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PHYLOGENETIC RELATIONSHIPS AMONG THE TROGONS

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ABSTRACT.—The order Trogoniformes currently is divided into six genera: *Apaloderma, Pharomachrus, Euptilotis, Priotelus, Trogon,* and *Harpactes.* For this study, the question of intergeneric relationships was addressed based on mitochondrial cytochrome *b* and 12S ribosomal RNA genes. Maximum parsimony analyses confirmed the monophyly of currently accepted genera. A monophyletic clade encompassing the New World genera was the sister group to the Asian genus *Harpactes.* The sister group of these clades, in turn, was the African genus *Apaloderma.* Within the New World clade, the sister taxon of the genus *Trogon* was a clade formed by the Eared Trogon (*Euptilotis neoxenus*) and the Quetzals (*Pharomachrus* spp.). The most basal genus within the New World clade was *Priotelus.* These results suggest an Old World (Africa/Eurasia) origin for trogons, with the New World representing a secondary area of diversification. Patterns in plumage coloration concurred with relationships inferred from the molecular data. A hypothesis for the evolution of iridescent structures in trogon feathers suggests an increase in the complexity of these structures in the youngest lineages. *Received 7 July 1997, accepted 12 March 1998.*

THE TROGONS AND QUETZALS (order Trogoniformes) are among the most colorful of birds. They have dense, lax plumage and a well-developed aftershaft on their contour feathers. The color pattern of males is brown or metallic green with a blue-green gloss on the dorsal region, and the head can be metallic green, black, gray, blue, violet, chestnut, pink, or red. In many species, the upper part of the chest is separated from the lower part and the belly by a conspicuous white band. The lower chest, belly, and undertail coverts can be red, yellow, or orange. The wings are completely black, and the tail is black with very distinctive patterns of white. Some species have colored bare periocular skin with tonalities ranging from light yellow to deep purple. The quetzals (*Pharomachrus* spp.) are characterized by having a crested head, elongated upperwing coverts, and uppertail coverts exceeding the length of the tail, which, in the Resplendent Quetzal (*P. mocinno*) can reach up to 70 cm. The bill is short but broad basally, usually brightly colored, has a strongly arched culmen, and, in several species, has a serrated maxillary tomium. The long tail is graduated, broad at the base, and truncated.

Morphological features said to be characteristic of trogons and quetzals (Ridgway 1911, Sibley 1955, Sibley and Ahlquist 1990) include a schizognathous palate, basipterigoid processes, a large vomer, 15 cervical vertebrae, two pairs of deep sternal notches, four to five pairs of ribs, a metasternum with four notches, separated coracoids, a tracheo-bronchial syrinx, holorhinal nostrils having an ossified nasal septum, Gadow's type VIII deep plantar tendon arrangement, intestinal convolutions of type VI (Gadow 1889), pelvic muscle formula AX (Garrod 1873), a well-developed caecum, left carotid artery only, a well-defined spinal pterila extending from the nape to the oil gland, 10 primaries, 11 to 12 secondaries, 12 rectrices, and an unfeathered uropygial gland. All of these features, however, also are found in various combinations in other groups of birds (Sibley and Ahlquist 1990). Perhaps the only character that differentiates trogons and quetzals (hereafter trogons) from other groups is their heterodactyl foot in which digits 1 and 2 are directed backward and digits 3 and 4 are united for their basal half and directed forward.

The trogons are widely distributed in the tropics of both the Old and New Worlds. Sibley and Monroe (1990) recognized 39 species in 6 genera. The African trogons in the genus *Apaloderma* (three species) are endemic to mountain forests in Liberia, Nigeria, Cameroon, An-

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gola, Zaire, Uganda, Kenya, Tanzania, Mozambique, and Malawi. The second largest genus, *Harpactes,* contains 11 species that occur in southeastern Asia from India and Sri Lanka to southeastern China, and south along the Malay Peninsula through Sumatra, Borneo, Java, and the Philippines. The monotypic genus *Euptilotis* is endemic to mountain forests of western Mexico and southern Arizona. The five species of the genus *Pharomachrus* are distributed from southern Mexico to Peru, Bolivia, Colombia, Venezuela, Ecuador, and Amazonian Brazil. *Priotelus* includes two species endemic to the Caribbean islands of Cuba and Hispaniola. Finally, the largest genus in the order, *Trogon* (17 species), is distributed from southwestern New Mexico and southeastern Arizona south through Mexico and Central America to northern Argentina.

Although the natural history of some trogons is well known (e.g. Skutch 1942, 1944, 1948), their phylogenetic relationships remain poorly understood. Systematic studies have been restricted mainly to descriptions of subspecies (e.g. Clark 1918, Zimmer 1948, Clancey 1959, Parkes 1970). Moreover, technical diagnoses of the different genera do not clearly define the boundaries of these taxa; instead, genera and subgenera are diagnosed primarily using poorly defined morphological characters that frequently unite conflicting groups or are so ambiguous as to be useless for inferring monophyly. Characters such as the amount of feathering on the tarsi, serration of the tomium, presence of patches of bare skin, color patterns, and some skeletal features have been used to infer relationships among trogons (Ogilvie-Grant 1892, Ridgway 1911, Clark 1918, Parkes 1970). Many of these characters show a greater range of variation within taxa than among them, thus leading to some conflicting conclusions. Some early classifications lumped most of the species in the genus *Trogon* and placed the few remaining species in *Pharomachrus* (Gould 1875). On the other hand, the use of the characters listed above has led other ornithologists to propose multiple subdivisions within the Trogoniformes. Swainson (1837), for example, recognized *Trogon, Harpactes, Apaloderma, Temnurus,* and *Calurus;* Ogilvie-Grant (1892) split the Asian trogons into two genera (*Harpactes* and *Hapalarpactes*); Sharpe (1900) divided the African trogons into *Hapaloderma* and *Heterotrogon;* Ridgway (1911) divided the genus *Trogon* into four different genera (*Trogon, Curucujus, Trogonurus,* and *Chrysotrogon*); and Peters (1945) split *Priotelus* into two genera (*Priotelus* and *Temnotrogon*) and the African trogons into two genera (*Apaloderma* and *Heterotrogon*).

I used mitochondrial cytochrome-*b* (cyt-*b*) and 12S ribosomal RNA (12S) gene sequences to study phylogenetic patterns in the Trogoniformes. Variation in nucleotide substitution rates in DNA sequences has been correlated with codon position, gene region, and substitution type. Thus, phylogenetic relationships among recently divergent taxa can be studied using rapidly evolving third-codon positions, as well as transition substitutions in general. For taxa that have diverged long ago, more slowly evolving transversions or non-silent substitutions can be used. The cyt-*b* gene has been shown to contain phylogenetic signal at several different phylogenetic levels (Edwards et al. 1991, Smith and Patton 1991, Moritz et al. 1992). Some investigators have concluded that the information contained in cyt *b* is inadequate to resolve all phylogenetic problems (Graybeal 1993, Avise et al. 1994), and others have suggested that analyses based on individual genes have a low probability of recovering entire genome trees. Cummings et al. (1995) proposed that at least 8,000 contiguous nucleotide sites would be required to reach a 95% probability of obtaining the entire genome phylogeny. As a consequence of these considerations, the mitochondrial 12S gene was included in this study to complement the cyt-*b* data. The 12S gene has a slower evolutionary rate than cyt *b*, making it suitable for resolving deep divergences (Hay et al. 1995, Heise et al. 1995).

