PHYLOGENETIC RELATIONSHIPS AND MORPHOLOGICAL DIVERSITY IN DARWIN'S FINCHES AND THEIR RELATIVES

Kevin J. Burns,[1] Shannon J. Hackett,[2] and Nedra K. Klein[3,4]

[1]*Department of Biology, San Diego State University, San Diego, California 92182-4614*
E-mail: kburns@sunstroke.sdsu.edu
[2]*Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605-2496*
[3]*Division of Science, Truman State University, Kirksville, Missouri 63501*

Abstract.—Despite the importance of Darwin's finches to the development of evolutionary theory, the origin of the group has only recently been examined using a rigorous, phylogenetic methodology that includes many potential outgroups. Knowing the evolutionary relationships of Darwin's finches to other birds is important for understanding the context from which this adaptive radiation arose. Here we show that analysis of mitochondrial DNA sequence data from the cytochrome *b* gene confirm that Darwin's finches are monophyletic. In addition, many taxa previously proposed as the sister taxon to Darwin's finches can be excluded as their closest living relative. Darwin's finches are part of a well-supported monophyletic group of species, all of which build a domed nest. All but two of the non-Darwin's finches included in this clade occur on Caribbean islands and most are Caribbean endemics. These close relatives of Darwin's finches show a diversity of bill types and feeding behaviors similar to that observed among Darwin's finches themselves. Recent studies have shown that adaptive evolution in Darwin's finches occurred relatively quickly. Our data show that among the relatives of Darwin's finches, the evolution of bill diversity was also rapid and extensive.

Key words.—Adaptive radiation, biogeography, Caribbean, Darwin's finches, Galápagos, morphological evolution, phylogeny.

Darwin's finches of the Galápagos and Cocos Islands are a classic example of speciation and adaptive evolution. Since the formation of these islands less than five million years ago, Darwin's finches have evolved a diversity of bill shapes and associated dietary preferences (Grant 1999). Bill morphology ranges from the large bills of *Geospiza* capable of crushing hard seeds to the slender bills of *Certhidea* that are used to pick arthropods off substrates. Despite the importance of this group for understanding and illustrating evolutionary principles (Futuyma 1998; Grant 1999), the phylogenetic context from which this diversity arose is largely unknown. Identifying the foundation from which this remarkable variation of feeding types evolved would help provide a better understanding of the nature of bill morphology change within the finches themselves.

Traditional classifications of Darwin's finches place them within the subfamily Emberizinae (Paynter and Storer 1970) with other New World finches and sparrows. Using DNA-DNA hybridization, (Sibley and Ahlquist 1985, 1990) and Bledsoe (1988) showed that some taxa historically considered part of Emberizinae are actually more closely related to tanagers (Thraupinae). Thus, Sibley and Monroe (1990) placed many species of Emberizinae (including Darwin's finches) with traditional tanagers and called this group the tanager-finches (tribe Thraupini). Using DNA sequence data, Sato et al. (2001) confirmed an association between Darwin's finches and members of Thraupini.

Numerous studies have more specifically identified likely close relatives to Darwin's finches. Species that have been suggested include the Blue-black Grassquit (*Volatinia jacarina*) (Steadman 1982), other grassquits (genus *Tiaris*) (Sushkin 1925; Lowe 1936; Sato et al. 1999; Sato et al. 2001), seedeaters (genus *Sporophila*) (Salvin 1876; Ridgway 1897),

the Bananaquit (*Coereba flaveola*) (Harris 1971), and the St. Lucia Finch (*Melanospiza richardsoni*) (Bond 1948; Baptista and Trail 1988). Only one of these previous studies (Sato et al. 2001) was accompanied by phylogenetic analyses using multiple outgroups. These authors specifically identified *Tiaris obscura* as the sister taxon to Darwin's finches. However, because their taxon sampling did not include all members of the genus *Tiaris*, they considered their conclusions tentative.

In this study, we use cytochrome *b* sequences and multiple outgroups (including all species of *Tiaris* and related genera) to reconstruct a phylogeny of Darwin's finches and close relatives. We then use this phylogeny to explore the biogeographic history of the group as well as investigate historical changes in bill morphology.

METHODS

Taxon Sampling

A combination of new sequences (GenBank Accession Nos. AF489878–AF489903; Table 1) and previously published sequences (Hackett 1996: U15717, U15718; Burns 1997: AF006211–AF006258; Sato et al. 1999: AF108772, AF108777, AF108790, AF108792, AF108796, AF108802, AF108806, AF108807; Lougheed et al. 2000: AY005206, AY005218, AY005219, AY005220, AY005221; Sato et al. 2001: AF310041–AF310043, AF310049, AF310053–AF310055) was used in this study. We focused our sampling on Sibley and Monroe's (1990) tanager-finches (tribe Thraupini) and included 91 individuals of 88 species representing the diversity seen within this group. Thus, we included representatives of 71 of the 104 genera listed in Sibley and Monroe's (1990) Thraupini. Our sampling included representatives of all taxa that have recently been suggested as the closest living relative to Darwin's finches: *Volatinia*, *Tiaris*, *Sporophila*, *Coereba*, and *Melano-*

[4] Nedra K. Klein is deceased.

TABLE 1. Species names, voucher numbers, and locality information of sequences not previously reported. AMNH, American Museum of Natural History; LSUMNS, Louisiana State University Museum of Natural Science; CAS, California Academy of Sciences; MVZ, Museum of Vertebrate Zoology at the University of California, Berkeley; FMNH, Field Museum of Natural History; UMMZ, University of Michigan Museum of Zoology.

Species	Museum	Number	Locality
Acanthidops bairdii	LSUMNS	B-16267	Costa Rica: Provincia San José, Cerro de la Muerte, km 113 Pan American Highway
Basileuterus tristriatus	UMMZ	227798	Costa Rica: Provincia San José, Pan American Highway, km 120, direction S San José
Coereba flaveola	UMMZ	227691	Puerto Rico: Mun. Guayama, Bahia de Jobos, 17°55′N 66°17′W
C. flaveola	UMMZ	225179	Jamaica: Trelawny Par., Cornwall, Good Hope Plantation
C. flaveola	UMMZ	227711	Venezuela: Distrito Federal, highway between Colonia Tovan and Chichiriviche
Conirostrum speciosum	FMNH	334602	Bolivia: Santa Cruz, Chiquitos
Dendroica pensylvanica	UMMZ	227790	Michigan: Cheboygan Co., Dingman's Marsh, 45°47′N 84°43′W
Euneornis campestris	FMNH	331119	Jamaica: Surrey, Portland, Hollywell Park
Loxigilla portoricensis	LSUMNS	B-11351	Puerto Rico: Cabo Rojo, Boqueron, Penones de Melones, 1 km WNW intersection routes 301 and 303
L. violacea	AMNH	25433	Dominican Republic: Provincia Independencia, Parque Nacional Sierra de Baoruco, Zapoten, Sawmill Clearing
Loxipasser anoxanthus	FMNH	331107	Jamaica: Surrey, Portland, Hollywell Park
Nesospingus speculiferus	LSUMNS	B-11375	Puerto Rico: San German, along route 120 near Mt. Alegrillo; LSUMZ 150230
Oryzoborus crassirostris	FMNH	339668	Venezuela: Sucre, Guaraunos, 14 km SSE
Phaenicophilus palmarum	AMNH	831246	Dominican Republic: Provincia La Vega; Jarabacon
Saltatricula multicolor	MVZ	179401	Aviary of Luis F. Baptista, CAS Accn. 5067
Sicalis luteola	FMNH	389274	Brazil: Roraima, Fazenda Santa Cecilia, E bank Rio Branco, across from Boa Vista
Spindalis zena	AMNH	NKK862	Bahamas: New Providence; 1 mi W Adelaide Village
Sporophila collaris	FMNH	334566	Bolivia: El Beni, Laguna Suarez, 5 km SW Trinidad
S. ruficollis	FMNH	334582	Bolivia: Santa Cruz, Chiquitos Purubi, 30 km S San Jose de Chiquitos
Tangara chilensis	MVZ	169699	Peru: Departamento Cajamarca, 1 mi N San José de Lourdes, Cordillera del Condor
Thraupis bonariensis	LSUMNS	B-3587	Peru: Departamento Huanuco: Nuevas Flores (Cullquish) on Rio Maranon
Tiaris bicolor	MVZ	179402	Aviary of Luis F. Baptista, CAS Accn. 5067
T. fuliginosa	LSUMNS	B-12612	Bolivia: Departamento Santa Cruz; Velasco; 50 km ESE Florida, Arroyo del Encanto
T. olivacea	AMNH	25429	Dominican Republic: Provincia Independencia, Parque Nacional Sierra de Baoruco, El Aceitillar, Alcoa Road
Vermivora celata	MVZ	169123	California: San Benito County, 0.5 mi N San Benito Mountain
Volatinia jacarina	FMNH	394403	Bolivia

