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# Molecular Systematics of Tanagers (Thraupinae): Evolution and Biogeography of a Diverse Radiation of Neotropical Birds

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**The tanagers (Passeriformes: Emberizidae: Thraupinae) are a diverse group of mostly Neotropical birds with a wide range of feeding morphologies, behaviors, plumage patterns and colors, and habitat preferences. Phylogenetic relationships of genera in this lineage were investigated using cytochrome *b* sequence data. This study indicates that the genera *Euphonia* and *Chlorophonia* (traditionally considered part of Thraupinae) do not form a monophyletic group with the other tanagers. Within the rest of Thraupinae, several monophyletic groups are identified that agree with traditional sequential taxonomies. Other monophyletic groups provide novel interpretations of biogeographic patterns and morphological evolution within tanagers. In several lineages, plumage patterns and colors persist despite dramatic changes in bill morphology. Phylogenetic structure and estimated timings of divergence events indicate that tanagers probably originated on Caribbean islands and later diversified throughout Central and South America during the mid-Tertiary.** © 1997 Academic Press

## INTRODUCTION

The tanagers (Passeriformes: Emberizidae: Thraupinae) represent a major Neotropical radiation (Sibley and Ahlquist, 1985, 1990) encompassing a diversity of feeding morphologies and behaviors. The 242 species (Storer, 1970; Isler and Isler, 1987) in this group are primarily tropical and occur in South, Central, and North America as well as islands in the Caribbean. Although often thought to be primarily fruit-eating, they include a wide variety of feeding specializations. Some species are primarily nectar-feeding, others are largely seed-eaters, and some feed on insects. Many species have a more generalized diet, feeding on various combinations of these items. This diversity of feeding types corresponds to that of Galapagos finches and Hawaiian honeycreepers, but in tanagers this evolution has occurred on a continental scale (Sibley and Ahlquist, 1985). Perhaps the most striking feature of this subfamily is the brilliance and variety of colors seen in many of the species. Often these colors are present in conspicuous, contrasting patterns. Although most species are colorful, many tanagers have nondescript, cryptic plumage. Tanagers also vary in whether or not these plumage colors are sexually dimorphic. Roughly half of the species are sexually dichromatic with males having more brightly colored plumage than females. Ranging in mass from 9 to 114 g (Isler and Isler, 1987), tanagers also vary greatly in overall body size. Tanagers also show differences in their nesting habits, breeding biology, foraging strata, tendency to migrate, and other aspects of behavior (Isler and Isler, 1987). The study of the evolution of this morphological and behavioral diversity, and the biogeographic history of this group, has been hindered by the lack of a phylogeny.

Several linear classifications of tanagers (e.g., Sclater, 1886; Ridgway, 1902; Hellmayr, 1936; Storer, 1970) have been proposed in which species are listed sequentially according to presumed evolutionary relationships. Studies which provide more rigorous phylogenies and phenograms included relatively few representatives of Thraupinae as the goals of these studies were often broader in scope than the phylogeny of this subfamily. Raikow (1978; 1985), for example, included 14 of the 59 genera of Thraupinae (as defined by Storer, 1970) in his phylogeny of nine-primaried oscine passerines. He devised hypotheses about relationships among these taxa based on limb musculature, bill shape, and feeding behavior. Using DNA–DNA hybridization data, Bledsoe (1988) also investigated relationships among nine-primaried oscines. He included only six tanagers in his study. Sibley and Ahlquist's (1985, 1990) monumental DNA–DNA hybridization study of the birds of the world included more taxa than Bledsoe's (1988) study, but sampled only 25 representatives of Thraupinae. To identify the outgroup to the tanager genus *Phaenicophilus*, McDonald (1988) surveyed allozyme variation in 9 genera and morphologic variation among

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8 genera. Webster (1988) provided the only comprehensive character study of Thraupinae. He described 36 skeletal characteristics of 191 species from 57 genera of Thraupinae; however, he did not include a character matrix or a phylogeny based on these characters. No previous study has involved both a comprehensive survey of Thraupinae and a cladistic analysis of character state data. Using a 1045-bp region of the cytochrome *b* gene from the mitochondrion, this study presents the first comprehensive phylogeny for genera in this lineage.

## MATERIALS AND METHODS

### *Taxon Sampling and Outgroup Choice*

Individuals representing 47 of the 57 genera currently placed within Thraupinae (Storer, 1970) were used in this study (Table 1). Also included as tanagers in this study are an individual of *Nephelornis* (a monotypic genus described since Storer (1970)) and an individual of *Tersina* (placed in the monotypic subfamily Tersininae by Storer (1970)). For two genera (*Piranga* and *Ramphocelus*) and for two species (*Spindalis zena* and *Phaenicophilus palmarum*), more than one individual was used to determine the appropriateness of representing each genus by only a single exemplar. Sequences of *Ramphocelus passerinii passerinii* and *R. sanguinolentus* were obtained from GenBank (Accession Nos. U15717 and U15718; Hackett, 1996) and sequences of *P. palmarum, S. zena* (from the Bahamas), *Nesospingus speculiferus* and *Thraupis bonariensis* were provided by N. K. Klein (personal communication). Sequences of four other tanagers used in this study (*Piranga erythrocephala, Piranga olivacea, Habia rubica,* and *Chlorothraupis carmioli*) are from a previous study (Burns, 1996; Burns, submitted for publication).

Choosing an outgroup to Thraupinae is problematic because the monophyly of tanagers is questionable (Sclater, 1886; Ridgway, 1902; Storer, 1969; Sibley and Ahlquist, 1990). Currently, this group is considered a subfamily of the family Emberizidae (AOU, 1983), which includes five other subfamilies: Icterinae (blackbirds), Parulinae (wood warblers), Emberizinae (sparrows), Coerebinae (bananaquits), and Fringillinae (cardinals and grosbeaks) (AOU, 1983). Of these subfamilies, two studies have shown that tanagers are monophyletic with respect to warblers (Bledsoe, 1988; Sibley and Ahlquist, 1990). In addition, morphological (Raikow, 1978) and DNA hybridization (Sibley and Ahlquist, 1990) studies have shown warblers to be basal to tanagers. Therefore, as outgroups to the tanager genera, I used three species of wood warblers: *Vermivora celata,* (this study), *Basileuterus culicivorus* (C. Cicero and N. K. Johnson, personal communication), and *Dendroica coronata* (C. Cicero and N. K. Johnson, personal communication). Several representatives of warblers were included to increase tree balance and to reduce the effects of long branch lengths on rooting the tanager taxa (Smith, 1994). Because the relationships of some tanager taxa to other Emberizidae have been questioned, the tree of warbler and tanager relationships was rooted using a nonemberizine passerine of the family Corvidae, *Cyanocitta cristata* (Helm-Bychowski and Cracraft, 1993; GenBank Accession No. X74258).

### *DNA Isolation and Sequencing*

DNA extracts were prepared from liver or muscle tissue preserved in 95% ethanol (*P. erythrocephala*), preserved in phenoxyethanol (*P. palmarum*), or frozen at −80°C (all other taxa included in this study). Extractions were performed using a 5% Chelex solution (Walsh *et al.*, 1991) or by NaCl extraction (Miller *et al.*, 1988). Specific fragments of the cytochrome *b* gene were then amplified using polymerase chain reaction (PCR) and six different primers (Burns, 1996, submitted for publication). A typical double-stranded amplification involved an initial denaturing at 92°C for 3 min, 3 initial cycles (45 s at 93°C, 45 s at 45°C, 45 s at 72°C), 32 additional cycles (1 min at 93°C, 1 min at 50°C, 1 min at 72°C), and a final extension of 72°C for 3 min.

For some fragments, agarose plugs of double-stranded products were taken using Pasteur pipets and diluted in 250 μl of low TE buffer. Plugs were then melted and 25 μl of this solution was amplified asymmetrically (Gyllensten and Erlich, 1988) in a 50-μl total reaction under the following conditions: an initial denaturing at 92°C for 3 min, 36 cycles (1 min at 93°C, 1 min at 50°C, 1 min at 72°C), and a final extension of 72°C for 3 min. The resulting single-stranded DNA product was cleaned in a spin column (MicroSpin s-300 HR Columns, Pharmacia Biotech, Inc.) to remove excess primers. Seven microliters of the cleaned product was then sequenced using DNA polymerase (Sequenase version 2.0, United States Biochemical Corp.) and Sanger dideoxy chain-termination (Sanger *et al.*, 1977). Sequencing products were run for 2–7 h on a 6% polyacrylamide–8.3 M urea gel and then visualized using autoradiography.