METHODS

Taxa examined.—Sequences of the cyt-*b* and the 12S genes were determined for 20 species of trogons. Sequences were deposited in GenBank and are available through the following accession numbers (cyt *b* and 12S, respectively): Narina Trogon (*Apaloderma narina* [U94798, U94812]), Bar-tailed Trogon (*A. vittatum* [U89200, U89234]), Crested Quetzal (*Pharomachrus antisianus* [U89204, U89235]), Golden-headed Quetzal (*P. auriceps* [U94799, U94813]), Pavonine Quetzal (*P. pavoninus* [U94800, U94814]), Eared Trogon (*Euptilotis neoxenus* [U89203, U89236]), Cuban Trogon (*Priotelus temnurus* [U89202, U89237]), Black-tailed Trogon (*Trogon melanurus* [U94805, U94819]), White-eyed Trogon (*T. comptus* [U94804, U94818]),

White-tailed Trogon (*T. viridis* [U94803, U94817]), Mountain Trogon (*T. mexicanus* [U94809, U94823]), Elegant Trogon (*T. elegans* [U94806, U94820]), Collared Trogon (*T. collaris* [U94808, U94822]), Masked Trogon (*T. personatus* [U89201, U89238]), Black-throated Trogon (*T. rufus* [U94807, U94821]), Blue-crowned Trogon (*T. curucui* [U94801, U94815]), Violaceous Trogon (*T. violaceus* [U94802, U94816]), Diard's Trogon (*Harpactes diardii* [U94797, U94811]), Philippine Trogon (*H. ardens* [U94796, U94810]), and Orange-breasted Trogon (*H. oreskios* [U89199, U89239]). The Lesser Roadrunner (*Geococcyx velox* [U89198, U89212]), Hodgson's Hawk-Cuckoo (*Cuculus fugax* [U89197, U89210]), Greater Coucal (*Centropus sinensis* [U89196, U89211]), Speckled Mousebird (*Colius striatus* [U89175, U89218]), White-headed Mousebird (*C. leucocephalus* [U89173, U89217]), and White-backed Mousebird (*C. colius* [U89174, U89216]) were employed as outgroups for character polarization and for rooting the phylogeny. Tissue samples were obtained from: Genetic Resources Collection, Academy of Natural Sciences of Philadelphia; Institute of Zoology, University of Copenhagen; Department of Ornithology, American Museum of Natural History; Museum of Natural Science, Louisiana State University; Bird Collection, University of Arizona; Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México; and Zoological Reference Collection, National University of Singapore.

DNA extraction and sequencing.—Total genomic DNA was extracted from frozen tissue using a Chelex 5% solution following the protocol suggested by Singer-Sam et al. (1989). Target genes were amplified and isolated as single fragments using specifically designed PCR primers. This first amplification was conducted in Peltier-effect thermocyclers (MJ Research) according to the parameters and conditions suggested by Nunn et al. (1996). PCR products were subjected to horizontal electrophoresis in a 2% NuSieve low-melting point agarose gel (FMC Bioproducts). Gels were stained for 10 min in a solution of 2 pg/mL of ethidium-bromide and visualized under UV light. The double-stranded DNA (dsDNA) products were cut directly from the gel and resuspended in 150 μL of ultrapure water by heating to 73°C for 15 min. The genes were reamplified as subfragments of about 400 bp using internal oligonucleotide primers. LPhe (L1243) 5'-CAAACAAAGCATGGCACTGAAG-3' and 12Sd (H1883) 5'-TTCGATTATAGAACAGGCTCCTC-3' primers were designed by J. Groth (unpubl. data; numbered following the chicken mitochondrial genome [Desjardins and Morais 1990]). The remaining primers used are described elsewhere (Helm-Bychowski and Cracraft 1993, Knight and Mindell 1993). An air thermocycler (Idaho Technologies) was used to perform 40-μL amplifications of these subfragments in glass microcapillary tubes using standard buffers (Wittwer 1992). Subfragments were amplified using the following conditions: 2 s at 94°C, 0 s at 47°C, and 15 s at 71°C for 35 cycles at slope 7. All PCR experiments were conducted along with positive and negative controls to test for contamination. Aliquots of 3 μL were visualized as described above. The remainder was purified to eliminate PCR primers, dNTPs, enzyme, and buffer components using the GeneClean II kit (BIO 101, Inc.). Purified PCR products were subjected to cycle sequencing using the ABI Prism Dye Terminator Cycle Sequencing Ready Reaction kit with AmpliTaq DNA Polymerase FS on the GeneAmp PCR System 9600 (Perkin Elmer). Amplifications were performed in 6-μL reaction volumes containing 2.5 μL of the Prism kit reagent, 1 pmole of sequencing primer, 5 ng/μL dsDNA template, and 2 μL of ultrapure water. Cycle sequencing was performed using the following conditions: 10 s at 95°C, 5 s at 50°C, and 3 min at 60°C for 32 cycles. The excess of *Taq* dideoxy terminators was removed with Centri-Sep spin columns (Princeton Separations) in a variable speed microcentrifuge at 2,500 rpm for 2 min. Final purifications were dried in a vacuum centrifuge and resuspended in 2.5 μL of the loading buffer (6× deionized formamide, 1× 50 mM EDTA pH 8.0). Resuspended sequencing products were subjected to 4% polyacrylamide denaturing gel electrophoresis in the ABI Prism 377 DNA Sequencer (Perkin Elmer). Sequence files were analyzed with the aid of the program Sequencher version 3.0 (Gene Codes Corporation). A large degree of fragment overlap, as well as sequencing both DNA strands, ensured accurate data collection. Initial alignment of the 12S sequences was performed using the program Malign (Wheeler and Gladstein 1992). Structural regions in the 12S sequences were delimited according to the proposed secondary structure for the 12S molecule (Springer and Douzery 1996, Houde et al. 1997, Mindell et al. 1997).

Phylogenetic analysis.—All cyt-*b* nucleotide positions and only alignment-stable nucleotides of the 12S were used in parsimony analyses conducted with the program PAUP 3.1.1 (Swofford 1993). Because of the large number of taxa used, it was necessary to use a heuristic algorithm for searching the tree space. Input order bias was minimized by performing 1,000 replicate heuristic searches with random addition of taxa. During all analyses, nucleotide transformations were considered unordered. Character states were optimized using delayed transformation (DELTRAN), which favors contemporaneous changes (i.e. parallelisms over reversals). Branch swapping was made by the tree bisection-reconnection algorithm. Retention and consistency indices were computed to evaluate the level of homoplasy in the most-parsimonious tree. Finally, tree robustness was examined using 500 bootstrap replications (Felsenstein 1985, Hillis and Bull 1993) and branch support (Bremer 1988, 1994).