spiza. Sato et al. (2001) specifically identified *Tiaris obscura* as the sister taxon to Darwin's finches. In addition, these authors found that the other two species of *Tiaris* they included in their study as well as *Melanospiza richardsoni* and the one included species of *Loxigilla* consistently clustered with Darwin's finches. Therefore, we included all species of these genera as well as all the species in the morphologically, behaviorally, and geographically similar genera *Coereba*, *Melopyrrha*, *Euneornis*, and *Loxipasser*. For *Coereba flaveola*, we included three individuals because a previous study (Seutin et al. 1994) has shown this species to possess extensive intraspecific divergence. Seven species of Darwin's finches were included, representing the diversity found within the group including the warbler finch (*Certhidea*), the vegetarian finch (*Platyspiza*), two tree finches (*Camarhynchus*), two ground finches (*Geospiza*), the woodpecker finch (*Cactospiza*), and the Cocos Island finch (*Pinaroloxias*). As outgroups to all sequences, we used three species of wood warblers (*Basileuterus tristriatus*, *Vermivora celata*, *Dendroica pensylvanica*). Sibley and Ahlquist (1990) considered the wood warblers a separate tribe (Parulini) within the same subfamily (Emberizinae) as tanager-finches (Thraupini). DNA sequencing studies (Klicka et al. 2000; Sato et al. 2001) also show that wood warblers are a separate monophyletic group that is closely related to the ingroup taxa sampled for this study.

DNA Isolation and Sequencing

Specific fragments of cytochrome *b* were amplified from extracted DNA using PCR and an assortment of primers (Hackett 1996; Groth 1998). Reactions were performed in 10 µl capillary tubes and typically involved 40 amplification cycles (3 sec at 94°C, 1 sec at 43–50°C, 30 sec at 71°C). Agarose plugs were taken and diluted in 250 µl of water. Re-amplification of melted plugs took place in 40 µl reactions at a higher (52°C) annealing temperature. Double-stranded products were cleaned and cycle sequenced (ABI Prism™ Dye Terminator Cycle Sequencing Ready Reaction kit with AmpliTaq DNA Polymerase, FS; Perkin Elmer, Foster City, CA) for 32 cycles under the following conditions: 10 sec at 96°C, 5 sec at 50°C, and 3 min at 60°C. Samples were run on polyacrylamide gels for 3–7 hours on an ABI Prism™ 377 (Applied Biosystems, Foster City, CA). Sequence Navigator version 1.0.1 (Applied Biosystems, Perkin Elmer) and Sequencher (Gene Codes, Ann Arbor, MI) were used to reverse complement opposing directions, to align different fragments from the same individual, and to translate complete sequences into amino acids. For each new sequence, 1045 base pairs of cytochrome *b* were used (from base 14,991 to base 16,035 relative to the published sequence of *Gallus gallus* [Desjardins and Morais 1990]).

Phylogenetics

Phylogenetic analyses were performed at two taxonomic levels. Initial analyses involved a larger dataset with the goal of defining a well-supported clade that contained Darwin's finches and their close relatives. Once such a well-supported clade was defined, a second series of more computationally

intensive analyses was performed with the goal of reconstructing relationships within this clade.

At the first level of taxonomic sampling, we used both parsimony and Bayesian approaches. For the Bayesian analyses, we used ModelTest, version 3.06 (Posada and Crandall 1998) to choose the best fit model for the dataset containing all individuals. We used an iterative approach whereby a starting tree (determined initially by neighbor joining based on Kimura 2-parameter distances) was entered into ModelTest and a model and parameters were chosen. We then used the chosen model in conjunction with MrBayes 2.0 (Huelsenbeck and Ronquist 2001) to perform Bayesian analyses on the dataset. Because ModelTest identified the GTR + I + gamma model as most appropriate for our data, our analysis used this model and did not specify values for specific nucleotide substitution model parameters. Thus, parameters were treated as unknown variables with uniform prior values and estimated as part of the analysis. All Bayesian analyses were run for one million generations and sampled every 100 generations. Thus, each analysis resulted in 10,000 samples. Four Markov Chain Monte Carlo chains were run for each analysis. Resulting log-likelihood scores were plotted against generation time to identify the point at which log-likelihood values reached a stable equilibrium value. Sample points prior to this point of stationarity were discarded as ''burn-in'' samples. The remaining samples were used to produce a majority rule consensus tree with the percentage values indicating the percentage of samples that identified a particular clade (the clade's posterior probability). We repeated the analyses several times to insure that results were not dependent on the initial random starting tree used. For these repeated analyses, we compared log-likelihood values and posterior probabilities of each repeated analysis to confirm that using a different starting tree did not alter our results significantly.

To confirm the results of the Bayesian analyses using a more traditional phylogenetic method, we also analyzed this larger dataset using parsimony (PAUP*, Swofford 2001). Using the Bayesian analysis as a guide, we pruned the dataset to 60 individuals to make the dataset more computationally manageable. For parsimony analyses, we used the heuristic search option with 1000 random addition replicates and the tree-bisection-reconnection branch-swapping algorithm. For this dataset, scatter plots (not shown) of overall divergence against sequence divergence for transitions and transversions at the three base positions revealed that third position transitional changes may be saturated. Therefore, in addition to equal weighted analyses, we performed several additional parsimony analyses in which third position transitions were downweighted relative to the other sites. To explore the sensitivity of different weighting schemes, we downweighted third position transitions by factors of 2, 5, 10, and 50. All of these parsimony analyses were bootstrapped with 10 random addition replicates per each of 100 bootstrap replicates. Both parsimony and Bayesian analyses revealed a strongly supported clade of 22 individuals (see results) that contained Darwin's finches and a variety of other birds.

We then subjected this clade to additional Bayesian analyses as well as more computationally intensive maximum-likelihood analysis. For maximum-likelihood analyses, we again used ModelTest, version 3.06 (Posada and Crandall 1998) and an iterative approach to choose the best fit model for this smaller dataset. This information was then used for maximum-likelihood analyses as implemented in PAUP* (Swofford 2001), using 10 random addition replicates. The topology that resulted from the maximum-likelihood analyses was then entered into ModelTest as a starting tree and the process repeated until the same model and parameters were chosen consistently. To assess support for different nodes in the topology, the maximum-likelihood tree was bootstrapped for 100 replicates.