For most fragments, double-stranded products were cycle sequenced using fluorescent dye-labeled terminators. Prior to cycle sequencing, double-stranded DNA fragments were cleaned using a spin column (MicroSpin s-300 HR Columns, Pharmacia Biotech, Inc.). The resulting product was cycle sequenced (ABI Prism Dye Terminator Cycle Sequencing Ready Reaction kit with AmpliTaq DNA Polymerase, FS; Perkin Elmer) for 24 cycles under the following conditions: 30 s at 96°C, 15 s at 50°C, and 4 min at 60°C. DNA was precipitated using 70% ethanol and resuspended in formamide/blue dextran. Samples were run on a 4.8% Page Plus (Amresco) acrylamide gel for 7 h on an ABI Prism 377 using the Run 2XA module. Sequence Navigator Version 1.0.1 (Applied Biosystems, Perkin–Elmer) was used to reverse complement opposing directions, to align differ-

**TABLE 1**

**Species Names, Voucher Numbers, and Locality Information of Individuals Sequenced for This Study**

| Species | Museum | Number | Locality |
|---|---|---|---|
| *Anisognathus flavinuchus* | LSUMNS | B-566 | Peru: Dept. Puno, Abra de Maruncunca, 10 km SW San Juan del Oro |
| *Buthraupis montana* | LSUMNS | B-365 | Peru: Dept. Cajamarca, Cerro Chinguela, 5 km NE Sapalache |
| *Calochaetes coccineus* | LSUMNS | B-6134 | Ecuador: Prov. Morona-Santiago, W Slope de Cutucci Yapitya |
| *Chlorochrysa calliparaea* | LSUMNS | B-8103 | Peru: Dept. Pasco, Playa Pampo, 8 km NW Cushi |
| *Chlorophanes spiza* | LSUMNS | B-2838 | Peru: Dept. Loreto, 1 km N Rio Napo, 157 km by river NNE Iquitos |
| *Chlorophonia flavirostris* | LSUMNS | B-11778 | Ecuador: Prov. Esmeraldas, El Placer |
| *Chlorornis riefferii* | LSUMNS | B-1859 | Peru: Dept. Pasco, Cumbre de Ollon, about 12 km E Oxapampa |
| *Chlorospingus pileatus* | LSUMNS | B-19947 | Costa Rica: Prov. San Jose, Villa Mills, km 95 Pan American Hwy |
| *Chlorothraupis carmioli* | LSUMNS | B-5510 | Peru: Dept. San Martin, 28 km NE Tarapoto |
| *Chrysothlypis chrysomelas* | LSUMNS | B-2189 | Panama: Prov. Darien, about 6 km NW Cana |
| *Cissopis leveriana* | LSUMNS | B-1143 | Bolivia: Dept. La Paz, Rio Beni, ca. 20 km by river N. Puerto Linares |
| *Cnemoscopus rubrirostris* | LSUMNS | B-5624 | Peru: Dept. Amazonas, 30 km by road E Florida on road to Rioja |
| *Conothraupis speculigera* | LSUMNS | B-5127 | Peru: Dept. Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 km by road from Olmos |
| *Creurgops dentata* | LSUMNS | B-580 | Peru: Dept. Puno, Abra de Maruncunca, 10 km SW San Juan del Oro |
| *Cyanerpes caeruleus* | LSUMNS | B-14737 | Bolivia: Dept. Santa Cruz, Serrania de Huanchaca, 25 km SE Catarata Arco Iris |
| *Cypsnagra hirundinacea* | LSUMNS | B-15290 | Bolivia: Dept. Santa Cruz, Velasco, Parque Noel Kempff Mercado, 30 km E Aserradero Moira |
| *Dacnis cayana* | LSUMNS | B-15077 | Bolivia: Dept. Santa Cruz, Velasco, 13 km SW Piso Firme |
| *Delothraupis castaneoventris* | LSUMNS | B-6931 | Peru: Dept. Huanuco, Quebrada Shugush, 30 km on Huanuco-La Union road |
| *Diglossa lafresnayii* | LSUMNS | B-351 | Peru: Dept. Cajamarca, Cerro Chinguela, 5 km NE Sapalache |
| *Dubusia taeniata* | LSUMNS | B-7710 | Peru: Dept. Huanuco, Unchog Pass NNW Acomayo |
| *Eucometis penicillata* | LSUMNS | B-6551 | Bolivia: Dept. Santa Cruz, Rio Quizer |
| *Euphonia laniirostris* | LSUMNS | B-18375 | Bolivia: Dept. Santa Cruz, Velasco, Parque Nacional Noel Kempff Mercado, 86 km ESE Florida |
| *Habia rubica* | MVZ | 168909 | Paraguay: Dept. Itapu, El Tirol, 19.5 km by road NNE Encarnacion |
| *Hemispingus atropileus* | LSUMNS | B-1889 | Peru: Dept. Pasco, Cumbre de Ollon, about 12 km E Oxapampa |
| *Hemithraupis flavicollis* | LSUMNS | B-5102 | Peru: Dept. Loreto, S Rio Amazonas, ca. 10 km SSW mouth Rio Napo on E bank Quebrada Vainilla |
| *Heterospingus xanthopygius* | LSUMNS | B-2324 | Panama: Prov. Darien, Cana on E slope Cerro Pirre |
| *Iridosornis analis* | LSUMNS | B-1706 | Peru: Dept. Pasco, Santa Cruz, about 9 km SSE Oxapampa |
| *Lamprospiza melanoleuca* | LSUMNS | B-9678 | Bolivia: Dept. Pando, Nicolas Suarez, 12 km by road S of Cobija, 8 km W on road to Mucden |
| *Lanio versicolor* | LSUMNS | B-1014 | Bolivia: Dept. La Paz, Rio Beni, ca. 20 km by river N. Puerto Linares |
| *Mitrospingus cassinii* | LSUMNS | B-11802 | Ecuador: Prov. Esmeraldas, El Placer |
| *Nemosia pileata* | LSUMNS | B-7295 | Peru: Dept. Loreto, Amazonas I. Pasto, 80 km NE Iquitos |
| *Neothraupis fasciata* | LSUMNS | B-13914 | Bolivia: Dept. Santa Cruz, Serrania de Huanchaca, 45 km E Florida |
| *Nephelornis oneilli* | LSUMNS | B-8402 | Peru: Dept. Pasco, Millpo, E. Tambo de Vacas on Pozuzo-Chaglla trail |
| *Oreomanes fraseri* | LSUMNS | B-2069 | Peru: Dept. Lima, about 13 road km W. Milloc |
| *Phaenicophilus palmarum* | LSUMNS | B-20106 | Haiti: Artibonite Department, W of Boriqne Rt. from Pte-de-Paix to O'Kap, W Capitarian |
| *Pipraeidea melanonota* | LSUMNS | B-12070 | Ecuador: Prov. Pinchincha, Mindo |
| *Piranga erythrocephala* | MZUNAM | BMM 496 | Mexico: Sinaloa, La Laguna, 1 km E Loberas |
| *Piranga olivacea* | LSUMNS | B-19750 | USA: Louisiana, Iberville Parrish, 4 mi N St. Gabriel, 435 Pecan Drive |
| *Pyrrhocoma ruficeps* | MVZ | 165617 | Paraguay: Dept. Itapu, El Tirol, 19.5 km by road NNE Encarnacion |
| *Schistochlamys melanopsis* | LSUMNS | B-9669 | Bolivia: Dept. Pando, Nicolas Suarez, 12 km by road S of Cabija, 8 km W on road to Mucden |
| *Sericossypha albocristata* | LSUMNS | B-5630 | Peru: Dept. Amazonas, 30 km by road E Florida on road to Rioja |
| *Spindalis zena* | LSUMNS | B-11442 | Puerto Rico: Cabo Rojo, Llanos Costa, 0.5 km NNW mouth Arroyo Cazul |
| *Tachyphonus surinamus* | LSUMNS | B-4795 | Peru: Dept. Loreto, S Rio Amazonas, about 10 km SSW Rio Napo |
| *Tangara gyrola* | LSUMNS | B-4258 | Peru: Dept. Loreto, Lower Rio Napo region, E bank Rio Yanayacu, ca 90 km N Iquitos |
| *Tersina viridis* | LSUMNS | B-9680 | Bolivia: Dept. Pando, Nicolas Suarez, 12 km by road S of Cobija, 8 km W on road to Mucden |
| *Thlypopsis sordida* | LSUMNS | B-7260 | Peru: Dept. Loreto, Amazonas I. Pasto, 80 km NE Iquito |
| *Vermivora celata* | MVZ | 169123 | USA: California, San Benito Co. |
| *Xenodacnis parina* | LSUMNS | B-7760 | Ecuador: Prov. Azuay |

*Note.* LSUMNS, Louisiana State University Museum of Natural Science; MVZ, Museum of Vertebrate Zoology at the University of California at Berkeley; MZUNAM, Museo de Zoologia, Falcultad de Ciencias, Universidad Nacional Autonoma de Mexico.

ent fragments from the same individual, and to translate complete sequences into amino acids.

