Figure 1 and in the branch lengths on the phylogram in Figure 2. Mean Kimura two-parameter divergence among species of *Atelornis* was 8.9%, whereas species of *Brachypteracias* differed by 12.5%, a value greater than the mean for intergeneric comparisons in the family (10.9%, Table 3). Plots of Tamura-Nei distances versus uncorrected pairwise divergences in various partitions of data highlight differences between transitions and transversions as well as differences among codon positions and structural elements of the four genes (Fig. 1). In all genes, transitions accumulate more quickly than transversions. Among data partitions, all elements appear to be linear with the exception of third position transitions and, to a lesser extent, transitions occurring in loops, both of which may be saturated in comparisons among genera and families.

Phylogenetic analyses.—Results of partition homogeneity tests indicate that there is not significantly conflicting phylogenetic signal among all four genes (P = 0.15) nor between protein-coding genes versus 12S (P = 0.69); we combined the data into a single large set for phylogenetic analyses. Unweighted (or equal-weighted) maximum-parsimony (MP) analysis of all 2,992 unambiguously aligned characters for 18 individuals yielded six shortest trees (2,319 steps), all of which differed only with respect to relationships among individuals within species (Fig. 2). Bootstrap support for this topology is high for nodes indicating monophyly of *Atelornis*, Brachypteraciidae, *Eurystomus*, Coraciidae, and ground rollers plus true rollers. There is also moderate bootstrap support for *Uratelornis* plus *Brachypteracias squamigera* and *Atelornis* plus *B. leptosomus*, indicating paraphyly of *Brachypteracias*. In general, the MP tree is most weakly supported at nodes connecting ground roller genera at the base of the family. Lack of resolution of intergeneric nodes is common in family-level bird phylogenies based on mitochondrial DNA sequences (Sheldon et al. 1999), a pattern that has prompted much consideration of weighting of characters (Voelker and Edwards 1998). For that reason and because saturation plots (Fig. 1) indicated that 3rd position transitions are likely to exhibit a large amount of homoplasy, we performed a series of analyses under various weighting schemes on a data set pruned to a single individual from each species. Figure 3 shows the topology that resulted from MP analyses in which we downweighted 3rd position transitions by factors of 2, 5, 10, and 50. Each weighted analysis produced the same most parsimonious tree, but with differing levels of bootstrap support. This tree also places *B. squamigera* with *Uratelornis*, but differs from the unweighted tree (Fig. 2) in that it places *B. leptosomus* as the basal member of ground roll-