We also investigated relationships among these 22 individuals using Bayesian phylogenetic methods. Using Mr-Bayes 2.0 (Huelsenbeck and Ronquist 2001), we performed three separate analyses with different initial conditions to test the sensitivity of our data to different models and initial parameters. Because ModelTest identified the GTR + gamma model as most appropriate for our data, our initial analysis used this model and did not specify values for specific nucleotide substitution model parameters. We also performed an additional analysis in which we specified initial rates for the GTR model and initial shape of the alpha parameter according to those specified in our maximum likelihood analyses. Because our data involve a protein coding gene, in addition to the above two analyses we also performed an analysis where first, second, and third codon positions were placed into different character partitions and site-specific rates were estimated for each partition. All Bayesian analyses were run as described above (i.e., one million generations sampled every 100 generations, four Markov Chain Monte Carlo chains, multiple repeated analyses).

Different topologies as well as different a priori hypotheses about the closest living relative to Darwin's finches were compared using the Shimodaira-Hasegawa (SH) test statistic (Shimodaira and Hasegawa 1999; Goldman 2000). To conduct SH tests, we used PAUP* (Swofford 2001) with resampling estimated log-likelihood optimization and 100,000 bootstrap replicates.

Morphology

To explore patterns of morphological variation within Darwin's finches and relatives, we measured bill length, bill depth, and bill width in all species of Darwin's finches and 13 other species identified as their close relatives (see Results). All measurements were taken with digital calipers from museum specimens. Bill length was measured from the anterior end of the nostril to the tip of the bill; bill depth and width were taken at the anterior end of the nostril. Our bill length and bill depth measurements are described in more detail as ''length of bill from nostril'' and ''height of bill at base'' in Baldwin et al. (1931). These three measures were not meant to be a complete description of bill morphology but were specifically chosen because of their use in studies of evolution in birds (e.g., Karr and James 1975; Fitzpatrick 1985; Smith 1987; Richman and Price 1992) and in Darwin's finches in particular (Lack 1947; Grant 1999). One goal of our study was to compare bill variation within the lineage of Darwin's finches and their close relatives to other related lineages of a similar age (as suggested by similar levels of

genetic divergence). Therefore, as a comparison, we also measured bill length and bill depth in five other lineages of tanagers and finches for which genetic data were available. To explore the range of bill sizes and shapes occupied by Darwin's finches and their relatives in comparison to the five other lineages of roughly similar age, we plotted bill depth versus bill length. To test, statistically, whether or not these similarly aged clades differed in the degree of bill morphospace occupied, we performed a linear regression of bill depth on bill length and examined the residuals of points from the least-squares line. The residuals were tested for normality and then the means of the residuals for each clade were tested for differences using a one-tailed t-test. Our null hypothesis was that Darwin's finches and their relatives would occupy significantly more morphospace than would the other clades of roughly similar age.

Another goal was to compare the evolution of bill size among Darwin's finches and their closest relatives. We were interested in examining whether change in bill morphology along some branches was greater than that seen in other branches. We used CAIC version 2.6.8 (Purvis and Rambaut 1995) to look at patterns of character change within Darwin's finches and their close relatives in a phylogenetic context. This method uses Felsenstein's (1985) method of independent contrasts and incorporates topology and branch length information from the phylogenies to reconstruct patterns of change in characters. This method computes contrast values, which estimate the amount of evolution that has occurred at each sister node in the tree. Larger contrast values, at a particular node indicate that a greater amount of evolution has occurred per unit time at that point in the tree. Independent contrast analysis requires a fully resolved phylogeny. However, relationships among *Geospiza* and among species of *Camarhynchus*, *Cactospiza*, and *Pinaroloxias* are uncertain (Sato et al. 1999; Sato et al. 2001). Therefore, although we included bill measurements of all species, we did not examine transformations of bill size within these clades. We treated these clades as soft polytomies (lack of information) and broke them into bifurcating clades using the method of Pagel (1992) as implemented in CAIC. Branch lengths for these nodes were estimated by taking an average of the branch lengths of the species belonging to that clade that were included in the phylogenetic analysis. For example, to estimate branch lengths for all the *Geospiza* species, we averaged the branch lengths leading to *Geospiza fortis* and *Geospiza magnirostris* in our maximum-likelihood phylogeny.

Biogeography

To infer the biogeographic history of Darwin's finches and their relatives, we used three alternative methods that allow for the consideration of both dispersal and vicariant events: ancestral area analysis of Bremer (1992, 1995), Hausdorf's (1998) modification of Bremer's method (termed weighted ancestral area analysis), and dispersal-vicariance analysis (DIVA) of Ronquist (1997). These methods adopt a parsimony approach and use a phylogeny and the current geographic range of the taxa to infer the historical areas of origin of ancestors of a monophyletic clade of organisms. These methods do not assume vicariance as the sole divergence

method, but instead allow that some members of a group may have dispersed from smaller centers of origin. These methods are useful for studying historical biogeography of this clade of birds because of the role that dispersal must have played in this radiation of mostly island birds. We assigned the distributions of taxa to the following areas: Caribbean, Central America, South America, Galápagos, and Cocos Island. Taxa that were found in multiple areas were coded as existing in multiple areas; for example, we coded *Coereba* as present in three areas (Caribbean, Central America, and South America). Bremer's ancestral area analysis (Bremer 1992, 1995) compares the number of gains under forward Camin-Sokal parsimony relative to the number of losses under reverse Camin-Sokal parsimony. Areas having a higher number of gains relative to losses for a particular clade (a higher gain/loss quotient) have a higher probability of being part of the ancestral area of that clade. This procedure is performed on a node-by-node basis so that the contributions of each area to the ancestral area at any particular node can be assessed. Hausdorf's (1998) method is similar to that of Bremer's, except that gains and losses are weighted by their basal or apical position in the tree with greater weight being given to basal branches and less weight being given to more apical branches. Thus, each area is assigned a *PI* value (the relative probability that that area was part of the ancestral area). The larger the *PI* value, the greater the probability that the area was part of the ancestral distribution of a particular clade. Dispersal-vicariance analysis (Ronquist 1997) reconstructs ancestral distributions and dispersal events on a phylogeny such that the number of dispersal and extinction events are minimized. We used DIVA version 1.1 (Ronquist 1996) to reconstruct the biogeographic history of this clade using Ronquist's method.

RESULTS

Sequence Variation

As expected for a protein coding mitochondrial gene, all sequences aligned without gaps or insertions. Of the 1045 sites, 479 (46%) were variable. Levels of uncorrected sequence divergence (*p*-distance of Nei [1987]) within all the non-warbler taxa varied from 0.2% (between two individuals of *Phaenicophilus palmarum*) to 16.5% (between *Chlorophonia flavirostris* and *Habia rubica*). Base composition (guanine 13.6%, adenine 26.5%, thymine 24.2%, cytosine 35.7%) was similar to that reported in other studies of cytochrome *b* in passerine birds (Edwards et al. 1991; Helm-Bychowski and Cracraft 1993; Burns 1997). Changes at third position sites were more common than changes at second and first position sites. Of the 450 variable sites, 97 were first positions, 26 were second positions, and 327 were third positions. Transitions between individual sequences were approximately twice as common as transversions.

Phylogenetics

In the Bayesian analyses of all individuals, log-likelihood values reached a stable equilibrium well before 250,000 generations. Thus, we chose a burn-in value of 2500 samples and constructed a majority rule consensus tree using the re-

maining samples (Fig. 1). The repeated analyses had similar posterior probabilities and likelihood values, indicating insensitivity to initial starting tree. Darwin's finches were identified as a monophyletic group with a posterior probability of 84%. Strong support (posterior probability = 100%) was observed for a previously unrecognized clade of birds containing Darwin's finches and 13 other species, including several Caribbean endemics (Fig. 1).