Accuracy of DNA sequencing was verified in five ways: (1) sequencing both heavy and light strands of most PCR fragments, (2) using overlapping fragments of cytochrome *b* (approximately 30% of the total sequence is overlapped by two fragments), (3) sequencing some individuals more than once, (4) comparing sequences of *Phaenicophilus* and *Spindalis* with samples of the same species sequenced in another lab (N. Klein, personal communication), and (5) comparing levels of sequence divergence separately for the three fragments sequenced in each individual (as suggested by Hackett *et al.* (1995)).

To check for the presence of nuclear copies, mtDNA was purified from four individuals (*Habia rubica, Nephelornis oneilli, Cypsnagra hirundinacea,* and *Euphonia laniirostris*) using the Magic Miniprep Kit from Promega. Cytochrome *b* sequences from these samples were identical to those obtained from the same individuals using extractions that did not purify mtDNA.

The resulting sequences include 1045 base pairs of cytochrome *b* and part of the threonine t-RNA with the intervening spacer region. For this study, only the cytochrome *b* portion of the sequences were used (from base 14,991 to base 16,035 relative to the published sequence of *Gallus gallus;* Desjardins and Morais, 1990). Percentage sequence divergence was calculated as the number of nucleotide differences between two sequences divided by the total number of nucleotides compared (*p* distance of Nei, 1987). The distance between two sequences was also calculated using Kimura's (1980) 2-parameter model of sequence evolution. This measure of distance is a maximum-likelihood estimate of sequence difference that corrects for multiple substitutions at sites and the higher rate of transition relative to transversion changes.

### *Phylogenetic Analyses*

Phylogenetic analyses were carried out using parsimony as implemented in test version 4.0d54 of PAUP* provided by D. L. Swofford. Sequences were analyzed using the heuristic option with 200 random addition replicates for each analyses. Data were analyzed with all characters given equal weight and using weighting schemes designed to correct for multiple substitutions at a given site. Relative support for different nodes was assessed using 100 bootstrap replicates (Felsenstein, 1985) with 10 random addition replicates per bootstrap replicate.

For molecular sequence data, only five possible characters can occur at a given site (four nucleotides or a gap). Thus, a site may easily become saturated if changes at that site repeat themselves. To explore the possibility that some types of base substitutions have become saturated, I plotted *p* distance versus Kimura's 2-parameter distances for first-, second-, and third-position sites. Saturation was judged to have taken place if the resulting scatterplots did not indicate a linear relationship between the two types of distances and if the data did not fall on the line $y = x$ (see Berbee *et al.,* 1995). A nonlinear relationship would indicate that the Kimura estimate has adjusted the original distance estimate based on the differences in substitution rates between transitions and transversions.

After determining that third-position sites were saturated for transitions (see below), I performed additional analyses using *a priori* and *a posteriori* methods of weighting characters. I first attempted to correct for noise at third-position sites by giving third-position transitions a weight one-sixth of the weight given to other characters. To accomplish this, I gave third-position transitions a weight of one and all other characters a weight of six using the stepmatrix option in PAUP. The ratio of 6:1 was obtained empirically from examining multiple sequences from each of two of the genera used in this study: *Piranga* (Burns, 1996; Burns submitted for publication) and *Ramphocelus* (Hackett, 1996). Different approaches to downweighting transitions include using the observed ratio among all taxa included in the study, arbitrarily choosing a ratio, or using a ratio observed in a set of taxa distantly related to the ones currently being studied. Because close relatives will have fewer multiple substitutions at a given site, examining the transition bias among closely related individuals is a more accurate way of determining actual transition bias than using the ratio observed among all species included in the study (Edwards, 1997). Using an arbitrarily chosen ratio or a ratio determined from distantly related taxa does not take advantage of the existing data and ignores differences in transition bias among taxonomic groups (Edwards, 1997).

I also weighted characters using the method of successive approximation (Farris, 1969, 1989; Carpenter, 1988). Trees were first constructed by giving all characters equal weight. Weights were then assigned *a posteriori* by using the maximum value of the rescaled consistency index. This process was repeated until a stable topology or set of topologies was reached (Farris, 1969, 1989; Carpenter, 1988). Thus, successive approximation of characters gives less weight to more variable characters. This method ignores the type of character change (transition or transversion) occurring at a site. Thus, if many transition changes occur at a particular site, all changes at that site (including transversions) would be downweighted. However, one advantage of successive approximation over weighting characters based on observed transition bias is that successive approximation does not assume a particular constant weight across all parts of the gene. Thus, if rates of substitution vary in different regions of the cytochrome *b* gene, successive weighting would downweight those areas that are more variable.

## RESULTS

### *Sequence Variation*

As expected for a protein coding mitochondrial gene, all sequences (GenBank Accession Nos. AF006211–AF006258) aligned without gaps or insertions. Of the 1045 sites, 489 (47%) were variable. Levels of uncorrected sequence divergence (*p* distance) among different genera of Thraupinae ranged from 6.2 to 16.4%. The highest levels of intergeneric divergence were between *Chlorophonia* or *Euphonia* and the other genera, while the lowest level was between the genera *Cissopis* and *Schistochlamys.* Low levels of sequence divergence were also found among mountain tanagers and relatives (the genera *Delothraupis, Dubusia, Buthraupis, Anisognathus,* and *Chlorornis*) and among *Hemispingus* and relatives (Fig. 1). Low levels of sequence divergence were also observed between individuals of the same species (*p* distance: *Spindalis zena* 6.7%; *Phaenicophilus palmarum* 0.2%) and of the same genus (*p* distance: *Piranga:* 8.2%; *Ramphocelus:* 9.6%). Base composition (guanine 13.5%, adenine 26.6%, thymine 24.9%, cytosine 35.0%) was similar to that reported in other studies of birds (Edwards *et al.,* 1991; Helm-Bychowski and Cracraft, 1993; Kornegay *et al.,* 1993; Hackett, 1996; Zink and Blackwell, 1996). Changes at third-position sites were more common than changes at second- and first-position sites (Fig. 2). Of the 489 variable sites, 115 occurred at the first codon position, 40 occurred at the second position, and 334 occurred at the third position of a codon. Transitions between individual sequences were approximately twice as common as transversions. Plots of Kimura's distance versus uncorrected sequence divergence are linear and roughly fall along the line $y = x$ for first- and second-position sites (Fig. 2). For third-position sites, transitions are saturated relative to transversions (Fig. 2).

### *Phylogenetics*

Of the 489 variable sites, 408 (83%) were phylogenetically informative. The parsimony analysis in which all characters were given equal weight resulted in two most parsimonious trees, each of which requires 3343 nucleotide changes (consistency index excluding uninformative characters (CI) = 0.21, retention index (RI) = 0.30). As indicated by the strict consensus tree (Fig. 3), the two trees agree in topology at almost every node. Because of the evidence of saturation at third-position codon sites (Fig. 2), I did an additional parsimony analysis in which third-position transitions were given a weight one-sixth of that of other types of changes. This transversion-weighted parsimony analysis resulted in six most parsimonious trees of 10,302 steps (CI = 0.24, RI = 0.42).

These six trees (strict consensus shown, Fig. 4) agree with trees resulting from the equally weighted analysis at many nodes. Of the 45 clades recovered in the strict consensus tree of the transversion-weighted data, 26 are also recovered in the equally weighted analysis. In the successive approximation analysis, the same set of three trees was consistently obtained after the first round of reweighting. These trees (strict consensus shown, Fig. 5) share all of the 26 nodes shared between the equally weighted and the transversion-weighted trees. In addition, successive approximation and transversion-weighted analyses share three nodes not found in the equally weighted trees.