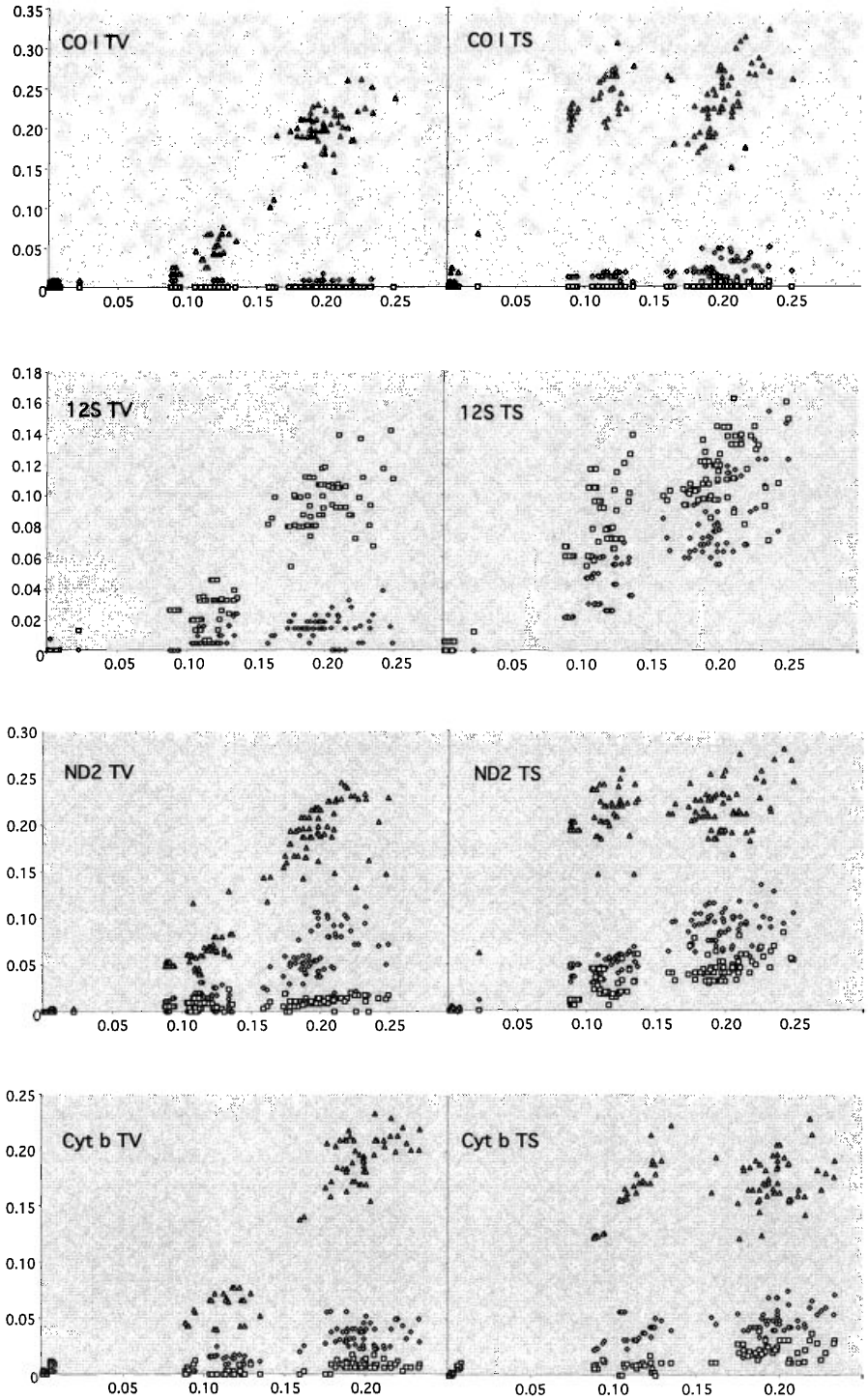

FIG. 1. Tamura-Nei distances (abscissa) versus uncorrected (*P*) distance (ordinate) for transitional (TS) and transversional (TV) pairwise changes among all individuals at 1st (diamonds), 2nd (squares), and 3rd (triangles) codon positions and in loops (squares) and stems (diamonds) of 12S.

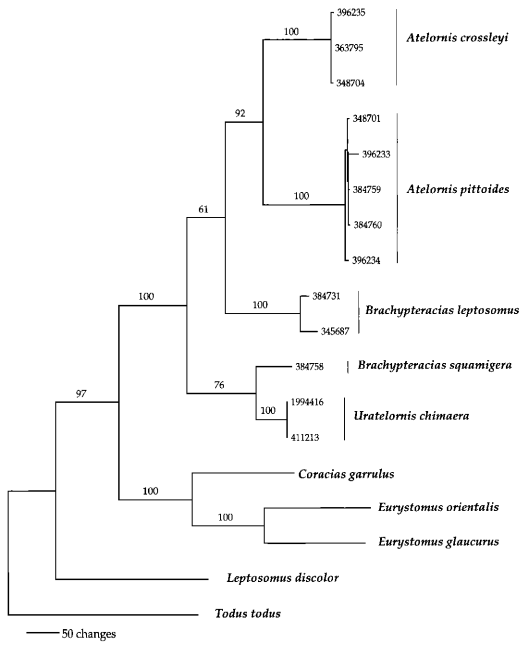

FIG. 2. Phylogeny of ground rollers and allies based on maximum-parsimony analysis of 2,992 equally weighted characters from four mitochondrial genes (one of six trees of length 2,319, other trees differ in relationships among individuals within species). Numbers above branches refer to bootstrap support (100 replicates). Numbers at branch tips identify individuals by voucher specimen number as in Appendix. Branch lengths are proportional to number of nucleotide substitutions with scale bar equal to a length of 50 changes.

ers. Bootstrap support is low for both of these nodes.

Analysis of the pruned data set using the MODELTEST program indicated that our data are best fit by a general-time-reversible model (6 substitution types, R[A–C] = 2.68, R[A–G] = 12.6727, R[A–T] = 2.20, R[C–G] = 0.72, R[C–T] = 17.68, R[G–T] = 1.00), in which proportion of sites assumed to be invariable was 0.50, and in which rates for variable sites followed a gamma distribution with a shape parameter of 1.30. Maximum-likelihood (ML) analysis of the pruned data set under the above model produced a tree with a negative natural-log likelihood of 13529.44 (Fig. 4). That tree differs from parsimony analyses in suggesting monophyly of *Brachpteracias*; however, that node receives <50% bootstrap support. The likelihood topology is consistent with both unweighted and weighted parsimony trees when nodes

TABLE 3. Pairwise gene sequence divergences for ground rollers, rollers, and other endemic Malagasy groups.

Pairwise comparison (No. species)	Mitochondrial divergence (model[a])	Genes	Reference
Atelornis (2)	0.089 (K2), 0.083 (*p*)	ND2, CO I, cyt *b*, 12S	This study
Brachypteracias (2)	0.125 (K2), 0.119 (*p*)	ND2, CO I, cyt *b*, 12S	This study
Eurystomus (2)	0.115 (K2), 0.110 (*p*)	ND2, CO I, cyt *b*, 12S	This study
Neodrepanus (2)	0.145 (K2)	ND3, ATPase6	S. Hackett et al. unpubl. data
Among Brachypteraciidae genera (5)	0.010–0.125 (K2)	ND2, CO I, cyt *b*, 12S	This study
	0.094–0.112 (*p*)		
Among Coraciidae genera (3)	0.142–0.157 (K2)	ND2, CO I, cyt *b*, 12S	This study
	0.140–0.143 (*p*)		
Among Philepittinae genera (4)	0.186–0.198 (K2)	ND3, ATPPase6	S. Hackett et al. unpubl. data
Brachypteraciidae (5) to Coraciidae (3)	0.165–0.202 (K2)	ND2, CO I, cyt *b*, 12S	This study
	0.154–0.179 (*p*)		
"*Oxylabes* groups" (4) to non-Malagasy sylviids (12)	0.0749–0.1533 (*p*)	16S, cyt *b*	Cibois et al. 1999
Coua (6) to other cuckoos (20)	0.20–0.28 (*p*)	ND2	Johnson et al. 2000
Mesitornis (1) to other gruiforms (16)	0.122–0.208 (K2)	12S	Houde et al. 1997
Avian species in 88 genera	0.020–0.160 (K2)	cyt *b*	Johns and Avise 1998

[a] K2 = Kimura two parameter, *p* = uncorrected or "global" distance.