Based on the topology of the Bayesian analyses, we pruned our dataset to 60 taxa and performed parsimony analyses. The pruned dataset contained 450 variable sites, and 386 (86%) of these were phylogenetically informative. The following list indicates the number of trees and consistency indices (excluding uninformative characters) found in the equal weight, 2:1, 5:1, 10:1, and 50:1 analyses, respectively: 139, 0.25; 9, 0.26; 6, 0.27; 2, 0.28; 2, 0.28. In general, fewer most-parsimonious trees were found in the analyses that downweighted third position transitions to a greater degree. Except for the 50:1 analysis, all most parsimonious trees identified Darwin's finches as a monophyletic group. Because this dataset included 60 taxa, there were 59 nodes that potentially could be supported. In the bootstrap analyses, 18 to 22 of these 59 nodes showed bootstrap support greater than 50% in the various weighting schemes.

All of the most-parsimonious trees identified the same previously unrecognized clade of birds identified in Bayesian analyses that contained Darwin's finches and 13 other species. This clade had strong support in all of the bootstrap analyses. In the equally weighted analyses, this clade was supported in 89% of bootstrap replicates. In all other weighting schemes, this clade was supported in either 99% or 96% of bootstrap replicates. The species in this clade (including Darwin's finches) are unique among all other species included in this study in that they build covered or domed nests with side entrances (Lack 1947; Bond 1993; Isler and Isler 1999). In addition, this type of nest structure is not found among any other species of Thraupini (including those that were not sampled in this study). Although species in the ''tanager'' genera *Euphonia* and *Chlorophonia* build these types of nests, these taxa have recently been found to be more closely related to cardueline finches and thus are not related to Thraupini (Burns 1997; Klicka et al. 2000). Hereafter, for ease of discussion, we will refer to the clade of Darwin's finches and their relatives that build this unique type of nest as the ''domed nest clade.'' The species within the domed nest clade are genetically quite similar to each other, indicating they share a very recent common ancestry. Levels of sequence divergence range from 0.3% to 10.0% and average only 6.7%. By comparison, Johns and Avise (1998) compiled cytochrome *b* sequence data for 88 avian genera and found that congeners show on average 7.8% sequence divergence. Thus, most species within the domed nest clade exhibit levels of genetic divergence less than that of pairs of congeneric, closely related species of birds. This contrasts with the traditional taxonomies that have placed these species into 13 different genera and three different families based on dramatic morphological differences in bill size and other characters.

To further explore relationships among members of this domed nest clade, we performed maximum-likelihood and Bayesian analyses of the 22 individuals identified as being part of this clade. For maximum likelihood analyses, the GTR + gamma model was identified as the most appropriate by ModelTest. Using this model, the same topology (Fig. 2; −ln likelihood = 4421.933) was found in all 10 random addition replicates. To explore the sensitivity of the likelihood analyses to the starting topology, we used a neighbor-joining tree, a successive-approximation tree (using the rescaled consistency index; Farris 1969; Carpenter 1988), or an equally weighted-parsimony tree as the starting tree and also performed iterations where the Akaike information criterion was used instead of the hierarchical likelihood ratio test criterion. In all cases, although different topologies and different models of evolution were sometimes initially selected, the same topology was ultimately chosen in all likelihood analyses. Thus, we consider our data insensitive to starting tree and model, and this topology is our best likelihood estimate of relationships among these taxa.

For each of the three Bayesian analyses of the domed nest clade, repeated analyses of the same initial model and parameters had similar likelihood values and posterior probabilities, indicating our data were insensitive to the initial starting tree used. Log-likelihood values stabilized well before 50,000 generations. Thus, we chose a burn-in value of 500 samples for all analyses and constructed majority rule consensus trees using the remaining samples. The two analyses that specified the GTR + gamma model found the same topology (hereafter referred to as topology A; Fig. 3A). Posterior probability values of these two Bayesian analyses were also highly congruent (values for the rate-specified analysis shown in Fig. 3A). Although this topology did not conflict with that found in the maximum-likelihood analyses, this topology was more resolved than the maximum-likelihood tree. The maximum-likelihood analysis was unable to resolve the position of the clade containing *Loxigilla portoricensis*, *L. violacea*, and *Melopyrrha* with respect to *Euneornis* and the large clade containing *Loxipasser* and 13 other species. For the analyses in which site-specific rates were estimated for each codon position, a different topology was obtained (topology B; Fig. 3B). This topology was similar to topology A, but differed in the arrangement of taxa within two clades: the clade containing *Melopyrrha*, *Loxigilla violacea*, and *L. portoricensis* and the clade containing *Tiaris canora*, *T. fuliginosa*, *T. obscura*, *T. bicolor*, *Melanospiza richardsoni*, and *Loxigilla noctis*. Support for the nodes that conflicted between these two trees were low and the SH test could not distinguish between the log likelihoods of these two topologies (*P* = 0.325). Therefore, both of these topologies were considered in the biogeographic analyses below. In both topologies, the genera *Tiaris* and *Loxigilla* were paraphyletic.