In all trees, genera for which more than one individual was included (*Piranga* and *Ramphocelus*) and species for which more than one individual was in-

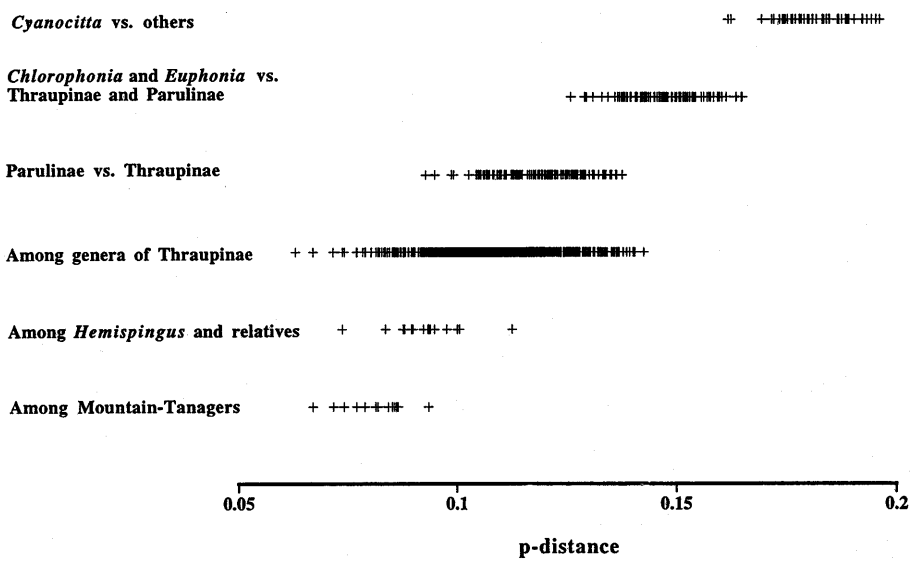


**FIG. 1.** Uncorrected percentage sequence divergence (*p* distance; Nei 1987) among individuals included in this study. Each cross represents a pairwise comparison between two individuals.

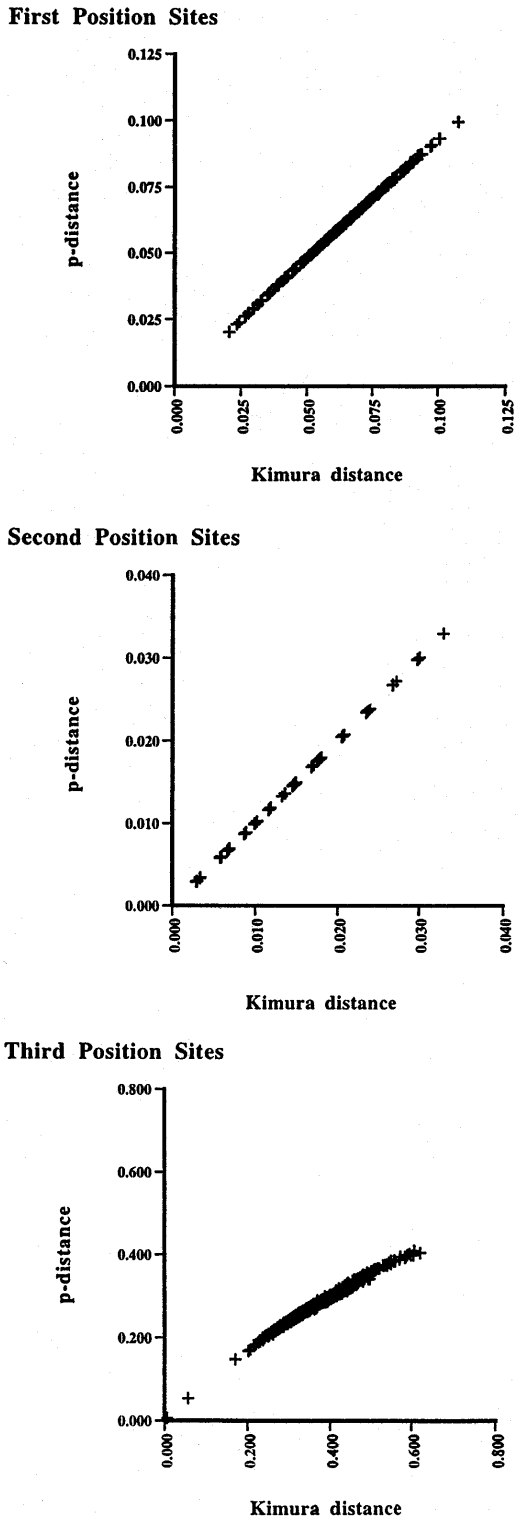


**FIG. 2.** Scatterplots of *p* distance versus Kimura distance indicating levels of saturation among tanager sequences for first-, second-, and third-position sites.

cluded (*S. zena* and *P. palmarum*) were monophyletic and showed strong bootstrap support for monophyly (Figs. 3–5). All analyses indicate that *Euphonia* and *Chlorophonia* (traditionally part of Thraupinae) form a monophyletic group outside of the warblers (Parulinae) and the rest of the Thraupinae. Thraupinae (excluding *Euphonia* and *Chlorophonia*) is monophyletic in all trees produced in this study. Within Thraupinae, the Caribbean genera *Spindalis*, *Phaenicophilus*, and *Nesospingus* form a basal paraphyletic assemblage. In general, deep nodes and more recently evolved nodes have stronger support (are more consistent across analyses or have higher bootstrap values) than nodes of intermediate age (Figs. 3–5).

## DISCUSSION

### *Comparisons with Other Data Sets*

Congruence in cladistic signal among data sets is a useful criterion for interpreting phylogenetic support of different nodes (Kluge, 1989; Miyamoto and Cracraft, 1991; Lanyon, 1993). Unfortunately, previous hypotheses of relationships among genera of Thraupinae have not been based on cladistic analyses of character state data. McDonald (1988) used phenetic analyses (UPGMA and Distance-Wagner) of morphology and allozyme frequencies. Sibley and Ahlquist (1985, 1990) and Bledsoe (1988) also used phenetics (UPGMA and Fitch algorithms) to analyze DNA hybridization data. Although Raikow's analysis of morphology is described as cladistic, his hypotheses of relationships were not entirely based on character state data (Bledsoe and Raikow, 1990). Despite differences in methods of analysis, these different data sets may recover the same set of relationships if the underlying cladistic signal is the same and if the different methods and types of data used are able to detect this signal. However, these data sets and the current data set show few similarities among themselves. Comparing previous analyses of tanager relationships (Raikow, 1978; Bledsoe, 1988; McDonald, 1988; Sibley and Ahlquist, 1990) to the current study reveals only one node in common between any previously published evolutionary tree of tanager relationships and the cytochrome *b* phylogenies. Furthermore, the previous studies bear little resemblance to one another in terms of their placement of tanager taxa. McDonald's allozyme tree shares a single node in common with Sibley and Ahlquist's (1985, 1990) studies, and the DNA hybridization studies (Sibley and Ahlquist, 1985, 1990; Bledsoe, 1988) share only a few nodes among themselves. Other than these cases, the previous studies do not have nodes in common among themselves. In addition, Webster (1988) found no correlation between his comprehensive skeletal survey and the DNA hybridization data (Sibley and Ahlquist, 1990). These observed incongruences may be