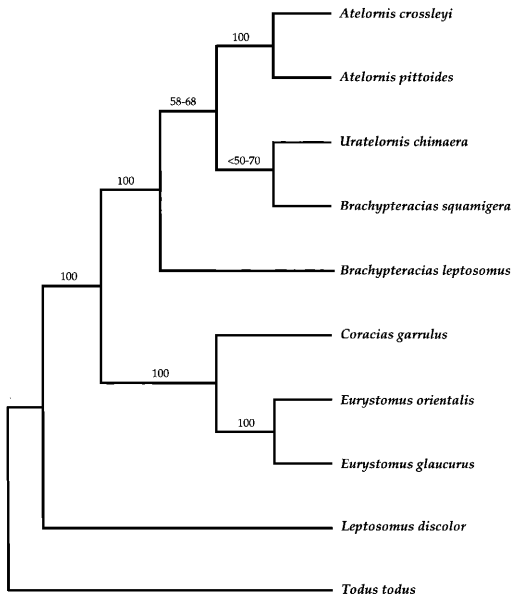

FIG. 3. Relationships of roller species determined by maximum parsimony with third position transitions downweighted by factors of 2, 5, 10, and 50. Each weighted-parsimony analysis produced one tree (lengths = 2,278, 5,311, 9,109, 39,469, respectively). Range of bootstrap support for nodes is presented above the nodes.

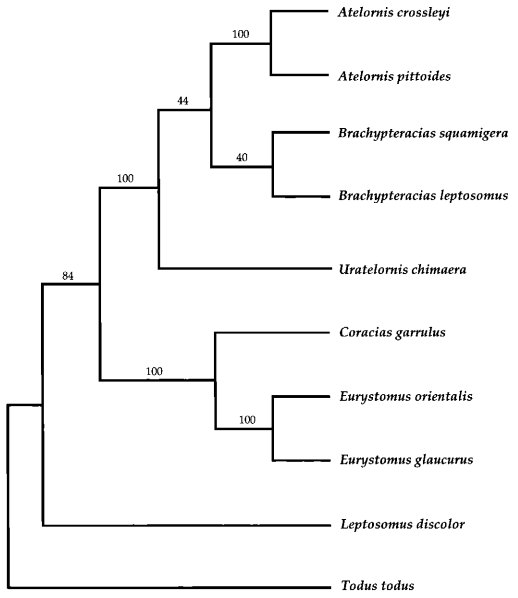

FIG. 4. Maximum-likelihood analysis under a GTR + I + G model (see text for more details). The topology shown has a −ln likelihood score = 13529.44. Numbers above branches refer to bootstrap support (100 replicates).

supported by <50% bootstrap are collapsed. Unfortunately, that level of scrutiny leaves many nodes within the family unresolved, supporting only monophyly of *Atelornis* and Brachypteraciidae. A likelihood-ratio test of clock-like evolution rejects possibility of a molecular clock in the combined-gene, pruned data set ($P < 0.05$). Results are similar ($P < 0.05$) when the five ground roller species are excluded from the test, but when the three true roller species are excluded, a molecular clock can not be rejected ($P > 0.05$). That result may indicate a difference in rate of evolution of those genes between Brachypteraciidae and Coraciidae, but it should be noted that the power of the test to reject a hypothesis of clock-like evolution may be compromised by reducing number of taxa.

DISCUSSION

Anomalous sequences.—In two individuals, PCR products obtained with cyt *b* primers were discovered to contain two copies of the gene. In both cases, the two copies, despite having >20% sequence dissimilarity, appeared to be functional genes on the basis of the fact that protein translations contained no stop codons or gaps. We initially suspected that we had coamplified a nuclear homologue of cyt *b* in those individuals because such sequences are known to be taxonomically ubiquitous (reviewed in Quinn 1997) and because nuclear copies of mitochondrial genes do not necessarily contain insertions, deletions, or stop codons (Sorenson and Fleischer 1996). However, in investigating highly divergent sequences for similarity to sequences deposited in GenBank using the BLAST search program (Altschul et al. 1997), we uncovered a pattern that indicates the source of multiple copies may be low-level contamination of tissue samples. The BLAST search of the *B. leptosomus* sequences indicated that one version of cyt *b* (which was more similar to other ground roller cyt *b* sequences) was a close match with other coraciiforms in the database, whereas the other version shared 99% sequence similarity with *Oxylabes madagascariensis*, a passerine bird endemic to Madagascar. The BLAST of *A. crossleyi* also indicated that one of the sequences was most similar to coraciiforms but that the highly divergent sequence shared 100% similarity with *Eliurus mi-*

nor, a murid rodent endemic to Madagascar. Field notes of the collector indicate that tissues of the passerine and the rodent had been collected immediately prior to the preparation of the *B. leptosomus* and *A. crossleyi* specimens (respectively). Because the biochemical studies of *Oxylabes* and *Eliurus* were carried out in different labs, we can only conclude that the samples had been contaminated in the field. We speculate that the contaminant was in low concentration because it did not amplify in PCR for other genes. Further, we believe that the very quality of cyt *b* that makes it attractive to systematists—namely, its ability to be amplified via PCR using highly conserved primers—may explain why that gene and not the others highlighted the contamination.

Patterns of gene evolution.—Base compositional biases of mitochondrial protein-coding genes (mostly cyt *b*) have been reported from at least 15 avian families in seven orders (e.g. Ciconiidae *in* Slikas 1997, Hirundinidae *in* Sheldon et al. 1999, Anatidae *in* McCracken et al. 1999, data from 11 families reviewed by Moore and DeFilippis 1997). The pattern of bias observed in the present study conforms to that found in other birds and strengthens the conclusion that base composition varies little among taxa. It has been reported that for cyt *b,* the highest intertaxon compositional variation is that seen in 3rd position A and C (Edwards et al. 1991, Moore and DeFilippis 1997). Our values of A = 35.6% and C = 51.2% for cyt *b* third positions (Table 2) are closest to values Moore and DeFilippis (1997) reported for Galliformes and were closer, in general, to proportions found in nonpasserines than in passerines.