In general, clades with strong bootstrap support in the maximum likelihood analyses also had high posterior probability values (Fig. 3). Support was high for the monophyly of Darwin's finches (posterior probability = 100%) and for relationships among the genera of Darwin's finches. Support was also high for a relationship between *Tiaris olivacea* and *Coereba flaveola*, a relationship between *T. obscura* and *T. fuliginosa*, and for the monophyly of a clade containing all domed nest species to the exclusion of *T. olivacea* and *C. flaveola*. Based on Bayesian and parsimony analyses of the larger da-
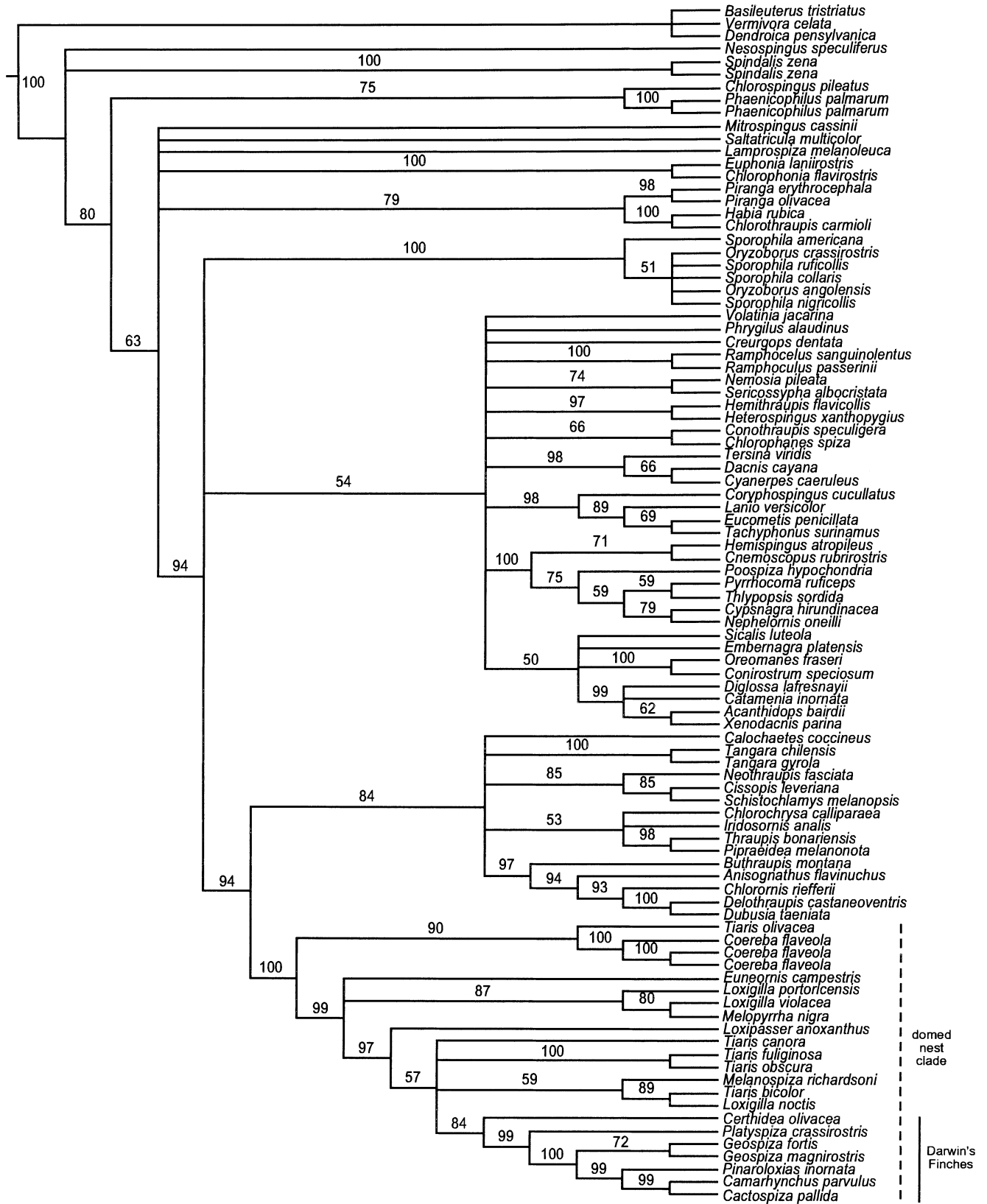
FIG. 1. Majority rule consensus tree of the 7500 trees resulting from the Bayesian analyses of the entire dataset. Numbers on nodes indicate the posterior probability of a particular clade. Short vertical line indicates the species belonging to Darwin's finches. Longer dashed line indicates species belonging to the domed nest clade defined in the text.
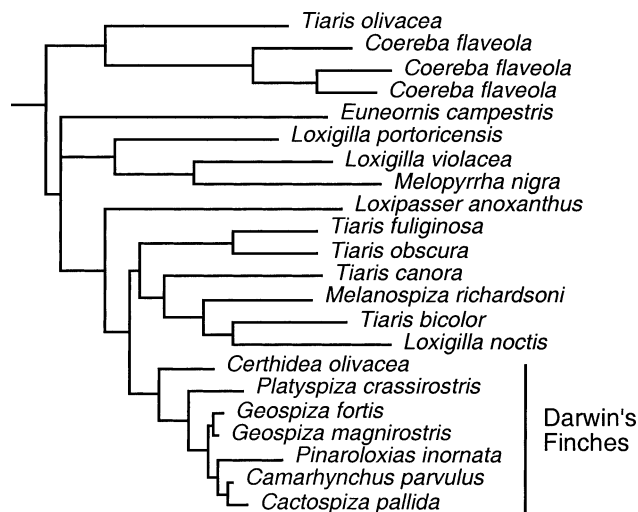
Fig. 2. Maximum likelihood topology resulting from phylogenetic analysis of the domed nest clade. Branch lengths are proportional to the amount of molecular change occurring along the branch.

taset, *Sporophila* and *Volatinia* can be excluded as the closest living relatives of Darwin's finches. Within the domed nest clade, Shimodaira-Hasegawa tests were used to determine whether other species previously proposed to be closely related to Darwin's finches are their closest living relative (Table 2). A tree in which all species of *Tiaris* were constrained to be a monophyletic sister group to Darwin's finches was significantly different from the best likelihood tree. In addition, we were also able to exclude *C. flaveola* as the sister clade to Darwin's finches.

Biogeography

Eleven of the 13 species found to be closely related to the Darwin's finches occur within the Caribbean (Fig. 4). Eight of the species are Caribbean endemics (*Tiaris canora* and all members of the following genera: *Euneornis*, *Loxigilla*, *Melopyrrha*, *Melanospiza*, and *Loxipasser*), and three of the other species (*T. bicolor*, *T. olivacea*, and *Coereba flaveola*) are more widespread but include the Caribbean islands in their distributions. Using the two trees identified using maximum-likelihood and Bayesian analyses and the three methods of biogeographic analysis, many ancestral nodes are identified as having their distributions in the Caribbean as well.

Strong support is provided for a Galápagos–Caribbean link among the branches leading up to Darwin's finches (Fig. 4). In the ancestral area analysis using topology A (Fig. 4A), a dispersal event is hypothesized from the Caribbean to the Galápagos prior to the evolution of the most recent common ancestor to Darwin's finches. Weighted ancestral area analysis (Fig. 4B) predicts a similar scenario, although the dispersal event occurred more recently in the tree. Using topology B, ancestral area analysis and weighted ancestral area analysis both identify this same pattern (Fig. 4C). Dispersal–vicariance analysis offers two alternative scenarios. Both trees identify one of these alternatives: dispersal from the Caribbean to the Galápagos along the branch leading up to the most recent common ancestor of Darwin's finches and its sister clade (Fig. 4D, E). Alternatively, the first tree also
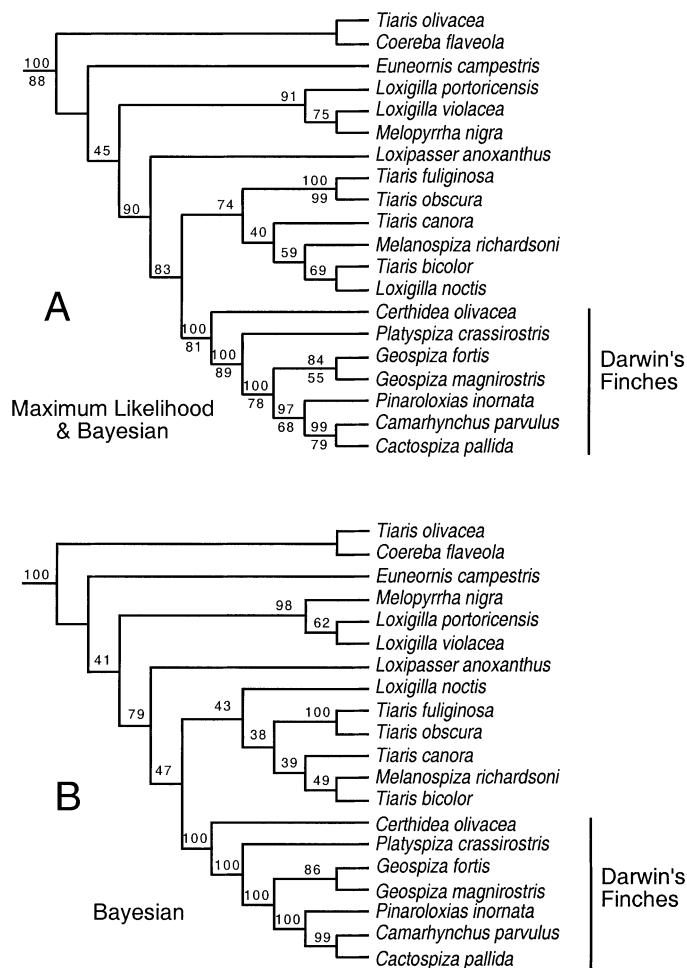

Fig. 3. Maximum-likelihood and Bayesian topologies resulting from phylogenetic analysis of the domed nest clade. In both trees, the three individuals of *Coereba flaveola* are shown as a single branch for ease of presentation. Numbers at nodes indicate posterior probabilities (above the branch) and maximum-likelihood bootstrap values (below the branch). Topology A indicates the tree found in the Bayesian analyses using the GTR + gamma model. The maximum-likelihood tree was similar except that the position of the clade containing *Loxigilla portoricensis*, *L. violacea*, and *Melopyrrha* could not be resolved with respect to *Euneornis* and the large clade containing *Loxipasser* and 13 other species (see Fig. 2). Topology B indicates the tree found in the Bayesian analyses that involved site-specific rates for codon positions.