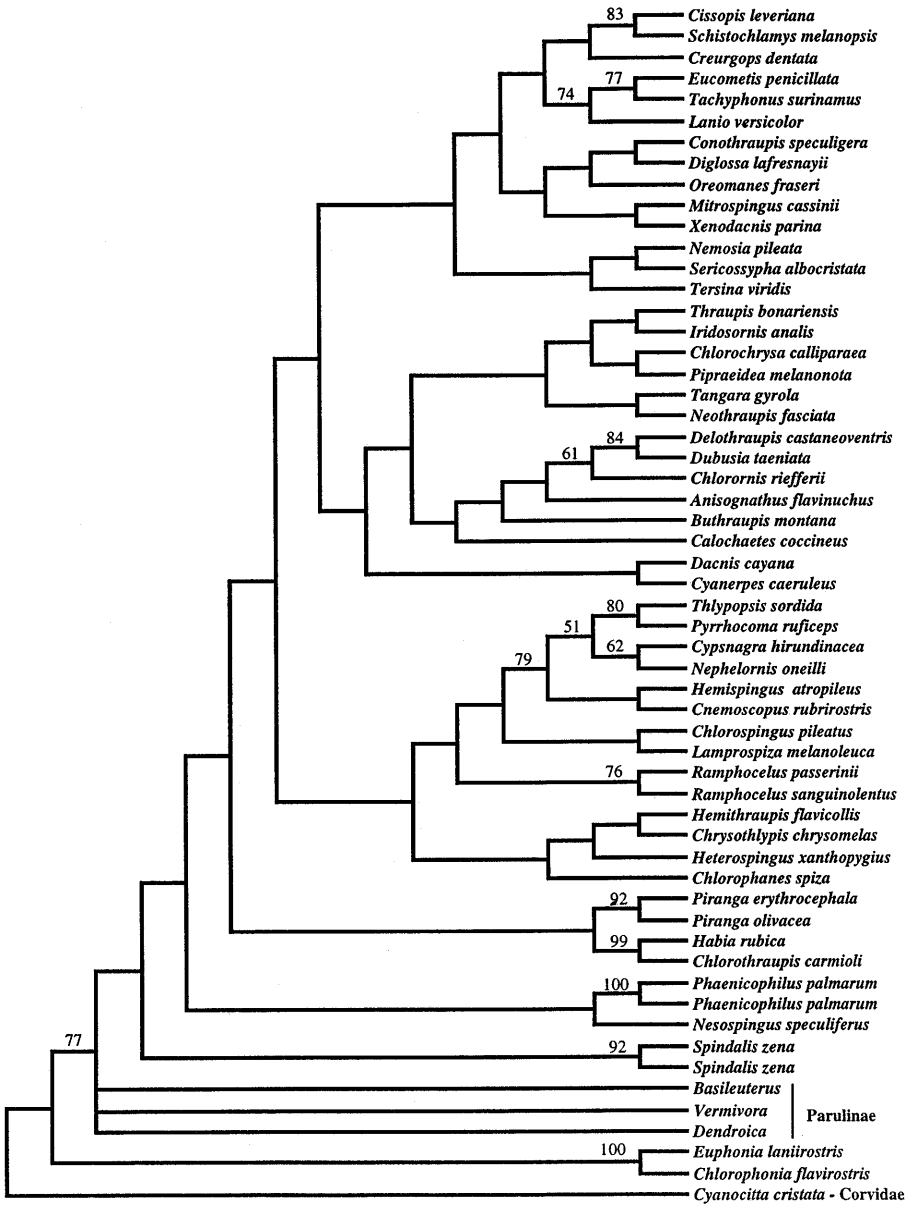


**FIG. 3.** Strict consensus tree of the two most parsimonious trees resulting from the equally weighted analysis. Tree is rooted with *Cyanocitta cristata*. Three other non-tanager taxa were also included in the analysis: *Basileuterus culicivorus, Dendroica coronata,* and *Vermivora celata* (all members of Parulinae). Numbers on tree indicate levels of bootstrap support for nodes retained by more than 50% of bootstrap replicates.

the result of differences in the ability of different kinds of data to recover phylogeny or may simply be an artifact of different methods of analyses and problems with taxon sampling.

Differences in taxon sampling have likely had a major effect on creating conflicting topologies. Missing taxa in phylogenetic studies can have a profound effect on final topological structure (Gauthier *et al.*, 1988; Weller, 1992; Lecointre *et al.*, 1993). Previous studies of thraupine genera were not comprehensive in scope and included relatively few taxa. Studies of appendicular musculature (Raikow, 1978), allozyme and morphological variation (McDonald, 1988), and DNA hybridization (Bledsoe, 1988; Sibley and Ahlquist, 1990) included 14, 9, 8, 6, and 25 genera of Thraupinae, respectively. Of the 25 genera included in Sibley and Ahlquist's study, only 3 Thraupinae were included in the more appropriate Fitch analyses (see critique in Harshman, 1994). The relatively few genera sampled in previous studies makes comparisons in topology difficult.

The cytochrome *b* data set also suffers from problems of taxon sampling. Missing from the current data set

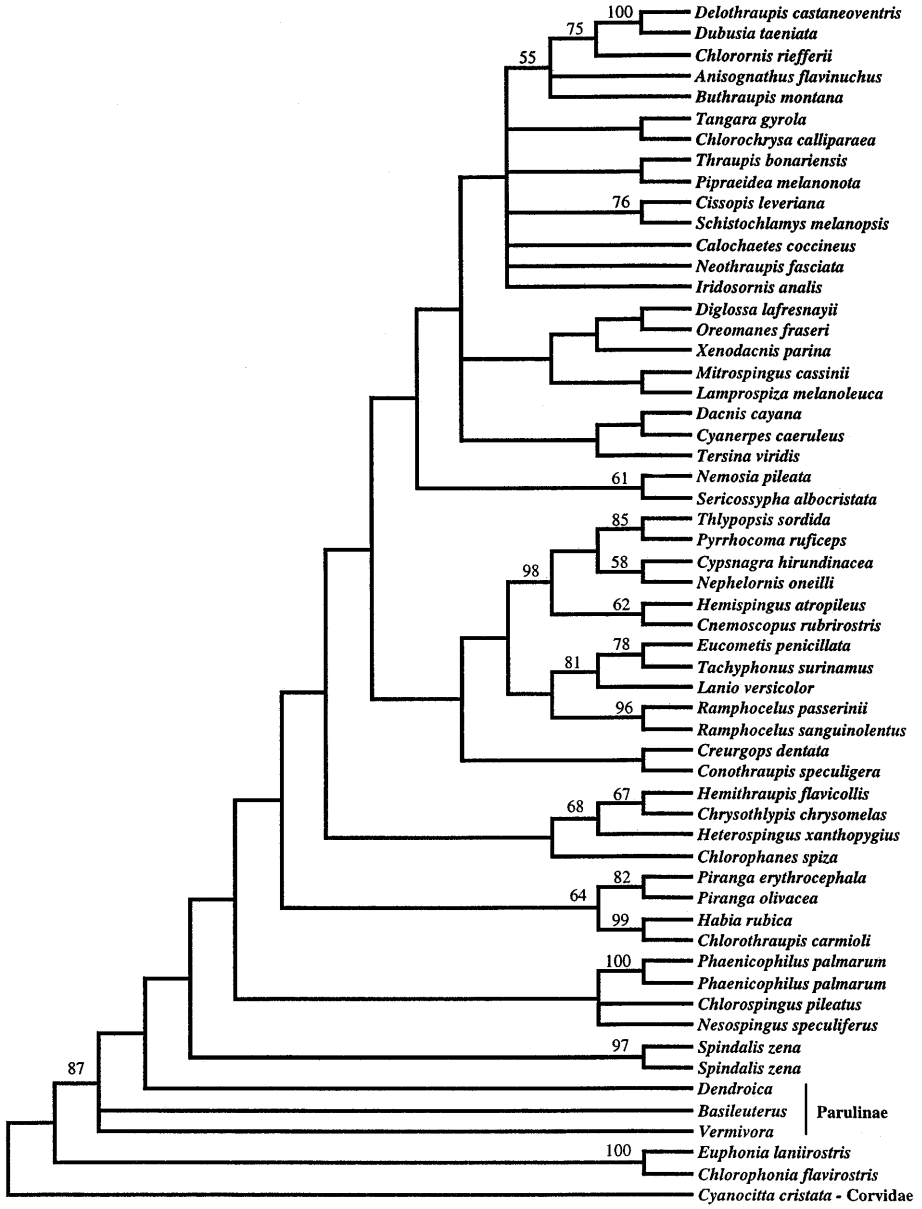


**FIG. 4.** Strict consensus tree of the six most parsimonious trees resulting from the transversion-weighted analysis. Tree is rooted with *Cyanocitta cristata*. Three other non-tanager taxa were also included in the analysis: *Basileuterus culicivorus*, *Dendroica coronata*, and *Vermivora celata* (all members of Parulinae). Numbers on tree indicate levels of bootstrap support for nodes retained by more than 50% of bootstrap replicates.

are representatives of the subfamily Emberizinae. DNA–DNA hybridization studies (Sibley and Ahlquist, 1985, 1990; Bledsoe, 1988) included many emberizines and showed that Thraupinae was polyphyletic relative to some South American emberizine finches such as *Sicalis*, *Diuca*, and *Urothraupis*. The monophyly of Thraupinae with respect to these emberizines is beyond the scope of the current study. Including some of these taxa with the current data set might break up some long branches and result in shifts in topology. Another potential problem common to all studies of tanager relationships is that in most cases only one individual is used to represent each genus. However, it is unlikely that many genera of Thraupinae are polyphyletic. Most genera are either monotypic or relatively small. The genera that contain many species are reasonably well defined by plumage or other morphological characters (e.g., *Tangara*, *Euphonia*, and *Chlorospingus*). When more than one individual from a genus was included in this study (*Ramphocelus*, *Phaenicophilus*, *Spindalis*, and *Piranga*), representatives from the same genus formed monophyletic groups. This suggests that