We compared the phylogenetic signal contained in each of the four genes by constructing MP trees based on single genes and by calculating indices of consistency (CI), homoplasy (HI), and retention (RI) (Table 4). Trees based on individual genes (not shown) were congruent with one another and with the MP and ML trees based on all genes (Figs. 2, 3, and 4) with respect to intraspecific and interfamilial relationships. However, gene trees differed by placing different ground roller species as basal members of the Brachypteraciidae, thus echoing differences among weighted and unweighted MP and ML trees based on the complete data set. The CO I tree also differed by placing *Coracias* with *Leptosomus* rather than *Eurystomus.* Failure of CO I to recover coraciid monophyly may be due to its high level of homoplasy as indicated by CI and HI (Table 4), though in general, all four genes exhibited similar scores. Calculations of parsimony-informative amino acid variation for the protein-coding genes (Table 2) indicate that the three protein-coding genes we sampled exhibit a wide range of amino acid constraint. For example, 37.3% of the amino acid residues in ND2 are variable, whereas only 5.3% of amino acid resides were variable in CO I (Table 2). Conservation of amino acid residues in CO I might suggest that the gene should be informative at higher taxonomic levels. However, CO I appeared to be a poor source of phylogenetic information for higher-level comparisons because the vast majority of informative sites occur at 3rd positions (Table 2) which quickly become saturated (Fig. 1). Thus, nucleotide variation in CO I is structured such that little information remains to resolve divergent nodes.

TABLE 4. Statistical comparisons of phylogenetic signal among four mitochondrial genes and among codon positions. Values in parentheses exclude uninformative characters.

	CI	HI	RI
ND2	0.6761 (0.5929)	0.3239 (0.4071)	0.5157
1st position	0.7707 (0.6713)	0.2293 (0.3287)	0.6519
2nd position	0.6914 (0.5370)	0.3086 (0.4630)	0.5536
3rd position	0.6511 (0.5845)	0.3489 (0.4155)	0.4832
Cyt *b*	0.6936 (0.5933)	0.3064 (0.4067)	0.6356
1st position	0.7705 (0.6706)	0.2295 (0.3294)	0.6889
2nd position	0.8780 (0.7222)	0.1220 (0.2778)	0.8184
3rd position	0.6695 (0.5792)	0.3305 (0.4208)	0.6248
CO I	0.6133 (0.5362)	0.3867 (0.4638)	0.4599
1st position	0.9375 (0.8000)	0.0625 (0.2000)	0.8333
2nd position	1.0000 (---[a])	---[a] (---[a])	---[a]
3rd position	0.5994 (0.5353)	0.4006 (0.4647)	0.4589
12S	0.6652 (0.5460)	0.3348 (0.4540)	0.5595
All data	0.6681 (0.5765)	0.3319 (0.4235)	0.5065

[a] The 2nd codon position in CO I contained no informative characters.

Phylogeny and classification.—Trees based on unweighted parsimony analysis of all characters from all individuals (Fig. 2) generally were well resolved for relationships both within ground rollers and among roller families. The topology of this tree is consistent with trees constructed with weighted parsimony (Fig. 3) and maximum-likelihood criteria (Fig. 4) with respect to monophyly of *Atelornis,* and the sister relationship of Brachypteraciidae to Coraciidae. The two parsimony trees further agree

in that *B. squamigera* is sister to *Uratelornis*. Although a single analysis (Fig. 4) supports a monophyletic *Brachypteracias*, that node is extremely poorly supported as assessed by bootstrap support. Despite using weighted parsimony and maximum likelihood analyses, basal relationships among ground rollers are not well resolved. This result is consistent with Voelker and Edwards' (1998) suggestion that problems that plague family-level avian phylogenies may prove resistant to improvement via character weighting.

Cracraft's (1971) statement that *Uratelornis* is closer to *Atelornis* than to *Brachypteracias* is not supported by our genetic data. However, Cracraft's contention that *Brachypteracias* represents the primitive condition in the family may have merit if one limits that interpretation to species from which he had skeletal material, namely *B. leptosomus*. Weighted-parsimony analyses suggest *B. leptosomus* as the basal member of the family. Our analyses support evidence from osteology (Cracraft 1971) and anatomy of the feeding apparatus (Burton 1984) that true rollers plus ground rollers are a clade. Our taxonomic sampling does not allow us to specify placement of Leptosomatidae within the Coraciiformes except to say that it is outside the other two roller families.

In proposing a phylogenetic classification for ground rollers based on our analyses of mitochondrial DNA, we were faced with having to choose between a treatment that would lump all five species into a single genus or a treatment that would place five species in four genera (*Atelornis* being the only clearly defined clade within the group). We reject the current classification in which *Brachypteracias* includes *squamigera* and *leptosomus* because only one weakly supported analysis indicates a monophyletic *Brachypteracias*. All other analyses specifically reject *Brachypteracias* monophyly; therefore, leaving *Bracypteracias* to include *squamigera* and *leptosomus* may be positively misleading on the basis of the phylogenetic results of our data. We feel it is more conservative and informative to place *squamigera* in a separate genus from *leptosomus*. That classification appropriately reflects uncertainty of basal relationships in the family and lack of support for a monophyletic *Brachypteracias*. It also would not conflict with a sister relationship between *leptosomus* and *squamigera* if such a relationship were found to be strongly supported by additional data.