Genetic distance and partition-homogeneity test.—I calculated corrected pairwise distances for the nucleotide sequences to test for saturation effects (Arctander 1991, Maynard-Smith and Smith 1996). Distances were computed with the program DNADIST from the Phylip 3.5p package (Felsenstein 1993) using Kimura's two-parameter model (Kimura 1980) and assuming a 10:1 transition-transversion bias. This bias is considered a conservative estimate for birds (Kocher et al. 1989, Nunn and Cracraft 1996, Espinosa de los Monteros and Cracraft 1997).

Using simulation analysis, Bull et al. (1993) showed that phylogenies are less accurate when combining DNA partitions having different evolutionary rates compared with analysis of data sets consisting only of slowly evolving partitions of the genome. Following this suggestion, I conducted a partition-homogeneity test. This analysis was performed with the aid of the program PAUP* (Swofford 1995). One thousand replicates were generated, and the sum of tree lengths was estimated using heuristic searches.

RESULTS

Sequence variability.—The combined sequences of the cyt-*b* and 12S genes resulted in an alignment of 2,159 nucleotides. The cyt-*b* sequences contained 590 invariant positions (52%), 85 autapomorphic characters (7%), and 468 phylogenetically informative characters (41%). The variability within the three codon positions was similar to that reported for other cyt-*b* genes (Edwards et al. 1991, Irwin et al. 1991, Graybeal 1993). Second positions were the least variable codon sites, with 57 nucleotide substitutions, followed by first positions with 137. Third positions were the most variable, with 362 nucleotide substitutions. Although the highest variation was present in third-codon positions, only a few of these changes involved amino acid replacements. Among the translated sequences, 118 (31%) of the 380 amino acid residues were variable. Based on the structural model for cyt *b* proposed by Howell (1989), the highest incidence of hypervariable amino acid residues was located inside the transmembrane regions of the molecule, especially in the fourth, fifth, and eighth segments. This replacement pattern is consistent with that reported for cyt *b* in other organisms (Diegli-Espoti et al. 1993).

Empirical pairwise differences between species of trogons in cyt *b* ranged from 62 (5.4%) between *Trogon violaceus* and *T. curucui* to 208 (18.2%) between *T. elegans* and *A. narina* (Table 1). The smallest distance between different genera was 144 nucleotide substitutions (12.6%) between *E. neoxenus* and *P. pavoninus.* Similar patterns were observed when only transversion substitutions were analyzed. Transversion distances in cyt *b* ranged from six (0.5%) between *T. curucui* and *T. violaceus* to 78 (6.8%) between *H. oreskios* and *T. mexicanus.* Transversion differences within *Trogon* differed by an order of magnitude (six [0.5%] between *T. violaceus* and *T. curucui* to 52 [4.6%] between *T. viridis* and *T. mexicanus*).

Multiple insertions and deletions characterized the hypervariable regions within the 12S gene. Although the multiple alignment for the 26 taxa sequenced had a length of 1,016 positions, the number of nucleotides ranged from 949 in *P. temnurus* to 975 in *A. narina.* Functional regions (i.e. stems and loops) in the sequences were easily identified following the model proposed for the secondary structure of the 12S molecule (Springer and Douzery 1996, Houde et al. 1997, Mindell et al. 1997). The alignment contained 590 invariant positions (58%), 72 autapomorphies (7%), and 354 phylogenetically informative characters (35%). The stem regions of the molecule were more conservative than the loops. Stems encompassed 315 of the invariant characters (53%), 20 of the autapomorphies (28%), and 134 of the phylogenetically informative characters (30%). Hypervariable fragments producing ambiguous alignments were located mainly inside the loops.

Variation in the 12S gene between trogon species ranged from 19 (1.9%) between *P. auriceps* and *P. antisianus* to 150 (14.8%) between *A. vittatum* and two species of *Trogon* (Table 2). The average distance between species belonging to different genera was 130 nucleotide substitutions (12.8%). Transversion distances ranged from 1 (0.1%) between *T. curucui* and *T. violaceus* to 48 (4.7%) between *A. vittatum* and *T. collaris.*

Variation in the transition-transversion ratio due to differences in selection pressure within mitochondrial DNA produces a characteristic nucleotide bias especially at silent positions (Brown 1985, Sueoka 1988). The nucleotide composition and bias (C) in cyt *b* reported for other birds (Nunn and Cracraft 1996, Nunn et al. 1996) and for mammals (Irwin et al. 1991) are almost identical to those observed in this

TABLE 1. Pairwise empirical differences among trogons for the sequences of cytochrome *b*. Total differences below the diagonal, transversion differences above the diagonal.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 *Harpactes oreskios*	—	49	54	69	62	59	52	57	59	67	67	69	68	59	57	69	65	73	78	69
2 *Harpactes ardens*	170	—	19	64	61	56	47	46	48	52	64	60	67	54	50	64	68	66	67	62
3 *Harpactes diardii*	172	110	—	67	70	65	56	55	55	59	69	67	70	59	57	69	63	71	72	67
4 *Priotelus temnurus*	195	189	181	—	63	64	55	46	60	62	70	66	69	56	54	68	66	68	67	66
5 *Apaloderma narina*	177	191	197	201	—	25	58	57	61	67	61	61	62	45	47	61	61	67	62	63
6 *Apaloderma vittatum*	164	179	189	189	124	—	59	62	60	70	62	60	65	50	50	64	64	68	65	62
7 *Pharomachrus antisianus*	164	155	151	172	168	160	—	15	11	37	57	55	58	47	43	61	57	65	66	61
8 *Pharomachrus auriceps*	179	169	169	150	177	168	83	—	22	44	62	58	63	48	50	66	60	70	65	64
9 *Pharomachrus pavoninus*	184	168	171	180	188	170	64	107	—	38	58	56	59	50	48	62	60	70	67	66
10 *Euptilotis neoxenus*	188	172	181	206	204	195	147	158	144	—	70	70	71	62	58	68	68	70	73	68
11 *Trogon curucui*	182	171	175	199	194	195	177	191	180	200	—	6	25	28	28	44	42	50	51	44
12 *Trogon violaceus*	175	173	178	190	191	188	173	192	174	194	62	—	25	26	24	44	42	50	51	44
13 *Trogon viridis*	178	169	175	194	176	176	169	179	187	197	137	139	—	31	29	47	47	49	52	47
14 *Trogon comptus*	177	155	171	195	178	171	161	169	167	179	145	143	136	—	10	36	36	42	39	36
15 *Trogon melanurus*	176	156	168	181	179	158	151	171	166	174	143	132	129	81	—	32	32	38	39	32
16 *Trogon elegans*	188	192	187	198	208	183	190	195	195	199	177	174	159	154	151	—	30	20	21	18
17 *Trogon rufus*	176	171	183	189	194	174	171	180	177	184	165	159	152	147	134	134	—	34	35	30
18 *Trogon collaris*	178	184	178	188	201	199	185	196	197	201	172	163	140	156	147	129	141	—	27	12
19 *Trogon mexicanus*	206	185	194	195	193	198	190	186	189	200	175	184	169	161	157	126	131	129	—	23
20 *Trogon personatus*	194	193	199	191	194	199	185	197	194	195	185	179	151	168	143	134	130	109	128	—