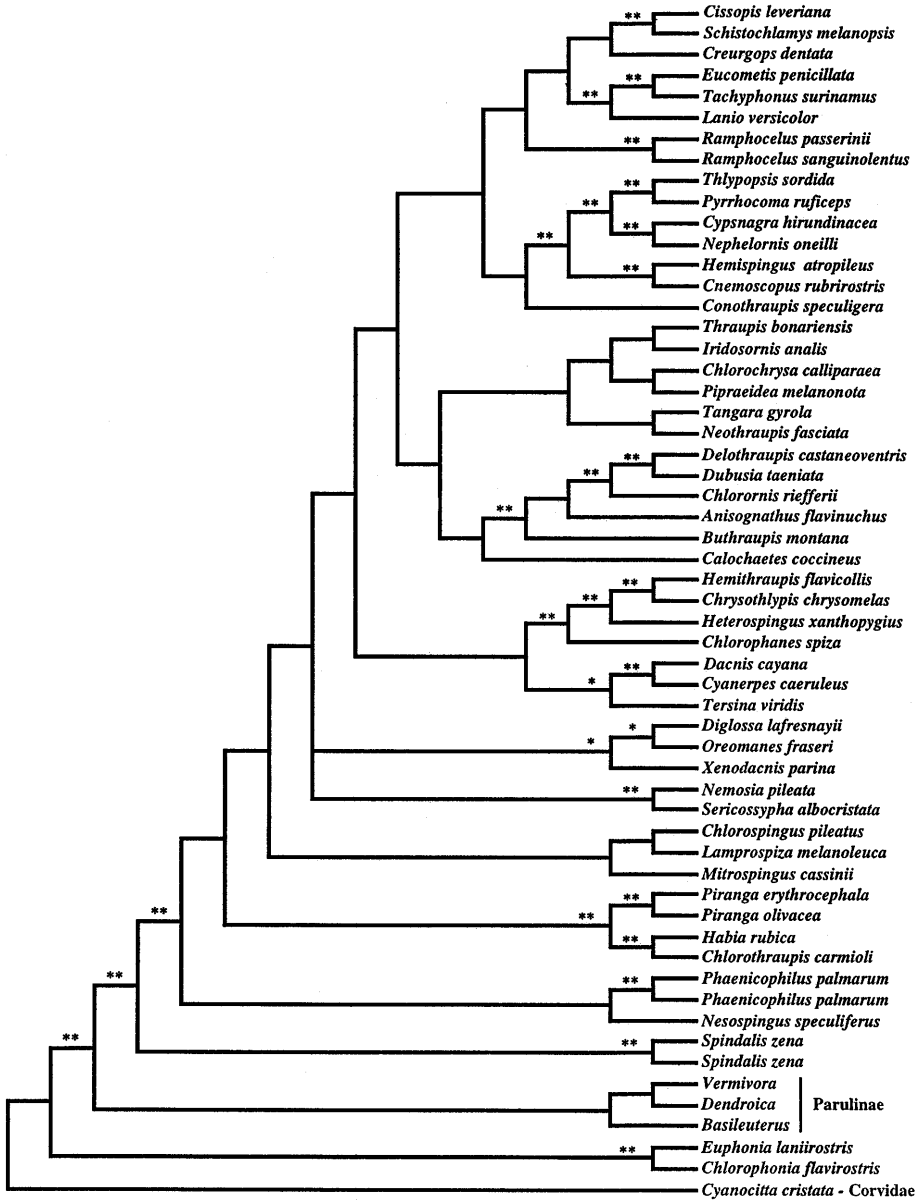


**FIG. 5.** Strict consensus of the three trees resulting from the successive approximations analysis. Tree is rooted with *Cyanocitta cristata*. Three other non-tanager taxa were also included in the analysis: *Basileuterus culicivorus, Dendroica coronata,* and *Vermivora celata* (all members of Parulinae). Double asterisks on tree indicate nodes found in all analyses, and single asterisks indicate nodes not found in the equally weighted analyses but found by both the transversion-weighted and successive approximation analyses.

problems associated with polyphyly (Lanyon, 1994) are not widespread within genera of Thraupinae.

In addition to recovering intrageneric relationships among thraupines, the cytochrome *b* data also show numerous similarities to previous sequential arrangements of taxa within Thraupinae (Sclater, 1886; Ridgway, 1902; Hellmayr, 1936; Storer, 1970). These sequential taxonomies were based on features such as plumage, other characteristics of morphology, and geographic distribution and were intended to reflect relationships among taxa. Many taxa adjacent to each other in these arrangements are sister taxa in the cytochrome *b* phylogenies (e.g., *Chlorophonia* and *Euphonia*, *Delothraupis* and *Dubusia*, *Hemispingus* and *Cnemoscopus*, *Hemithraupis* and *Chrysothlypis*, *Dacnis* and *Cyanerpes*). In some cases, groups of adjacent taxa in the sequential taxonomies are distinct clades in the cytochrome *b* phylogenies (e.g., *Diglossa, Oreomanes,* and *Xenodacnis; Piranga, Chlorothraupis,* and *Habia*). Some of these similarities are discussed in the following sections. The ability of the cytochrome *b* data to recover intrageneric relationships and to recover many of the relationships proposed by the sequential taxonomies indicates that the cytochrome *b* data are tracking

phylogenetic signal. These similarities also suggest that the cytochrome *b* data are reconstructing relationships among species and are not simply recovering a gene tree (Pamilo and Nei, 1988; Doyle, 1992).

*Phylogenetic Conclusions*

*Euphonia and Chlorophonia.* *Euphonia* and *Chlorophonia* share two features not found in other tanagers: a specialized digestive tract and an unusual type of nest. Species in both genera have stomachs that are highly reduced and modified for digesting fruit such as mistletoe berries (Forbes, 1880; Wetmore, 1914; Desselberger, 1931). While most tanagers build open cup nests, species in *Euphonia* and *Chlorophonia* build domed, globe-shaped nests with side entrances. In addition, Webster (1988) observed that *Euphonia* and *Chlorophonia* have extremely similar skeletal morphologies. These features and similarities in external morphology have led many authors to consider these two genera to be closely related. Thus, they have been placed adjacent to each other in the linear classifications (Sclater, 1886; Ridgway, 1902; Hellmayr, 1936; Storer, 1970; AOU, 1983). In addition, Sclater (1886) placed these two genera in their own subfamily.

In the phylogenetic analyses of the cytochrome *b* data (Figs. 3–5), *Chlorophonia* and *Euphonia* form a well-supported monophyletic group distinct from all other Thraupinae. Levels of sequence divergence between these genera and the other genera of Thraupinae are high (Fig. 1). This agrees with the morphological and behavioral differences shared by *Euphonia* and *Chlorophonia* to the exclusion of the other genera. *Euphonia* was also found to be highly divergent in allozyme loci from other tanager genera (McDonald, 1988), and Sibley and Ahlquist (1990) found *Euphonia* to be basal to all other tanager taxa included in their study.

All analyses in the current study show that *Euphonia* and *Chlorophonia* form a monophyletic group outside of other tanagers and warblers (Figs. 3–5). This agrees with McDonald's (1988) results which showed that tanagers were more closely related to warblers than they were to *Euphonia*. Based on the results of these independent data sets, species in the genera *Euphonia* and *Chlorophonia* should not be included within Thraupinae as doing so makes Thraupinae a nonmonophyletic group. The large genetic divergences observed between the *Euphonia* and *Chlorophonia* clade and the warblers and tanagers included in this study suggest that *Euphonia* and *Chlorophonia* may not be closely related to other members of Emberizidae. Their relationship to other passerine birds outside of Emberizidae should be explored further.

*The Swallow-Tanager.* The monotypic genus *Tersina* (the Swallow-Tanager) is also morphologically and behaviorally distinct. Unlike other tanagers, Swallow-Tanagers place their nests in horizontal cavities in banks, cliffs, trees, or manmade structures (Schaefer, 1953; Isler and Isler, 1987). They also have an atypical palatal structure (Lucas, 1895; Webster, 1988), unusually long wings, and a uniquely flattened bill that is broad at its base. These characteristics have led the Swallow-Tanager to be described in linear arrangements as a monotypic family (Hellmayr, 1936; Wetmore, 1960; Meyer de Schauensee, 1970), subfamily (Sclater, 1886; Storer, 1970), or tribe (AOU, 1983). Webster (1988) also argued for subfamily- or family-level status for *Tersina* based on several unique skeletal characters. DNA hybridization data (Sibley and Ahlquist, 1990) contradict these assessments by placing *Tersina* as the sister taxon to *Tangara* well within other genera of Thraupinae. The cytochrome *b* phylogenies (Figs. 3–5) also indicate that *Tersina* does not have a special phylogenetic status relative to other Thraupinae. The species is not the sister taxon to the rest of Thraupinae; thus, because classification should define historical entities, placing this species in a separate category relative to other Thraupinae is not justified.