Recognizing inherent subjectivity of categories above species level, we propose the following classification that is consistent with our hypothesis of phylogeny and that fosters stability by introducing the fewest changes:

Family Brachypteraciidae
Brachypteracias leptosomus (Lesson 1832)
Geobiastes squamigerus (Lafresnaye 1838)
Uratelornis chimaera Rothschild 1895
Atelornis pittoides (Lafresnaye 1834)
Atelornis crossleyi Sharpe 1875

We resurrect the genus *Geobiastes*, proposed by Sharpe (1871), to highlight lack of a clear sister relationship between *squamigera* (*-us*) and *B. leptosomus*. That classification, which closely follows early treatments of Sharpe (1871) and Hartlaub (1877), is further favored (over placing all five species in *Brachypteracias*) because it is informative with respect to hypothesized genetic divergences among genera (Table 3) and it highlights behavioral and morphological differences. Johns and Avise (1998) surveyed genetic distances in cyt *b* sequences between species in 88 genera of birds and found that bird genera contain less genetic differentiation than do genera of other vertebrates and that the vast majority of bird genera studied contain <10% sequence divergence. Although our decision to retain *Atelornis* as the only polytypic genus is not based on genetic divergence alone, it is consistent with the breadth of genetic divergence encompassed by most avian genera.

Given that many aspects of ground roller natural history remain unknown, it is difficult to compare aspects of their ecology to the proposed phylogeny of the group. For example, the humid forest-dwelling genera *Atelornis*, *Geobiastes*, and *Brachypteracias* have similar single-note guttural "*boop*" or "*whoop*" calls, whereas *Uratelornis* gives a descending series of repeated notes. Whether similarity in calls of the humid forest species has a phylogenetic basis or is the result of convergence associated with forest structure (Chapuis 1971) is an open question.

Radiations, rates, and fossils.—Madagascar currently supports at least five endemic avian groups that are believed to be monophyletic and thus may have diversified since reaching Madagascar. This includes Brachypteraciidae,

Philepittinae (two genera, four species, order Passeriformes), Mesitornithidae (two genera, three species, order Gruiformes), and *Coua* (nine species, order Cuculiformes). In addition, recent and ongoing work indicates that vangas are likely not a monophyletic group (Fjeldså et al. 1999, Schulenberg 1995), but that a group of genera (*Oxylabes, Thamnornis, Cryptosylvicola,* and *Hartertula flavoviridis*) formerly considered to be divided among the Timaliidae and the Sylviidae constitutes a previously unrecognized Malagasy radiation (Cibois et al. 1999). Addition of our ground roller phylogeny to recent phylogenetic hypotheses for Philepittinae (Prum 1993) and *Coua* (Johnson et al. 2000), and genetic data on Mesitornithidae (Houde et al. 1997), Philepittinae (S. Hackett et al., unpubl. data), and a mixed assemblage of birds formerly placed in a variety of families (Cibois et al. 1999) provides a basis for discussing patterns of avian evolution on Madagascar.

Prum's (1993) morphological study of the Eurylamidae and Philepittidae indicated that the latter is a monophyletic subfamily of the former, and that the ancestor of the Philepittinae colonized Madagascar from Africa. He did not speculate on how recently that colonization may have taken place, but indicated that differentiation of bill morphology may have occurred after colonization in response to selective pressures on diet. Such a change could have occurred rapidly depending on intensity of selection, but genetic data (S. Hackett et al. unpubl. data, Table 3) indicate that splits between philepittinine genera and between species of *Neodrepanis* are quite old. Johnson et al.'s (2000) mitochondrial DNA phylogeny of cuckoos indicated that divergence (among six of nine species) within the monophyletic *Coua* was associated with arboreality but was not correlated with habitat distribution. Their findings that the couas are basal to the subfamilies Cuculinae, Coccyzinae, and Crotophaginae, and that genetic divergence between *Coua* and other cuckoo genera was very high (Table 3) lead them to conclude that the endemic Malagasy genus split from other cuckoos a long time ago. That result is similar to Houde et al.'s (1997) finding that the Mesitornithidae (represented by *Mesitornis*) are as genetically divergent from other gruiforms and allies as from galliforms (*Gallus gallus*) and this group too may represent an ancient lineage. We found that genetic divergence of ground rollers from true rollers also fits this pattern. Thus, with respect to the endemic Malagasy groups that have been demonstrated to be monophyletic and for which mitochondrial DNA data exist (Table 3), only the clade identified by Cibois et al. (1999) is not widely divergent from its putative sister taxon. We conclude that most endemic Malagasy nonpasserine groups show long histories of isolation on the island, but that recently hypothesized clades of passerines may be more recent colonists.

Fossils attributed to the Brachypteraciidae have been reported from the mid-Eocene in Europe. Those fossils provide an estimate for a minimum age of 46–49 Ma before present (Carroll 1988) for timing of divergence between ground rollers and true rollers. Combining the 46 Mya date for those fossils with corrected mitochondrial genetic distances between true rollers and ground rollers (range 16.5 to 20.2%, Table 3) provides a rough calibration of 0.37–0.44% genetic divergence per million years. That estimated rate of sequence divergence is surprisingly low; typically, rates of evolution are five-fold higher (Klicka and Zink 1997). Our calibration of a mtDNA molecular clock may be compromised by variation in rates of molecular evolution among some roller lineages. Our calibration may also be an underestimation because saturation seen at high levels of divergence (Table 3) obscures true genetic divergence between true rollers and ground rollers; however, we believe it unlikely that saturation alone would result in such a dramatic (five-fold) underestimate. In addition, although variation in rates of molecular divergence is known to exist in vertebrate genomes, it seems unlikely that factors known to affect rates, such as metabolism and body size (Mindell et al. 1996), would produce such a drastic slow down in ground rollers. An alternative hypothesis that could explain the apparent discrepancy between rates of mitochondrial DNA evolution in ground rollers and in other birds is that fossils attributed to that family are in fact not brachypteraciids. Identification of fossils from Europe as members of a clade that (currently) is endemic to Madagascar in itself raises questions about the identity of those specimens. Furthermore, as identification of those fossils as ground rollers is not supported by a character-based phylogenetic analysis, it is simply not