TABLE 2. Pairwise empirical differences among trogons for the sequences of 12S rRNA. Total differences below the diagonal, transversion differences above the diagonal.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 *Harpactes oreskios*	—	25	19	32	34	34	28	26	24	28	39	40	41	35	37	40	35	42	32	35
2 *Harpactes ardens*	88	—	17	38	36	35	34	34	32	34	42	41	44	37	39	40	39	44	40	38
3 *Harpactes diardii*	91	58	—	38	37	36	33	33	31	33	39	38	41	33	35	36	35	41	36	34
4 *Priotelus temnurus*	118	126	127	—	40	40	36	34	32	34	36	37	38	36	35	39	35	39	35	33
5 *Apaloderma narina*	121	126	131	122	—	9	36	36	34	38	41	42	44	41	43	44	39	45	42	40
6 *Apaloderma vittatum*	119	126	134	120	58	—	38	38	36	40	41	42	44	41	43	47	43	48	46	43
7 *Pharomachrus antisianus*	112	119	124	117	122	128	—	4	4	20	37	36	38	38	38	40	35	40	36	34
8 *Pharomachrus auriceps*	109	117	128	120	124	125	19	—	2	18	37	36	38	38	40	40	35	42	36	34
9 *Pharomachrus pavoninus*	107	116	124	118	121	123	23	23	—	18	35	34	36	36	38	38	33	40	34	32
10 *Euptilotis neoxenus*	111	125	124	115	136	134	84	75	81	—	38	37	39	37	37	39	36	40	37	34
11 *Trogon curucui*	136	139	143	128	142	145	138	138	136	128	—	1	8	13	16	21	18	24	19	18
12 *Trogon violaceus*	133	142	147	126	138	144	136	141	139	132	28	—	9	14	17	22	19	25	20	19
13 *Trogon viridis*	122	132	141	126	139	143	131	133	129	126	68	61	—	15	18	25	22	28	23	22
14 *Trogon comptus*	124	135	133	129	137	132	135	134	134	133	89	90	89	—	7	25	22	28	23	21
15 *Trogon melanurus*	129	138	142	125	142	137	129	129	128	125	83	78	81	43	—	27	24	28	25	23
16 *Trogon elegans*	126	136	137	128	133	139	129	127	125	121	103	104	96	105	105	—	12	13	11	8
17 *Trogon rufus*	123	144	144	133	140	150	131	127	124	126	103	101	100	107	106	54	—	11	11	8
18 *Trogon collaris*	127	141	144	134	141	150	141	144	140	130	103	103	99	105	105	59	58	—	12	8
19 *Trogon mexicanus*	125	127	131	132	139	145	131	134	134	125	88	86	95	106	100	71	61	66	—	7
20 *Trogon personatus*	126	135	139	119	132	140	130	129	126	125	93	90	93	103	105	60	55	45	63	—

TABLE 3. Nucleotide composition and base compositional bias in cytochrome-*b* and 12S rRNA genes.

	Cytochrome *b*												12S rRNA							
	First position				Second position				Third position				Stems				Loops			
	C	T	A	G	C	T	A	G	C	T	A	G	C	T	A	G	C	T	A	G
Mean	28.5	23.7	27.0	20.8	26.7	39.7	20.8	12.8	42.4	15.4	38.6	3.5	27.0	23.7	23.0	26.3	25.1	20.1	39.2	15.6
SD	1.2	1.2	1.1	0.9	0.5	0.6	0.2	0.3	2.6	3.1	1.8	1.2	1.3	1.1	1.3	0.8	0.9	0.8	1.0	0.8
Nucleotide bias	0.073				0.22				0.414				0.044				0.191			

study (Table 3). Because third-codon position substitutions tend to be silent, and therefore the most variable, a higher nucleotide compositional bias was found ($C = 0.414$). Third positions are rich in cytosine (42.4%) and adenine (38.6%), much lower in thymine (15.4%), and lowest in guanine (3.5%). Second positions have an intermediate bias ($C = 0.22$), being rich in thymine (39.7%) and poor in guanine (12.8%), with intermediate percentages for cytosine (26.7%) and adenine (20.8%). First positions are the least biased ($C = 0.073$), being relatively rich in cytosine (28.5%) and poor in guanine (20.8%), but intermediate in adenine and thymine (27% and 23.7% respectively).

Of the two structural regions of the 12S (Table 3), loops possessed the highest bias ($C = 0.191$). The bias is mainly produced by an overabundance of adenine (39.2%), which is explained by the hypothesis that the low polarity of adenine may favor hydrophobic interactions with proteins (Gutell et al. 1985). Following adenine are cytosine (25.1%), thymine (20.1%), and guanine (15.6%). A more uniform nucleotide bias is observed in stems ($C = 0.044$), being slightly rich in cytosine (27%) and poor in adenine (23%), with intermediate percentages for guanine (26.7%) and thymine (23.7%). The nucleotide composition and bias observed in the 12S sequences were consistent with those reported previously for mammals (Springer et al. 1995, Springer and Douzery 1996).

Several molecular studies have shown the existence of nuclear pseudogenes formed by translocated fragments of the mitochondrial genome, especially from cyt *b* (Quinn 1992, Smith et al. 1992, Kornegay et al. 1993). Five observations indicate that the sequences used during this study were of mitochondrial origin only: (1) nonsense codons for protein-coding genes and frameshifts, which are typical indicators of nuclear copies, were not apparent; (2) genes were isolated initially as a single fragment including flanking regions of the tRNA-Thr and the last 90 bases of ND5 for cyt *b*, and the 3′ end of the tRNA-Phe for 12S; isolation of entire genes minimizes the potential risk of amplifying smaller fragments that are more likely to be translocated into the nuclear genome; (3) the 381 amino acid codons forming the cyt *b* were translated using the vertebrate mitochondrial code without ambiguities or intermediate stop codons; (4) the secondary

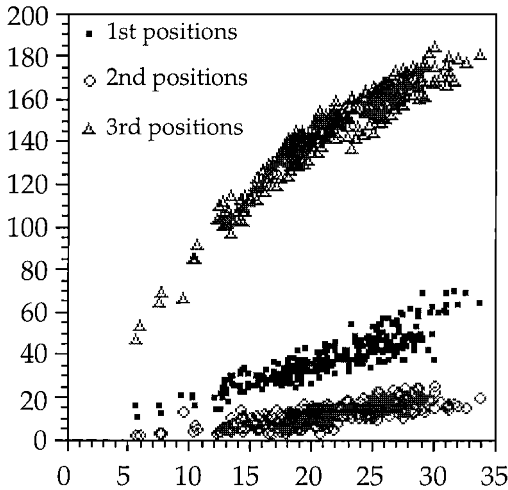

FIG. 1. Saturation plots for the cytochrome-*b* gene sequences constructed using empirical differences for each codon position as a function of corrected sequence divergence (%) and using the Kimura two-parameter model with a 10:1 transitions:transversion ratio.

structure deduced from the 12S sequences was entirely consistent with that proposed for other vertebrates (Springer and Douzery 1996, Houde et al. 1997, Mindell et al. 1997); and (5) the nucleotide bias observed in the different gene partitions is nearly identical to those reported for other birds (Moore and DeFilippis 1997).