Unlike the situation with *Euphonia* and *Chlorophonia*, the morphological differences between *Tersina* and other tanagers are not coupled with comparable genetic change. Levels of sequence divergence between *Tersina* and other genera of Thraupinae are not greater than those of other genera. Many of the morphological characters unique to *Tersina* are probably specializations associated with this species' swallow-like habit of catching insects in flight (Sibley, 1973); therefore, these characters may have evolved relatively rapidly in concert with each other.

In the transversion-weighted and successive approximation analyses (Figs. 4 and 5), the cytochrome *b* data place *Tersina* as the sister taxon to the honeycreeper genera *Cyanerpes* and *Dacnis*. The bill shapes of species in these genera are different from those of *Tersina*, but all three genera have similar plumage coloration and patterns of sexual dichromatism. In all of these genera, males are bright blue and females are greenish. The placement of *Tersina* adjacent to *Cyanerpes* and *Dacnis* indicates that bill shape evolution may be more labile than are plumage patterns within this lineage.

*Nectar-feeding tanagers.* Early workers (Sclater, 1886; Ridgway, 1902; Hellmayr, 1936) placed several genera of nectar-feeding passerines into a single family, Coerebidae. A detailed study of the anatomy of species in this family (Beecher, 1951) revealed that many of the similarities among the genera in this family were convergent adaptations for nectar-feeding. Based on this study, Beecher identified nine genera in this family as nectar-adapted tanagers (*Diglossa, Cyanerpes, Chlorophanes, Iridophanes = Tangara pulcherrima, Hemidacnis = Dacnis, Dacnis, Euneornis, Xenodacnis,* and *Oreomanes*) and three genera as nectar-adapted warblers (*Coereba, Conirostrum,* and *Atelodacnis = Conirostrum*). Raikow (1978) considered it likely that the

genera Beecher removed from Coerebidae and placed within Thraupinae were closely related. Limited data from DNA hybridization contradict these results. Sibley and Ahlquist (1985, 1990) included two of these genera (*Cyanerpes* and *Diglossa*) in their studies, and they were not sister taxa.

In agreement with the DNA hybridization studies, the cytochrome *b* data reveal that within tanagers, nectar-feeding specializations arose multiple times. Trees in the current study (Figs. 3–5) identify at least three separate lineages in which Beecher's nectar-adapted tanagers occur: one lineage including *Dacnis* and *Cyanerpes*, a second lineage including *Diglossa, Oreomanes,* and *Xenodacnis,* and a third lineage including *Chlorophanes* (*Tangara pulcherrima* and *Euneornis* were not included in the current study). Constraining the trees resulting from the current study to make these tanagers form a monophyletic group increases their length (e.g., equally weighted trees increase by at least 12 steps and transversion-weighted trees increase by at least 87 steps).

The closely related genera *Diglossa, Oreomanes,* and *Xenodacnis* share some plumage similarities, but have different bill morphologies and foraging behaviors. This pattern of having similar plumages, but differences in bill size and shape, is similar to that described above among *Tersina, Dacnis,* and *Cyanerpes* and again points to the relative conservative nature of plumage coloration compared to bill morphology.

*Chlorospingus and tanagers of the Greater Antilles.* In the cytochrome *b* phylogenies, *Spindalis, Nesospingus,* and *Phaenicophilus* form a paraphyletic basal assemblage relative to the other genera studied (Figs. 3–5). In the transversion-weighted tree (Fig. 4), *Chlorospingus* is included among these species as well. The close relationship of these genera is unexpected based on linear classifications (Sclater, 1886; Ridgway, 1902; Hellmayr, 1936; Storer, 1970) or allozyme data (McDonald, 1988), but agrees with many plumage characters. Species in these four genera all have olive-green, olive-brown, and yellowish plumages. In addition, both *Spindalis* and *Phaenicophilus* have striking black and white facial patterns which are also seen in some *Chlorospingus* in the form of postocular spots or stripes. Beyond these similarities among adults, fledglings of *Phaenicophilus* are similar in plumage to female *Spindalis* from Jamaica (McDonald, 1988).

In contrast to plumage similarities, species of *Nesospingus, Spindalis,* and *Phaenicophilus* average 50% larger than species of *Chlorospingus.* (Ranges and average weight of species in these genera are (from data compiled in Isler and Isler, 1987): *Spindalis,* 31.2 g (17–47.2 g); *Phaenicophilus,* 29.0 g (24–32 g); *Nesospingus,* 36 g (31–39.7 g); and *Chlorospingus,* 21.7 g (13.3–30 g).) The island distributions of *Nesospingus, Spindalis,* and *Phaenicophilus* may explain their larger size relative to *Chlorospingus.* While *Chlorospingus* tanagers occur throughout mountainous regions from Mexico to western South America, *Nesospingus, Spindalis,* and *Phaenicophilus* are largely restricted to islands in the Caribbean. Like many insular species, *Spindalis, Nesospingus,* and *Phaenicophilus* may have evolved their larger size as a consequence of such factors as absence of predators, availability of resources, or degree of competition (Foster, 1964; Grant, 1965; Case, 1978; Smith, 1992). This lineage represents a third instance within Thraupinae in which plumage coloration and patterns persist despite changes in other aspects of morphology.

*Mountain-tanagers and relatives.* The phylogenies reveal a clade representing an Andean radiation of tanagers consisting of the genera *Chlorornis, Dubusia, Buthraupis, Delothraupis,* and *Anisognathus* (Figs. 3–5). This clade contains 5 genera and 17 species of dramatically colored tanagers. All but one of the species are restricted to high elevations of the Andes and northern South America. Unlike many tanagers, all species in these genera are sexually monomorphic in plumage, with both sexes being brightly colored. The cytochrome *b* data agree with linear classifications (Sclater, 1886; Hellmayr, 1936) that have placed the genera *Buthraupis, Dubusia, Delothraupis,* and *Anisognathus* near one another. Some authors (e.g., Meyer de Schauensee, 1970; Fjeldså and Krabbe, 1990) have considered *Delothraupis* and *Dubusia* congeneric, and the cytochrome *b* data indicate that these two genera are sister taxa.

Different authors have disagreed on the phylogenetic position of the Grass-green Tanager, *Chlorornis.* Some linear arrangements (Hellmayr, 1936; Storer, 1970) of taxa have listed this species with other atypical tanagers of uncertain affinities; Sclater (1886) considered it related to the finch genus *Saltator,* DNA hybridization evidence places it as the sister taxon to *Catamblyrhynchus* (Sibley and Ahlquist, 1990), and other authors (Isler and Isler, 1987) have noted similarities in foraging behavior between *Chlorornis* and *Buthraupis.* In all analyses in the current study, *Chlorornis* is the sister taxon to a clade containing *Delothraupis* and *Dubusia.* The placement of *Chlorornis* within the clade containing *Anisognathus, Buthraupis, Delothraupis,* and *Dubusia* by the cytochrome *b* data is supported by similarities in geographic distribution and plumage patterns among these genera.

The cytochrome *b* data suggest that another genus of uncertain phylogenetic affinities, *Calochaetes,* may also belong to this clade of mountain-tanagers. *Calochaetes* clustered with these tanagers in the equally weighted trees, the successive approximation tree, and in four of the six transversion-weighted trees. *Calochaetes* has been traditionally placed adjacent to the genera *Piranga* and *Ramphocelus* due to similarities in plumage to *Ramphocelus* and similarities in overall shape to *Piranga.* However, *Calochaetes* is more similar in habitat, behavior, and vocalizations to mountain-tanagers than

it is to species of *Piranga* and *Ramphocelus* (Isler and Isler, 1987). The brilliantly colored, sexually monomorphic plumage of *Calochaetes* also suggests that this species is closely related to the other cloud-forest-dwelling mountain-tanagers.

*Hemispingus and relatives.* One of the most strongly supported clades (Figs. 3–5) in this study includes taxa representing another mostly Andean radiation, namely *Hemispingus, Cnemoscopus, Pyrrhocoma, Thlypopsis, Nephelornis,* and *Cypsnagra.* All species in these genera have relatively nondescript plumage and are confined to the Andes with the exception of *Pyrrhocoma, Cypsnagra,* and some species of *Thlypopsis. Nephelornis* is a recently described monotypic genus of uncertain phylogenetic affinities (Lowery and Tallman, 1976). Raikow (1978) considered *Nephelornis* to be relatively primitive in terms of its limb musculature. He placed this genus within Thraupinae, but considered it to have some affinities to wood warblers (Parulinae) as well. The cytochrome *b* data place *Nephelornis* within a clade containing *Cypsnagra, Thlypopsis, Pyrrhocoma, Hemispingus,* and *Cnemoscopus* (Figs. 3–5). *Nephelornis* was not closely related to the wood warblers included in this study; thus, its placement within Thraupinae is justified.