TABLE 2. Results of Shimodaira-Hasegawa test comparing likelihood tree to alternative hypotheses based on previous studies. Species listed under constraint indicate those constrained to be the sister taxon to Darwin's finches.

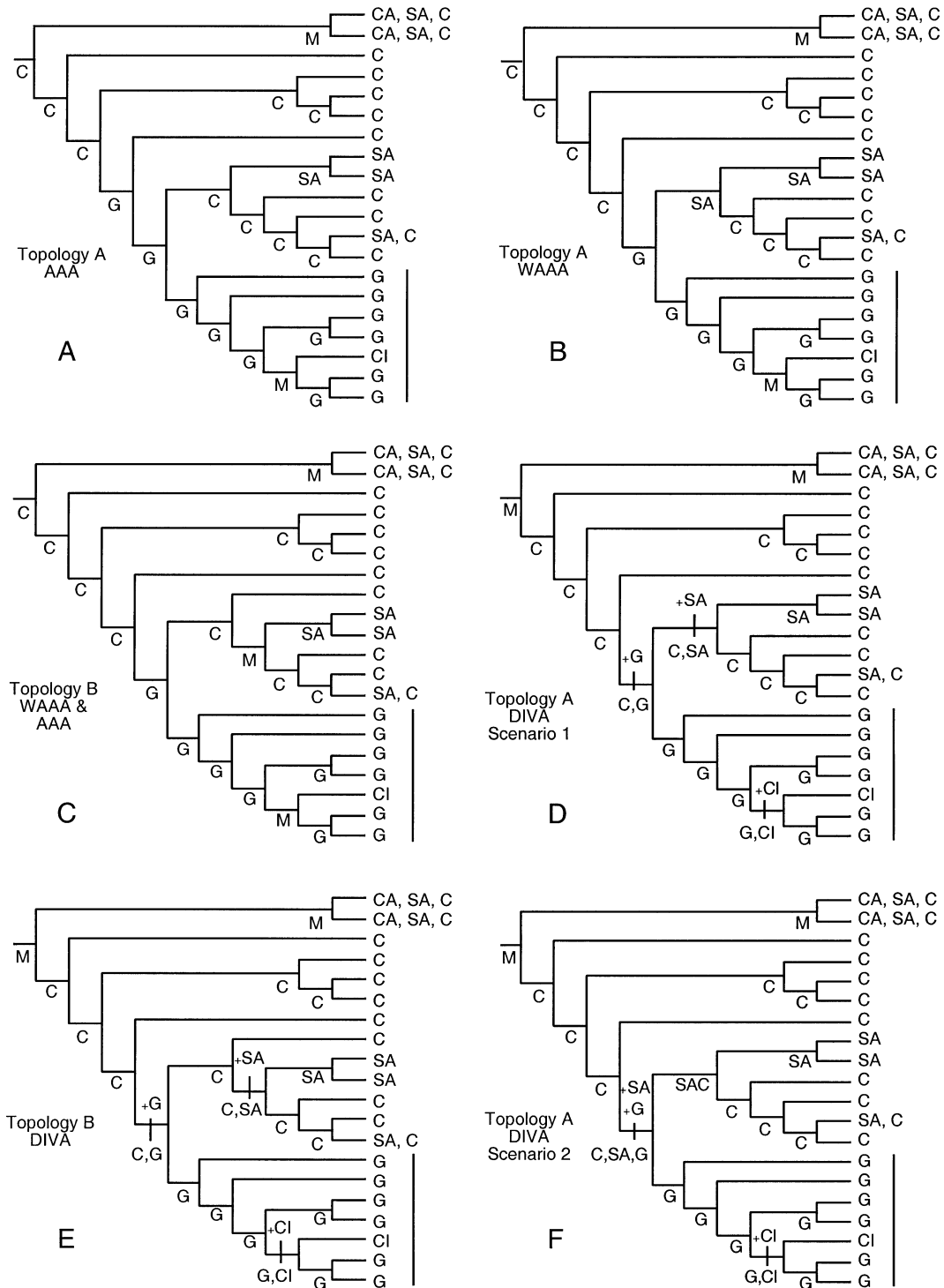| Constraint	$-\ln L$	P
Best tree	4421.93	(best)
Tiaris obscura	4443.69	0.06247
Coereba flaveola	4445.49	0.04771*
Melanospiza richardsoni	4426.27	0.62739
Tiaris (all species)	4473.94	0.00038*

* $P < 0.05$.

FIG. 4. Reconstruction of the biogeographic history of Darwin's finches and their close relatives. Order of taxa match that in Figure 2. (A) topology A, ancestral area analysis (AAA); (B) topology A, weighted ancestral area analysis (WAAA); (C) topology B, WAAA and AAA; (D) topology A, DIVA, Scenario 1; (E) topology B, DIVA; (F) topology A, DIVA, Scenario 2. Biogeographic regions were coded as follows: C, Caribbean; SA, South America; CA, Central America; G, Galápagos; CI, Cocos Island; M, multiple solutions possible.