possible to be certain whether those fossils represent ground rollers, true rollers, or perhaps a taxon ancestral to both of those modern groups. Brochu (2000) describes a similar situation in *Crocodylus*. Genetic distances suggested that species in *Crocodylus* were relatively closely related, but fossils assigned to the genus were as old as the Late Cretaceous. Brochu's parsimony analysis of morphological characters for both living and fossil crocodylians supported a recent radiation of *Crocodylus* and suggested that the oldest fossil diagnosable to *Crocodylus* was from the Miocene, a date in keeping with molecular results. Older fossils referred to as *Crocodylus* are not placed with those recent species. Historically, the name *Crocodylus* was applied as a general description of morphology, not as a clade in the modern phylogenetic sense.

Many authors have likened ground roller morphology to a primitive coraciiform condition (Cracraft 1971), and if coraciiforms were indeed the dominant group of arboreal birds in the Eocene (Feduccia 1999), it is possible that certain of their osteological characters would resemble modern ground rollers. Most modern bird orders are known from the Eocene and many others are surely older (Cooper and Penny 1997), but there is little evidence that any of those taxa belong to extant families (Padian and Chiappe 1998). Further investigation of ground roller divergence times should include analysis of a slowly evolving, constant-rate gene as well as a modern analysis of characters from extant and fossil rollers. Placing Eocene fossils on the coraciiform tree may shed light on the origin of Madagascar's "primitive" ground rollers.

ACKNOWLEDGMENTS

Fieldwork was supported by the World Wide Fund for Nature (Madagascar), the John D. and Catherine T. MacArthur Foundation, and the National Geographic Society. We are grateful to the Malagasy authorities, particularly the Association Nationale pour la Gestion des Aires Protégées and Direction des Eaux et Forêts, for permission to collect and export specimens. We thank The Pritzker Foundation for its generous support of this and other ongoing research in The Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution. We also thank Academic Affairs of The Field Museum for funding our studies of genetic diversity in Malagasy birds. For collecting tissues from taxa used as outgroups we acknowledge L. R. Heaney, S. M. Lanyon, and T. S. Schulenberg. G. F. Barrowclough (American Museum of Natural History) and E. Pasquet (Muséum National d'Histoire Naturelle) generously supplied tissue samples of *Uratelornis*, and T. Glenn provided useful advice concerning "antique" DNA. This paper benefited from the thoughtful comments of J. L. Cracraft and an anonymous reviewer.

LITERATURE CITED

ALTSCHUL, S. F., T. L. MADDEN, A. A. SCHAFFER, J. ZHANG, Z. ZHANG, W. MILLER, AND D. J. LIPMAN. 1997. Gapped BLAST and PSI-BLAST: A new generation of protein database search programs. Nucleic Acids Research 25:3389–3402.

APPERT, O. 1968. Zur brutbiologie der Erdracke *Uratelornis chimaera* Rothschild. Journal für Ornithologie 109:264–275.

BOCK, W. J. 1994. History and nomenclature of avian family-group names. Bulletin of the American Museum of Natural History, no. 222.

BROCHU, C. A. 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. Copeia 2000:657–673.

BRODKORB, P. 1971. Catalogue of fossil birds: Part 4 (Columbiformes through Piciformes). Bulletin of the Florida State Museum 15:163–266.

BURTON, P. J. K. 1984. Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes. Bulletin of the British Museum (Natural History) 47:331–443.

CARROLL, R. L. 1988. Vertebrate Paleontology and Evolution. W. H. Freeman and Company, New York.

CHAPUIS, C. 1971. L'influence du milieu sur les émissions vocales des oiseaux: L'évolution des chants en forêt équatoriale. La Terre et al Vie 36:183–202.

CHENU, J. C., AND O. DES MURS. 1852. Encyclopédie D'histoire Naturelle, vol. II. Marescq et Compagnie, Paris.

CIBOIS, A., E. PASQUET, AND T. S. SCHULENBERG. 1999. Molecular systematics of the Malagasy babblers (Passeriformes: Timaliidae) and warblers (Passeriformes: Sylviidae), based on cytochrome *b* and 16S rRNA sequences. Molecular Phylogenetics and Evolution 13:581–595.

COOPER, A., AND D. PENNY. 1997. Mass survival of birds across the Cretaceous-Tertiary boundary: Molecular evidence. Science 275:1109–1113.

CRACRAFT, J. 1971. The relationships and evolution of the rollers: Families Coraciidae, Brachypteraciidae, and Leptosomatidae. Auk 88:732–752.

DESJARDINS, P., AND R. MORAIS. 1990. Sequence and gene organization of the chicken mitochondrial genome. Journal of Molecular Biology 212:599–634.

DORST, J. 1972. The evolution and affinities of the birds of Madagascar. Pages 615–627 *in* Biogeography and Ecology of Madagascar (R. Battistini and G. Richard-Vindard, Eds.). Dr. W. Junk B. V., The Hague, The Netherlands.

EDWARDS, S. V., P. ARCTANDER, AND A. C. WILSON. 1991. Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. Proceedings of the Royal Society of London, Series B 234:99–107.

FEDUCCIA, A. 1999. The Origin and Evolution of Birds, 2nd ed. Yale University Press, New Haven, Connecticut.

FJELDSÅ, J., S. M. GOODMAN, T. S. SCHULENBERG, AND B. SLIKAS. 1999. Molecular evidence for relationships of Malagasy birds. Pages 3084–3094 *in* Proceedings 22nd International Ornithological Congress (N. J. Adams and R. H. Slotow, Eds.). Birdlife South Africa, Johannesburg.