Phylogenetic analysis.—The homogeneity test showed that the data matrices for the cyt-*b* and 12S sequences represent homogeneous partitions (P = 0.034). Therefore, a combined analysis approach was chosen for phylogeny estimation. In addition, empirical pairwise distances were plotted against Kimura distances to detect saturation in the different partitions of each gene. This analysis shows that the nucleotide substitution rate follows a linear relation in the 12S gene. Evidence of saturation occurred only in the cyt-*b* gene. Figure 1 presents comparative curves for the accumulation of total substitutions depending on codon position in the cyt *b*. Second positions showed a clear linear pattern and had the slowest rate of nucleotide substitution (best fitted line slope = 0.77). The nucleotide replacement rate in first positions (slope = 1.81) was more than twice that for second positions, but the accumulation maintained essentially a linear pattern. The nucleotide substitution rate at third positions increased rapidly in relation to corrected distances, but after 13% of difference it began to level off into a zone of saturation.

A global parsimony analysis of the two combined sequences, including all substitutional variation regardless of position and type, resulted in three equally parsimonious trees of 3,760 steps in length. The strict consensus tree (Fig. 2A) confirmed that each genus within the Trogoniformes is monophyletic, but the relationships among genera were only partially resolved. The 10 species in the genus *Trogon* are equally divided into two subclades that form one of the best supported lineages within the phylogeny. In one of the subclades (the "Violaceous subclade"), *T. curucui* is the sister taxon to *T. violaceus*; their closest relative is *T. viridis*, and at the base of this subclade are *T. melanurus* and its sister taxon *T. comptus*. The other subclade (the "Elegant subclade") is composed of *T. mexicanus*, *T. elegans*, *T. rufus*, *T. collaris*, and *T. personatus*. Excluding the last two species, which are each other's closest relative, the phylogenetic relationships in this subclade are unresolved. The sister group of *Trogon* is *Priotelus* (Cuban Trogon). The next node of the consensus tree is a polytomy formed by *Trogon-Priotelus*, *Pharomachrus-Euptilotis*, and *Harpactes*. Within quetzals, *Pharomachrus antisianus* and *P. pavoninus* are sister species, their sister group is *P. auriceps*, and the sister taxon to the quetzals is the monotypic *Euptilotis neoxenus*. In the clade formed by the Asian trogons, *Harpactes diardii* is the sister taxon to *H. ardens*, and their sister group is *H. oreskios*. The two African trogons (*Apaloderma*), the most basal species in the cladogram, are sister taxa to the rest of the order. Although the consensus tree shows an apparent lack of resolution, the nodes are supported with high bootstrap values at the genus level and above. Relatively low bootstrap values were registered for the clade comprising the Asian trogons (79%) compared with values for the other genera.

The African trogons, quetzals, and New World Trogons were each identified in 100% of the bootstrap replications. In contrast to interspecific patterns, intergeneric relationships were poorly supported (<50%). The only exception was the lineage relating *E. neoxenus* to the quetzals, which had a bootstrap value of 100%. Finally, the monophyly of the Trogoniformes was highly supported, scoring boot-

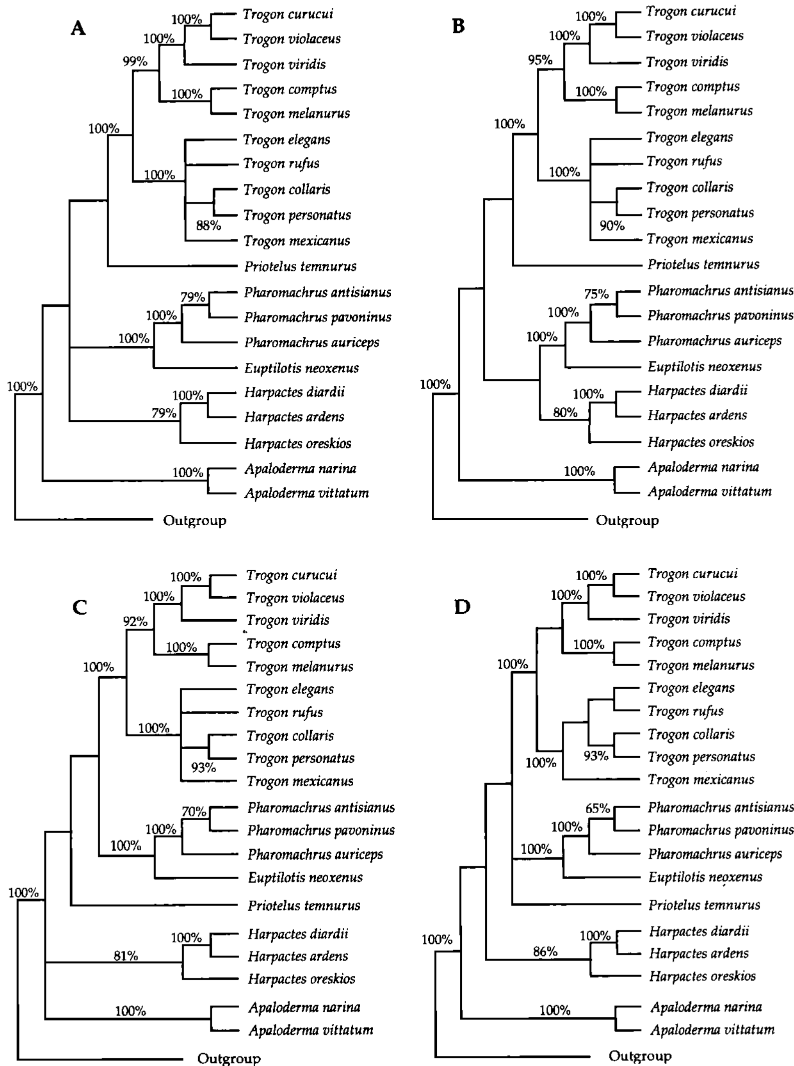

FIG. 2. Phylogenetic hypotheses for the Trogoniformes. (A) Strict consensus tree from three equally parsimonious trees obtained from equal-weighting analysis of all nucleotide positions in both genes (length, 3,760; consistency index, 0.407; retention index, 0.5). (B) Strict consensus tree from two equally parsimonious trees obtained after down-weighting third-position transitions (0.5:1) for cytochrome *b* (length, 3,157; consistency index, 0.466; retention index, 0.573). (C) Strict consensus tree from two equally parsimonious trees obtained after down-weighting third-position transitions (0.2:1) for cytochrome *b* (length, 2,795; consistency index, 0.464; retention index, 0.571). (D) Strict consensus tree from two equally parsimonious trees obtained after down-weighting third-position transitions (0.1:1) for cytochrome *b* (length, 2,673; consistency index, 0.465; retention index, 0.572). Percentages on branches are bootstrap values of 500 replications. For taxa included in the outgroup refer to *Taxa examined* in Methods.

strap values of 100% even when the outgroup was not constrained to be monophyletic.