The different sequential taxonomies (Sclater, 1886; Hellmayr, 1936; and Storer, 1970) predate the description of *Nephelornis* and place the other taxa in this clade near one another to different degrees. Although *Hemispingus* and *Chlorospingus* are thought to be closely allied (even considered congeneric by Sclater (1886)) and to be sister taxa by allozyme data (McDonald, 1988), the DNA sequence data clearly show that these two genera are distantly related. In fact, constraining the transversion-weighted trees to make *Hemispingus* and *Chlorospingus* sister taxa increases the length of the tree by at least 85 steps.

## BIOGEOGRAPHY

The phylogeny of Thraupinae presented in this study, together with information on DNA sequence divergence, provides a framework for addressing biogeographic hypotheses. If differences in DNA sequences accumulate at a roughly constant rate over time, levels of DNA sequence divergence can be used to date splitting events. Although using such a molecular clock is controversial, it provides a method for estimating approximate divergence times and formulating preliminary biogeographic hypotheses. Ideally, a molecular clock would be calibrated with fossils for the particular lineage being studied. Unfortunately, the fossil record of birds, and passerines in particular, is relatively poor compared to other groups. For studies of bird mtDNA, one widely used calibration (e.g., Hackett, 1992; Cicero and Johnson, 1995; Seibold and Helbig, 1995) is 2% sequence divergence per million years derived from divergence levels of mtDNA restriction fragment length polymorphism of geese (Shields and Wilson, 1987). This rate is similar to that observed in many mammalian and other lineages (Wilson *et al.,* 1985); thus, it has been applied generally. Other calibrations sometimes used (Helm-Bychowski and Cracraft, 1993; Smith and Patton, 1993; Arctander *et al.,* 1996) are based on a linear relationship observed between transversions in cytochrome *b* sequences and divergence dates of different taxa of ungulate mammals with a good fossil record (Irwin *et al.,* 1991). Irwin *et al.* (1991) observed a rate of roughly 0.5% divergence in third-position transversions per million years. This calibration is more appropriate for the current study than that of Shields and Wilson (1987) for three reasons. First, the current study and that of Irwin *et al.* (1991) are based on cytochrome *b* sequences, not overall mtDNA divergence. Second, properties of cytochrome *b* sequence divergence in birds have been found to be similar to those in mammals (Edwards *et al.,* 1991). Finally, given the levels of saturation observed in the current study (Fig. 2), using an estimate based on overall sequence divergence would lead to an underestimate of divergence times. Overall, rates of accumulation of third-position transversion differences correspond to the hierarchical structure observed in the phylogeny (Fig. 6). That is, levels of divergence are greater between *Cyanocitta* and Emberizidae (Parulinae and Thraupinae) than among genera of Thraupinae, and levels of divergence among older genera of Thraupinae are greater than among more recent clades within Thraupinae (such as the genera of mountain-tanagers and *Hemispingus* tanagers). This indicates that transversion differences are at least roughly tracking the relative ages of branching events (Helm-Bychowski and Cracraft, 1993).

Using a rate of 0.5% per million years for third-position transversions, corvids (represented by *Cyanocitta*) diverged from tanagers (Thraupinae) and warblers (Parulinae) between 40 and 50 million years ago and the genera of Thraupinae (excluding *Euphonia* and *Chlorophonia*) diverged from Parulinae beginning around 26 million years ago (Fig. 6). The DNA sequence data indicate that the genera of Thraupinae diverged from one another soon after diverging from warblers (Fig. 6). Most of the diversity among genera of Thraupinae evolved over a span of roughly 10 million years beginning about 25 million years ago (Fig. 6). Thus, the incredible range of morphology and behavior characteristics of the different genera evolved relatively rapidly during the Miocene. These divergence dates agree well with estimates based on DNA–DNA hybridization. Sibley and Ahlquist (1985) estimated that the different lineages of emberizines (including warblers and tanagers) diverged from one another 23 to 26 million years ago. In addition, the dates of divergence predicted by the sequence data are consistent with the idea of a

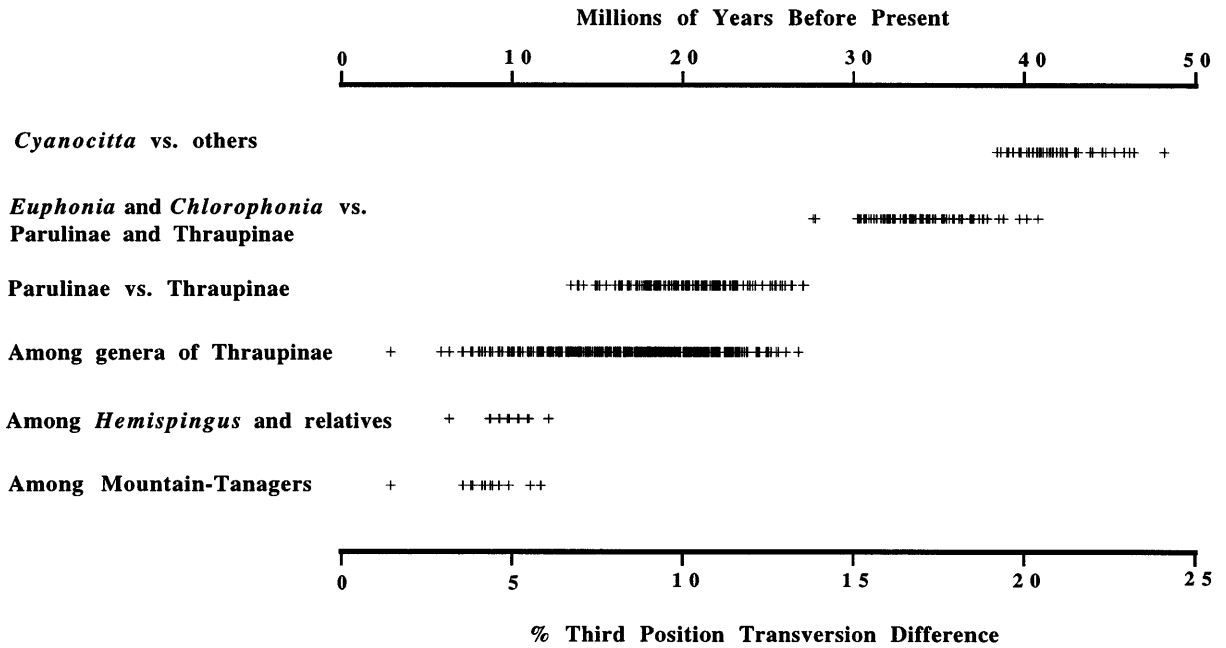


**FIG. 6.** Approximate divergence times of taxa included in this study based on third-position transversion sequence divergence and the calibration of Irwin *et al.* (1991).

mid-Tertiary radiation of passerine birds based on the fossil record (Feduccia, 1996).

Given the phylogenetic structure of the trees in this study (Figs. 3–5), tanagers first evolved on Caribbean islands and then radiated throughout South America. A similar scenario with similar divergence dates has been proposed for two groups of mammals, the caviomorph rodents and platyrrhine primates, based on the fossil record. Marshall and Sempere (1993) proposed that these two groups arrived in South America from Caribbean Islands beginning in the late Oligocene. Thus, similar geologic events may have influenced the evolution of these three groups.

Most of the currently recognized genera of tanagers shared a common ancestor prior to Pleistocene glaciation events and the formation of the Panamanian isthmus 3–5 million years ago. Therefore, these events probably had more of an effect on diversity within genera than among genera (as shown for the tanager genera *Diglossa* (Hackett, 1995), *Ramphocelus* (Hackett, 1996), and *Piranga* (Burns, 1996; submitted for publication)). Divergence dates of genera of Thraupinae correspond well with geologic events in the Andes. The major uplifts of the Andes during the late Oligocene and Miocene (Potts and Behrensmeyer, 1992; Marshall and Sempere, 1993) occurred at a time of extensive tanager diversification. The presence of clades largely restricted to the Andes with more recent divergence dates (such as the mountain-tanagers and *Hemispingus* tanagers) indicates that geologic events in the Andes have probably continued to have an important influence on tanager diversity.

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