GOODMAN, S. M. 2001. A description of a new species of *Brachypteracias* (Family Brachypteraciidae) from the Holocene of Madagascar. Ostrich 72: in press.

HACKETT, S. J. 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). Molecular Phylogenetics and Evolution 5:368–382.

HARTLAUB, G. 1861. Ornithologischer Beitrag zur Fauna Madagascar's. C. Schünemann, Bremen, Germany.

HARTLAUB, G. 1877. Die Vögel Madagascars. H. W. Schmidt, Halle, Germany.

HELM-BYCHOWSKI, K., AND J. CRACRAFT. 1993. Recovering phylogenetic signal from DNA sequences: Relationships within the Corvine assemblage (Class Aves) as inferred from complete sequences of the mitochondrial DNA cytochrome-b gene. Molecular Biology and Evolution 10:1196–1214.

HOUDE, P., A. COOPER, E. LESLIE, A. E. STRAND, AND G. A. MONTANO. 1997. Phylogeny and evolution of 12S rDNA in Gruiformes (Aves). Pages 121–158 *in* Avian Molecular Evolution and Systematics (D. P. Mindell, Ed.). Academic Press, San Diego, California.

JOHNS, G. C., AND J. C. AVISE. 1998. A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome *b* gene. Molecular Biology and Evolution 15:1481–1490.

JOHNSON, K. P., S. M. GOODMAN, AND S. M. LANYON. 2000. A phylogenetic study of the Malagasy Couas with insights into cuckoo relationships. Molecular Phylogenetics and Evolution 14:436–444.

JUKES, T. H., AND C. R. CANTOR. 1969. Evolution of protein molecules. Pages 21–132 *in* Mammalian Protein Metabolism (H. N. Munro, Ed.). Academic Press, New York.

KEITH, S. 1980. Origins of the avifauna of the Malagasy region. Pages 99–108 *in* Proceedings of the 4th Pan African Ornithological Congress (D. N. Johnson, Ed.). South African Ornithological Society, Johannesburg.

KLICKA, J., AND R. M. ZINK. 1997. The importance of recent ice ages in speciation: A failed paradigm. Science 277:1666–1669.

KOCHER, T. D., W. K. THOMAS, A. MEYER, S. V. EDWARDS, S. PAABO, F. X. VILLABLANCA, A. C. WILSON. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences USA 86:6196–6200.

KRAUSE, D. W., J. H. HARTMAN, AND N. A. WELLS. 1997. Late Cretaceous vertebrates from Madagascar: Implications for biotic change in deep time. Pages 3–43 *in* Natural Change and Human Impact in Madagascar (S. M. Goodman and B. D. Patterson, Eds.). Smithsonian Institution Press, Washington, D.C.

LANGRAND, O. 1990. Guide to the Birds of Madagascar. Yale University Press, New Haven, Connecticut.

MARTIN, L. D. 1983. The origin and early radiation of birds. Pages 291–338 *in* Perspectives in Ornithology (A. H. Brush and G. Clark, Eds.) Cambridge University Press, New York.

MAURER, D. R., AND R. J. RAIKOW. 1981. Appendicular myology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). Annals of the Carnegie Museum 50:417–434.

MCCRACKEN, K. G., J. HARSHMAN, D. A. MCCLELLAN, AND A. D. AFTON. 1999. Data set incongruence and correlated character evolution: An example of functional convergence in the hind-limbs of stifftail ducks. Systematic Biology 48:683–714.

MINDELL, D. P., A. KNIGHT, C. BAER, AND C. J. HUDDLESTON. 1996. Slow rates of evolution in birds and the metabolic rate and temperature hypothesis. Molecular Biology and Evolution 13:422–426.

MINDELL, D. P., M. D. SORENSON, C. J. HUDDLESTON, H. C. MIRANDA, JR., A. KNIGHT, S. J. SAWCHUK, AND T. YURI. 1997. Phylogenetic relationships among and within select avian orders based on mitochondrial DNA. Pages 213–247 *in* Avian Molecular Evolution and Systematics (D. P. Mindell, Ed.). Academic Press, San Diego, California.

MOORE, W. S., AND V. R. DEFILIPPIS. 1997. The window of taxonomic resolution for phylogenies based on mitochondrial cytochrome *b*. Pages 83–119 *in* Avian Molecular Evolution and Systematics (D. P. Mindell, Ed.). Academic Press, San Diego, California.

MOREAU, R. E. 1966. The Bird Faunas of Africa and its Islands. Academic Press, New York.

MUNDY, N. I., P. UNITT, AND D. S. WOODRUFF. 1997. Skin from feet of museum specimens as a nondestructive source of DNA for avian genotyping. Auk 114:126–129.

OLSON, S. L. 1985. The fossil record of birds. Pages 79–238 *in* Avian Biology, vol. 8 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, Orlando, Florida.

PADIAN, K., AND L. M. CHIAPPE. 1998. The origin and early evolution of birds. Biological Reviews 73: 1–42.

PALUMBI, S. R. 1996. Nucleic acids II: The polymerase chain reaction. Pages 205–247 *in* Molecular Systematics (D. M. Hillis, C. Moritz, and B. K. Mable, Eds.). Sinauer Associates, Sunderland, Massachusetts.

PETERS, J. L. 1945. Check-list of Birds of the World, vol. 5. Harvard University Press, Cambridge, Massachusetts.

POSADA, D., AND K. A. CRANDALL. 1998. MODELTEST: Testing the model of DNA substitution. Bioinformatics 14:817–818.