One possible reason for the lack of resolution in deeper nodes of the tree may be the homoplasy due to multiple hits in third positions of cyt *b*. More than 95% of third-codon positions have been hit multiple times (i.e. 362 of 381). To filter this saturation effect, I decided to down-weight transitions with respect to transversions. In the first analysis, third-position transitions (cyt *b* only) were down-weighted to half the value of third-position transversions. This

FIG. 3. Single most-parsimonious tree obtained for a combined analysis of both genes after removing third positions from the cytochrome-*b* sequences (length, 1,971; consistency index, 0.466; retention index, 0.574). Percentages are the values of 500 bootstrap replications; numbers in front of the nodes are branch support values.

resulted in two equally parsimonious trees of 3,157 steps. The consensus tree (Fig. 2B) did not support monophyly of the New World genera. In this tree, quetzals are placed as a sister group of the Asian trogons, a relationship not supported in the bootstrap test. Once third-position transitions were down-weighted to a ratio of 0.2:1 with respect to transversions, the New World genera formed a monophyletic clade (Fig. 2C). The interrelationships among the New World, Asian, and African trogons, however, were unresolved. Further down-weighting third-position transitions (from 0.1 to 0.025 transitions per transversion) consistently produced two alternative trees of 2,673 steps. The consensus of these trees placed the African trogons as the most basal lineage, and the Asian trogons as the sister taxa to the New World trogons (Fig. 2D). Although in this analysis, the polytomy in the "Elegant subclade" within *Trogon* was resolved, the relationships among the New World genera were ambiguous.

Based on the above results, I excluded third-position cyt *b* from the data matrix and performed a new parsimony analysis, which resulted in a single most-parsimonious tree of 1,971 steps in length (Fig. 3). In this phylogenetic hypothesis, all the genera were resolved as monophyletic and supported by high bootstrap values (>80%) as well as branch support (>6). The New World genera were monophyletic, and their sister taxon was *Harpactes* (Asian trogons). The most basal group was the African genus *Apaloderma*. Within the New World lineage, the two subclades of *Trogon* were recovered and the interspecies relation-

ships were congruent with those obtained in the previous analyses (Fig. 2D). The sister group to *Trogon* was the lineage formed by *Euptilotis-Pharomachrus*. Finally, *Priotelus temnurus* was the sister taxon to the rest of the New World genera. This phylogenetic hypothesis remained constant even when the taxa included in the outgroup were changed. By removing the saturated partition within cyt *b*, a considerable amount of noise was eliminated, reducing the length of the tree by 1,789 steps (i.e. from 3,760 steps equal weights to all nucleotides, to 1,971 steps without the 381 third-codon positions). In spite of the noise elimination, however, the support values for the nodes linking different genera did not improve significantly. The nodes linking the New World genera to *Priotelus* and then to *Harpactes* were lost in trees one step longer than the most-parsimonious solution.

Discussion

On the origin and distribution of Trogoniformes.—From the standpoint of biogeography, the trogons have been an enigma because of their Pantropical distribution (Darlington 1957). Their current distribution coincides with the distribution of several other avian families (e.g. Anhingidae, Capitonidae, Heliornithidae, Jacanidae, Psittacidae) and other vertebrates (e.g. crocodilians and caecilians). Congruent biogeographic patterns between or among taxa can be explained by two processes: speciation of widespread taxa after a vicariant event, or multiple dispersal events. Although vicariance requires the fewest ad hoc assumptions to justify distribution patterns, it depends on phylogenetic congruence using corroborated phylogenies for other taxa. These are currently unavailable.

Reconstruction of ancestral distribution areas can be addressed for trogons. Early hypotheses pointed to the New World as the center of origin for these birds (Swainson 1837, Ridgway 1911). This idea was based on the high diversity of trogons in the Neotropics (64% of species). Cain (1971), however, argued that the area in which most species of a particular group are distributed may be a secondary center of diversification. Therefore, relative species richness may be false evidence for inferring the ancestral area of a taxon. Traditional vicariance biogeography assumes that the ancestral area must be considered as the sum of all the areas in which the group is found. However, this implies that the distribution of the ancestor was more widespread than that of any of its descendants (Bremer 1992). Recently, Bremer (1992, 1995) proposed a method for estimating the relative probability that different areas were part of the ancestral area of the group. This relative probability is computed based on a gain-loss ratio of individual areas after being coded as binary characters on a cladogram assuming irreversibility.

Applying Bremer's method to the cladogram proposed here (Fig. 3), Africa has a probability of 1.0 because it has been gained once on the *Apaloderma* lineage and then lost once on the clade encompassing the remaining genera. Asia and the New World each receive a probability of 0.5. Asia is gained on the lineage leading to *Harpactes*, then is lost once in *Apaloderma*, and once in the New World clade. In the same manner, the New World is gained once in the clade formed by the Neotropical genera and then lost once in *Apaloderma* and once in *Harpactes*. Therefore, the idea of a Neotropical origin is not supported. Instead, an African origin for trogons seems a reasonable conclusion, with the New World representing a secondary center of radiation. Ronquist's (1994, 1995) method, as well as Brundin's (1981, 1988) progression rule, identify Africa as being the ancestral area of the Trogoniformes.

Additional evidence supporting an Old World origin for trogons comes from paleontology. The oldest described fossils within the family Trogonidae have been found in Tertiary deposits of Europe (Olson 1985). The earliest fossil comes from the middle Oligocene of Switzerland and has been referred to *Protornis glarniensis*. This species clearly shows the heterodactyl condition typical of the Trogonidae (Olson 1976). Another fossil species, *Paratrogon gallicus*, was recovered from lower Miocene deposits at Langy, France (Olson 1976). Currently, Gerald Mayr (pers. comm.) is describing a new fossil trogon from the Middle Oligocene (33 million years ago) of Céreste, France. In contrast, the oldest fossils discovered in the New World belong to two extant species (*Priotelus roseigaster* and *Trogon surrucura*), which are known from Pleistocene deposits from the Do-

minican Republic and Brazil, respectively (Brodkorb 1971).