indicates that there may have been simultaneous dispersal from the Caribbean to South America and the Galápagos along this branch (Fig. 4F). Later, this widespread taxon evolved into two separate lineages, one in the Galápagos and the other in South America and the Caribbean. Although this second scenario includes South America, it does not propose a direct link between the Galápagos and South America without including the Caribbean.
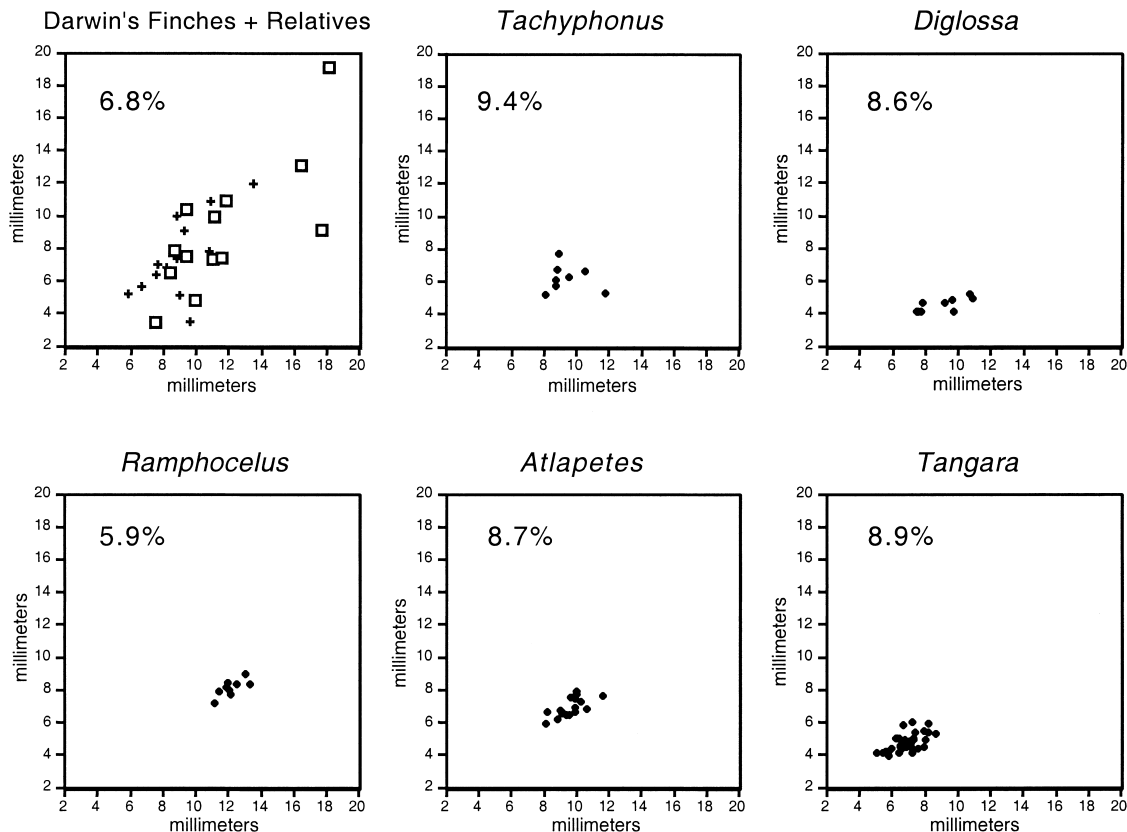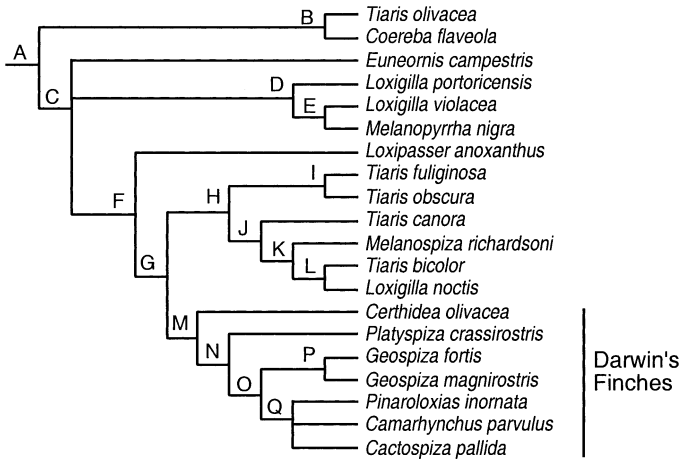
FIG. 5. Scatter plots of bill length (horizontal axis) and bill depth (vertical axis). All measurements are in millimeters and each graph is drawn at the same scale. Each point represents the mean value of data collected for a single species from museum skin measurements. Average uncorrected percent sequence divergence for each group is as follows: domed nest clade (open squares, Darwin's finches; +, close relatives), 6.8%; *Tachyphonus* tanagers, 9.4% (K. Burns, unpubl. data); *Diglossa* flowerpiercers, 8.6% (Hackett 1995); *Ramphocelus* tanagers, 5.9% (Hackett 1996); *Atlapetes* finches, 8.7% (Hackett 1992); and *Tangara* tanagers 8.9% (K. Burns and K. Naoki, unpubl. data).

Morphological Variation

Scatterplots of bill length and depth of species in the domed nest clade indicate that species within this group show substantial variation in bill size and shape (Fig. 5). This variation is not confined to Darwin's finches, but also extends to the other species of the domed nest clade found to be closely related to them. This extensive variation in bill size and shape is not found in other lineages of tanagers and finches that display levels of sequence divergence similar to or greater than those of Darwin's finches and their close relatives (Fig. 5). For example, species in the domed nest clade average 6.8% sequence divergence. By comparison, species in the genus *Tachyphonus* have on average 9.4% sequence divergence (K. Burns, unpubl. data), but have much less variation in bill size. Thus, members of the domed nest clade show much greater variation in bill size and shape than other lineages of tanager-finches of a similar age. Statistical analyses of bill size measurements support the pattern seen in the scatterplots. Residuals from the bill morphology regression analyses show normality of values for all clades. T-tests of mean residual values demonstrate that the domed nest clade exhibits significantly greater mean values and therefore significantly increased occupation of morphospace in comparison to the other similarly aged clades.

These plots (Fig. 5) and associated statistical analyses clearly demonstrate that there is a great diversity of bill types within the domed nest clade. However, they do not show where the evolution within this clade has been the greatest. To further explore the nature of this change within the domed nest clade, we used the branch lengths and topology of the maximum-likelihood phylogeny to compare independent contrast values among nodes within the domed nest clade. Although changes in bill length and depth are much greater within the domed nest clade than in other clades of tanager-finches (Fig. 5), the magnitude of change is not evenly distributed within this clade (Fig. 6). The largest contrast values for all three bill measures are within the Darwin's finches themselves. For example, for bill depth, the four largest contrast values all involve nodes within the Darwin's finches (nodes M, N, O, and P). Evolution of bill size within *Geospiza* appears to have been particularly rapid. The node contrasting the species of *Geospiza* has one of the highest contrast value for all three bill measurements. Another node with large contrast values is node M, which contrasts bill size among the warbler finch (*Certhidea*) and the other Darwin's finches. Thus, the independent contrast values indicate that bill change has been more rapid in the evolution of Darwin's finches than anywhere else in the domed nest clade. This
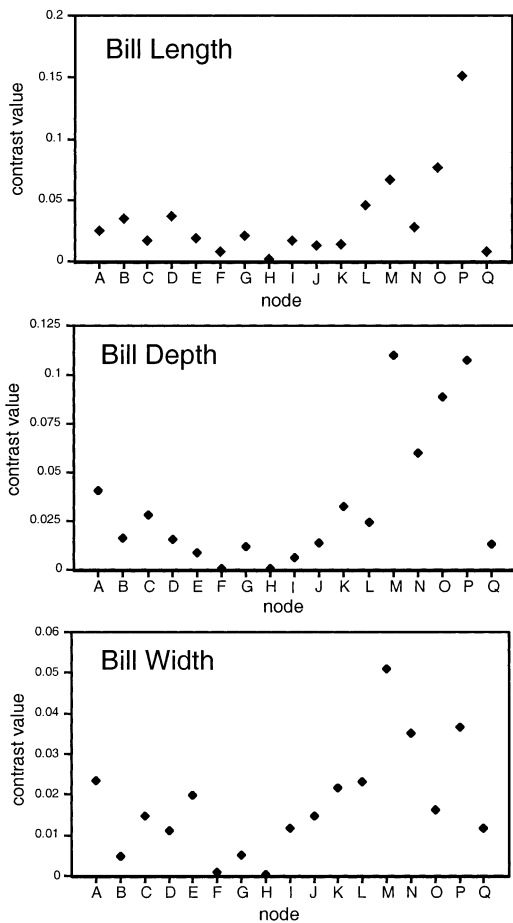
FIG. 6. Independent contrasts of bill length, depth, and width for Darwin's finches and relatives (domed nest clade). Topology shown is the maximum-likelihood topology except that relationships among *Pinaroloxias*, *Camarhynchus*, and *Cactospiza* have been drawn as unresolved based on other studies (see text). Vertical line indicates the Darwin's finch species. In the plots of bill dimensions, the horizontal axis indicates node letter as shown in the phylogeny and the vertical axis indicates the magnitude of the contrast.

pattern is also illustrated by inspecting the branch lengths themselves (Fig. 2). Branches leading to nodes connecting Darwin's finches are relatively shorter than those seen in other parts of the tree. These short branches coupled with the large morphological differences seen among Darwin's finches are driving the pattern seen in the independent contrast analyses. However, it is important to re-emphasize that the entire domed nest clade has undergone extensive bill evolution in a relatively short time frame (Fig. 5) compared to other Thraupini. In other words, bill evolution has been relatively rapid within the domed nest clade compared to other lineages of tanagers and finches of a similar age (Fig. 5), and within the domed nest clade, bill evolution has occurred at an even more accelerated pace among some of Darwin's finches (Fig. 6).