PRUM, R. O. 1993. Phylogeny, biogeography, and evolution of the broadbills (Eurylaimidae) and asities (Philepittidae) based on morphology. Auk 110:304–324.

QUINN, T. W. 1997. Molecular evolution of the mitochondrial genome. Pages 3–28 *in* Avian Molecular Evolution and Systematics (D. P. Mindell, Ed.). Academic Press, San Diego, California.

RAKOTOARISOA, J. E. 1998. Preliminary study on the nesting of Scaly Ground-Rollers *Brachypteracias squamiger* on the Masoala Peninsula. Working Group on Birds of the Madagascar Region Newsletter 8(1):9–11.

RAKOTOARISOA, J. E. 1999. Comportements des adults et caractéristiques des poussins du Rollier terrestre écailleux *Brachypteracias squamiger* sur la presqu'île Masoala. Working Group on Birds of the Madagascar Region Newsletter 9(1): 30–32.

RAZAFIMAHAIMODISON, J. C. 1995. Preliminary research on the Pitta-like Ground-Roller (*Atelornis pittoides*) in the Ranomafana National Park, Madagascar. Pages 24–25 *in* Environmental Change in Madagascar (B. D. Patterson, S. M. Goodman, and J. L. Sedlock, Eds.). Field Museum of Natural History, Chicago.

SCHULENBERG, T. S. 1995. Evolutionary history of the vangas (Vangidae) of Madagascar. Ph.D. dissertation, University of Chicago, Chicago.

SEUTIN, G., B. N. WHITE, AND P. T. BOAG. 1991. Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoology 69: 82–90.

SHARPE, R. B. 1871. On the Coraciidae of the Ethiopian region. Ibis 3:184–203,270–289.

SHELDON, F. H., L. A. WHITTINGHAM, AND D. W. WINKLER. 1999. A comparison of cytochrome *b* and DNA hybridization data bearing on the phylogeny of swallows (Aves: Hirundinidae). Molecular Phylogenetics and Evolution 11:320–331.

SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and Classification of Birds: A Study in Molecular Evolution. Yale University Press, New Haven, Connecticut.

SIBLEY, C. G., AND B. L. MONROE, JR. 1990. Distribution and Taxonomy of the Birds of the World. Yale University Press, New Haven, Connecticut.

SLIKAS, B. 1997. Phylogeny of the avian family Ciconiidae (storks) based on cytochrome *b* sequences and DNA-DNA hybridization distances. Molecular Phylogenetics and Evolution 8:275–300.

SORENSON, M. D., AND R. C. FLEISCHER. 1996. Multiple independent transpositions of mitochondrial DNA control region sequences to the nucleus. Proceedings of the National Academy of Sciences USA 93:15239–15243.

SWOFFORD, D. L. 1998. PAUP*: Phylogenetic Analysis Using Parsimony. Sinauer Associates, Sunderland, Massachusetts.

TAMURA, K., AND M. NEI. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10:512–526.

THOMPSON, J. D., D. G. HIGGINS, AND T. J. GIBSON. 1994. CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. Nucleic Acids Research 22:4673–4680.

THORSTROM, R., AND J. LIND. 1999. First nest description, breeding, ranging and foraging behaviour of the Short-legged Ground-Roller *Brachypteracias leptosomus* in Madagascar. Ibis 141:569–576.

TURNER, D. A. 1984. The ground-rollers of Madagascar. Pages 553–557 *in* Proceedings 5th Pan-African Ornithological Congress (J. Ledger, Ed.). South African Ornithological Society, Johannesburg.

VOELKER, G., AND S. V. EDWARDS. 1998. Can weighting improve bushy trees? Models of cytochrome *b* evolution and the molecular systematics of pipits and wagtails. Systematic Biology 47:589–603.

WETMORE, A. 1960. A classification for the birds of the world. Smithsonian Miscellaneous Collections 139(11):1–37.

Associate Editor: R. Prum

APPENDIX.

Taxa examined	Voucher specimen[a]	Locality[b]
Atelornis crossleyi	FMNH 363795	Fianarantsoa; Andringitra, 1210 m
	FMNH 396235	Antananarivo; Tsinjoarivo
	FMNH 384704	Antananarivo; Andranomay, 1300 m
Atelornis pittoides	FMNH 396234	Antananarivo; Tsinjoarivo
	FMNH 396233	Antananarivo; Tsinjoarivo
	FMNH 384759	Toliara; Parc National d' Andohahela, 1200 m
	FMNH 384760	Toliara; Parc National d' Andohahela, 1200 m
	FMNH 384701	Antananarivo; Andranomay, 1300 m
Brachypteracias squamigera	FMNH 384758	Toliara; Parc National d' Andohahela, 1200 m
Brachypteracias leptosomus	FMNH 384731	Antsiranana; Parc National de Marojejy, 1225 m
	FMNH 345687	Toliara; Parc National d' Andringitra, 750 m
Uratelornis chimaera	AMNH 411213	Toliara; Lac Ihotry
	MNHN 1994.416	Toliara; Ihotry
Leptosomus discolor	No voucher	Mahajanga; Ampijoroa Forestry Station
Coracias garrulous	FMNH 347816	Pakistan: NW Frontier Province; Swat District
Eurystomus glaucurus	FMNH 384689	Toliara; Foret de Vohibasia
Eurystomus orientalis	FMNH 350940	Philipines: Catanduanes Island, Gigmoto
Todus todus	FMNH 331066	Jamaica: Portland, Hollywell Park

[a] FMNH = Field Museum of Natural History, Chicago; AMNH = American Museum of Natural History, New York; MNHN = Muséum National d'Histoire Naturelle, Paris.

[b] Presented for sites in Madagascar as province; site.