Considering that Africa is one of the largest continents, how can one explain that only 8% of the extant species of trogons are distributed there? In general, the overall biological diversity of Africa is relatively low compared with other tropical areas (Keast 1973). Identifying all of the possible elements that determine diversity patterns though time and space is extremely difficult. Many different physical, historical, and biological factors have been correlated with almost every pattern of variation in species diversity (Huston 1994). The principle of competitive exclusion (Hardin 1960) might be one of the factors that could be invoked for the smaller number of species of trogons in Africa and Asia versus the Neotropics. The Old World species of trogons are insectivorous, whereas the New World species feed on a mixture of fruits and animals. Possibly, the fruit-eating niches in the Old World are taken by avian families that are poorly represented or completely missing in the New World (e.g. Bucerotidae, Musophagidae, Irenidae, Pycnonotidae). Consequently, a decrease in competition pressure may have resulted in radiation toward new niches in the New World.

Other factors that have been associated with species diversity are structural and climatic heterogeneity of the habitat (Schluter 1988, Huston 1994). During phases of glacial aridity, the rain forest in the Amazon and Southeast Asia shrank to isolated refugia (Roberts 1984), possibly constituting favorable conditions for the speciation of the populations restricted in these areas. Compared with Southeast Asia and the New World, the tectonic history of Africa was relatively stable during the last 40 million years without being affected by the rise of extensive mountain ranges (Potts and Behrensmeyer 1992). Thus, a high diversity in Southeast Asia and especially in the New World may be a direct consequence of the great orogenic activity during the late Cenozoic due to the collision of continental plates, and not the result of a long history of the avifauna within such areas.

Absolute dates of diversification for trogons are unknown owing to the lack of an extensive fossil record. Nonetheless, the problem of dating can be approached through molecular studies. Several authors have suggested that approximate times can be estimated based on differences in nucleotide substitutions in mitochondrial DNA (Brown et al. 1982, DeSalle et al. 1987, Miyamoto and Boyle 1989, Irwin et al. 1991). The existence of a molecular clock has been questioned because of evidence showing that different regions of the genome evolve at different rates in different lineages (Martin et al. 1992, Martin and Palumbi 1993). Most of these examples involve lineages whose species exhibit significant differences in body size, metabolic rate, or generation time. Trogons, by contrast, are rather uniform in body size and generation time.

Characteristics observed in the sequences of the cyt-*b* gene of trogons (Tables 1–3) are similar to those observed in albatrosses (order Procellariiformes), in which corrected third-position divergence was estimated at a rate of 1.58% and 2.86% for per million years (Nunn et al. 1996). Using these estimates, and assuming that the corrected third-position divergence among the trogons is linear with respect to time, a rough date for the separation times among genera can be suggested. The genera *Pharomachrus* and *Euptilotis* diverged 13.8 to 25 million years ago (Mya). If we compare these dates with others estimated for corvine birds (Helm-Bychowski and Cracraft 1993), the trogons represent a relatively old divergence within birds. A mean value of 51.5% for pairwise corrected third position divergence gives estimates of the date of origin for the Neotropical trogons between 18 and 32.6 Mya. The split of the African trogons with the rest of the genera occurred between 19.7 to 35.6 Mya. Even with such broad estimates, these data suggest that the radiation of the major clades of trogons, especially among Africa, Asia, and the New World may be characterized as a star phylogeny. If the major clades diversified rapidly, that might be responsible for the problems in recovering a stable signal during cladistic analysis. Finally, trogons diverged from their sister taxon (i.e. Coliiformes) between 25.5 to 46.1 Mya. This estimate is consistent with the date suggested by the oldest fossils described for trogons (Olson 1976, 1985). An undescribed fossil heterodactyl bird recovered from the Lower Eocene (53 Mya) London Clay of Essex (G. Mayr pers. comm.), however, indicates that the Trogoniformes origin should be earlier

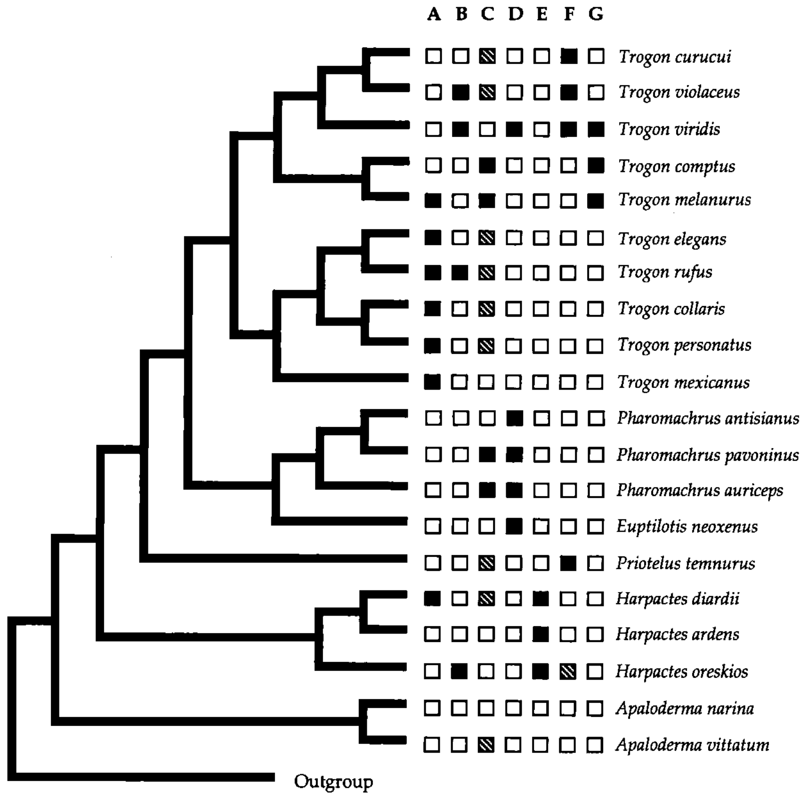

FIG. 4. Evolutionary tendencies in the coloration pattern of trogon feathers. (A) White pectoral line dividing the chest and belly color: absent (white); present (black). (B) Color of the belly: red (white); yellow (black). (C) Coloration pattern on tail feathers: one white spot at the tip of the feather (white); multiple white bands (hatched); no white pattern (black). (D) White spots on the secondary feathers: present (white); absent (black). (E) Color of the back: green (white); brown (black). (F) Color of the head: same color as the back (white); gray (hatched); violet (black), and (G) Color of the rump: same color as the back (white); violet (black).

than the date suggested by the present calibration.

Coloration patterns.—Without question, one of the most attractive features of trogons is their plumage. Indeed, the Resplendent Quetzal was considered a sacred bird in many pre-Columbian cultures of the New World because of its coloration. The brightest colors and more complex coloration patterns occur mainly on regions of the body that are involved during display (i.e. head, upper back, breast, tail, and surface of the wings). Less-exposed areas like the underparts of the body usually present dull colors and in most cases lack special patterns. A corroborated phylogeny reveals evolutionary tendencies in the coloration pattern of trogons. Because color and color patterns in trogons have a strong sexual component, the following discussion is based mainly on male plumages.

For most species, the ventral coloration pattern can be divided into two regions: (1) the chin, throat, and upper portion of the breast (which usually show the same color as the head or the back); and (2) the lower portion of the breast and the belly, which typically are red or yellow. These two regions are divided by a white band in some species. This white band has evolved independently at least three times within the order, once in the Asian trogons (*H. diardii*) and twice in the genus *Trogon*. This white band represents a synapomorphy for the Elegant subclade (Fig. 4A). "Red belly" can be interpreted as ancestral within the group, and the derived condition "yellow belly" evolved

once in the Asian trogons (*H. oreskios*) and independently (twice) in *Trogon* (Fig. 4B).

White bands on the tail are complex because patterns depend on sex and age. Nevertheless, the presence of this character can be interpreted as the primitive condition, apparently evolving in two contrasting directions. It has transformed either from a single band located at the tip of the feather to multiple bands, or from one band to no bands (Fig. 4C).

Multiple white spots on the secondary feathers, which are more evident in males, vary from a random distribution of tiny dots to clearly defined white bands. The presence of any of these patterns is the plesiomorphic condition for trogons, whereas the apomorphic state is the loss of white pattern (i.e. secondaries plain black). This derived condition has appeared independently twice, once in *T. viridis* and once in the *Pharomachrus-Euptilotis* clade, in which the loss of white pattern represents a synapomorphy (Fig. 4D).

Coloration of the dorsal region can be divided into three general areas: (1) the head, (2) the back, and (3) the rump. Brown back color in males is a synapomorphy for the Asian trogons. Thus, the presence of a green back is plesiomorphic (Fig. 4E). The color of the other two dorsal regions (head and rump) is correlated with the back color. The plesiomorphic state for these two regions is brown in the Asian trogons and green in the African and New World trogons. Head color presents at least two derived states, gray and violet. Violet heads evolved twice in the New World genera (*Priotelus temnurus*, and in three species of the Violaceous subclade), whereas gray heads evolved at least once within the Asian trogons (Fig. 4F).

Finally, for most of the species I examined the rump was the same color as the back, the only exception was for three species: *Trogon melanurus*, *T. comptus*, and *T. viridis* have violet rumps that represent the only derived condition observed for this character (Fig. 4G).

Evolution of iridescent structures in trogon feathers.—Plumage iridescence is widespread in birds. In most bird groups like hummingbirds and sunbirds, the interference granules responsible for the production of iridescent colors are relatively uniform in design and composition across species (Dorst 1951, Durrer and Villiger 1962). In trogons, Durrer and Villiger (1966) described four different levels of structural complexity in these granules. Quetzals have the most complex kind of iridescence, with barbules possessing from five to eight layers of elliptical platelets forming a continuous mosaic on the iridescent surface of the feather. These platelets are made of melanin filled with air capsules divided by extensions of the platelet wall. The layers of platelets are separated by layers of keratin. In *Trogon*, the melanin granules are air-filled rods that are packed so tightly that practically no keratin separates them. Trogons are less brilliant than quetzals because the rod arrangement only allows light to pass at an angle of 30°, thereby producing a relatively weak iridescent effect (Durrer and Villiger 1966). The difference in color intensity between the species of trogons is due mainly to changes in the diameter of the rods. Thick rods produce golden glows, whereas thin rods tend to produce blue tones. The other two structural patterns in the iridescent granules are variations from that described for *Trogon*. In *Priotelus*, the total diameter of the rod is similar to that in *Trogon* (0.2 μ), but the melanin wall is thicker in *Priotelus* than in *Trogon* (0.08 μ and 0.04 μ, respectively). Another difference between these genera is that in *Priotelus*, the melanin rods are clearly divided by keratin layers. Finally, in *Harpactes* and *Apaloderma*, the diameter of the rods is larger than in *Priotelus*, and the keratin layers dividing the rods are more than twice as thick as in *Priotelus* (Durrer and Villiger 1966).

According to the phylogeny obtained in the present study, the least-iridescent structures occur in African and Asian trogons, which are the most basal lineages (Fig. 5). These large rods divided by thick layers of keratin are relatively similar to the iridescent structures found in other birds (Dorst 1951; Durrer and Villiger 1962, 1966). In derived lineages, rod diameter and thickness of the melanin wall are reduced. Concomitant with this are a reduction in the thickness of the keratin layer, an increment in the number of rods, and a displacement of the rods toward the external surface of the barbules. The more complex structures found in quetzals can be explained as a step further in the tendency toward an increased number of rods on the surface of the barbules, finally leading to the fusion of multiple air-filled rods into elliptical platelets.

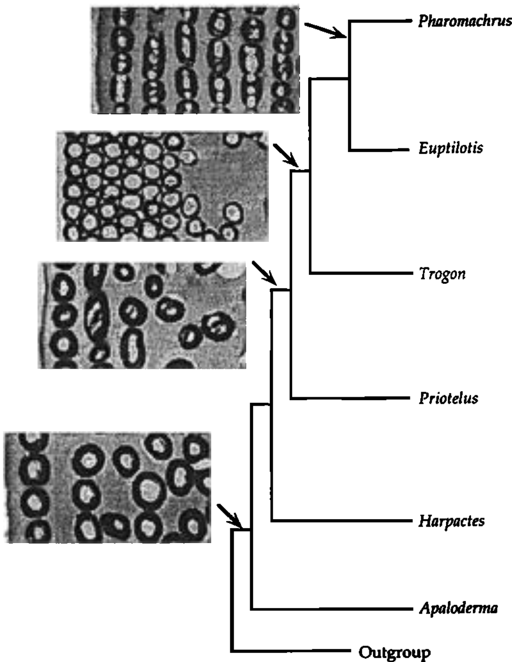

FIG. 5. Most-parsimonious scenario for the evolution of iridescent structures in the feathers of trogons. Electron microscope photographs were scanned from Durrer and Villiger (1966). Photographs were taken using a 30,000:1 magnification scale.

A phylogenetic classification of the genera of Trogoniformes.—Useful classifications should be based on a corroborated phylogeny, and the classification must reflect the historical relationships of the taxa encompassed within that group. Based on my tree (Fig. 3), I recommend the following phylogenetic classification for genera within the Trogoniformes:

ORDER Trogoniformes
FAMILY Trogonidae
Subfamily Apalodermінae
GENUS *Apaloderma*
Subfamily Trogoninae
Tribe Harpactini
GENUS *Harpactes*
Tribe Trogonini
GENUS *Priotelus*
GENUS *Trogon*
GENUS *Pharomachrus*

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