DISCUSSION

Phylogenetic and Taxonomic Conclusions

Taxon sampling can have a profound effect on topological relationships in a phylogeny (Smith 1994). Although many authors have speculated on the origin of Darwin's finches and tried to determine relationships among them, only one previous study of Darwin's finches (Sato et al. 2001) has used phylogenetic methods and multiple outgroups. However, Sato et al. (2001) did not include several of the species that are closely related to Darwin's finches (Fig. 1). Our study shows that both the monophyly of Darwin's finches and the general arrangement of genera of Darwin's finches are not sensitive to the more dense outgroup sampling of our study over that of Sato et al. (2001). Like Sato et al. (2001), we found strong support for the monophyly of Darwin's finches. All Bayesian, maximum-likelihood, and parsimony analyses (except the 50:1 weighting) identified Darwin's finches as a monophyletic group. Both likelihood bootstrap and Bayesian posterior probability values of this clade are high (Fig. 3). Thus, all species (including the Cocos Island finch and the Warbler finch) descended from a single common ancestor. In addition, there is broad congruence in the topological relationships of Darwin's finch genera between our study and that of previous sequence based studies that did not sample potential outgroups extensively (Sato et al. 1999; Sato et al. 2001). Thus, our study agrees with these previous studies in that a clade containing *Pinaroloxias*, *Cactospiza*, and *Camarhynchus* is the sister taxon of *Geospiza*; *Platyspiza* is the sister taxon of these genera; and *Certhidea* is the most basal Darwin's finch. All of these nodes have strong support; thus, this arrangement can be used for testing hypotheses about evolution within the finches.

Our analyses are able to show that several species previously proposed as sister taxa to Darwin's finches are not their closest living relatives. Although previous studies have suggested that either *Sporophila* or *Volatinia* is the sister taxon to the Darwin's finches, Bayesian analyses of the larger dataset and all of our parsimony analyses provide strong support for a clade that contains Darwin's finches and several other species but excludes these two genera. Furthermore, the cup-shaped nest built by species in *Sporophila* and *Volatinia* is further evidence that they do not belong in the domed nest clade that contains Darwin's finches. Within the domed nest

clade, SH tests were able to reject *Tiaris* and *Coereba flaveola* as the closest living relative to Darwin's finches (Table 2). Instead of identifying a single species as the closest living relative to Darwin's finches, our results identifies a clade of six species (*Tiaris canora*, *T. fuliginosa*, *T. obscura*, *T. bicolor*, *Loxigilla noctis*, and *Melanospiza richardsoni*) that together form the sister taxon to Darwin's finches.

The ''domed nest clade'' represents a strongly supported monophyletic group not previously recognized. Thus, we propose the Latin name Tholospiza (meaning dome finch) to assist future communication concerning this group of birds. Because of the importance of Darwin's finches in a variety of evolutionary and ecological studies, we anticipate that having a formal name to describe their phylogenetic position will be useful. We do not propose a rank for Tholospiza because of the current state of uncertainty in tanager phylogeny (Sibley and Ahlquist 1990, Burns 1997).

Biogeography

Most of the species identified as the closest living relatives to Darwin's finches occur on the Caribbean islands. The predominance of Caribbean species within this clade is not an artifact of our taxon sampling. We included a number of South American taxa in our study, several which have been previously suggested as closely related to Darwin's finches. In fact, most of the non-Darwin's finches included in our study occur in South America, and these species were not identified as closely related to Darwin's finches. Furthermore, the unusual nest type of this clade is strong corroborating evidence of the monophyly of this group to the exclusion of all other taxa, even those that we did not sample.

Because many of the species in the domed nest clade occur in the Caribbean, this region must have played an important role in the evolution of the group. Discussions of island radiations in birds have mostly focused on the Hawaiian and Galápagos Islands; however, our results indicate that similar processes may be occurring among birds in the Caribbean. Island radiations within the Caribbean are well documented for non-avian taxa (Hedges et al. 1994; Hedges 1996; Losos et al. 1998), but only a few avian groups have been studied in detail (Seutin et al. 1994; Hunt et al. 2001). Our results indicate that more attention should be given to the Caribbean as a source of avian adaptive radiations. Probably the reason for the lack of discussion of radiations within Caribbean birds is that the birds of this region are generally thought to represent a composite of different types of birds that managed to arrive through dispersal from other areas (Bond 1978). This idea is reflected in the traditional taxonomy of the birds of this clade, as members of this clade have typically been placed within three different families. Our results show that they are instead a closely related group, with comparatively little genetic divergence among the species.

Many authors have discussed the geographic origin of Darwin's finches (e.g., Harris 1971; Steadman 1982; Grant 1999). Most of the literature has focused on South America as being the source of the ancestor to Darwin's finches, with only a few authors suggesting a Caribbean origin. However, no previous studies have attempted to investigate the ancestral origin of Darwin's finches in a rigorous fashion using quantitative biogeographic methods and a variety of outgroups. Typically, these studies assumed that the distribution of the ancestor of Darwin's finches was the same as the distribution of their closest living relative. For example, because Sato et al. (2001) identified *T. obscura* as the closest living relative of Darwin's finches, the authors assumed a South American origin to the finches. However, this approach ignores the distribution of taxa on other branches of the tree. If only the closest living relative is considered, there are only two branches under consideration, that of Darwin's finches and that of their closest living relative. Therefore, it is equally likely that the common ancestor of these two lineages had its origin in either of these two areas (or perhaps both). However, if a number of lineages leading up to Darwin's finches are all found in the same area or if a number of separate lineages within the sister taxa are found in the same area, it would strengthen the argument that this area was the source of the ancestor of Darwin's finches. In this study, we used three common methods of biogeographic inferences that consider distributional information and branching structure. All three of the methods provide stronger support for a Caribbean origin to Darwin's finches than for South America. Thus, discussion of the evolution of Darwin's finches should be placed within the context of a larger radiation of birds whose distributions are centered in the Caribbean.

We do not think that the island distributions of Galápagos finches and their close relatives are coincidental. One possible explanation would be that these island taxa are remnants of an ancient widespread lineage that has since become extinct on mainland South America. This explanation would agree with the idea that the Caribbean species in this group are relictual taxa (Bond 1961, 1971). However, levels of genetic variation are low within species in this group; they probably originated more recently than other taxa in South America. Thus, the recent nature of this lineage may have led to greater success colonizing relatively new islands in which competing species were absent. As a result, more of these species are distributed on islands rather than in South America. Along with this, these species may have had a greater propensity for dispersal than other lineages and thus had greater capabilities of colonizing islands.

Morphological Evolution and Adaptive Radiation

Previous workers have not suspected a close relationship among all members of the domed nest clade because of the morphological diversity present among the species. The evolutionary relationships of *Euneornis*, *Loxigilla*, *Loxipasser*, *Melanospiza*, *Melopyrrha*, *Tiaris*, and *Coereba* have been problematic, leading some workers to conclude that each of these genera have no extant close relatives (e.g., Bond 1961, 1971). Thus, traditional taxonomists have included most of these species in separate genera or even in separate families. Like Darwin's finches, these close relatives of Darwin's finches differ dramatically in their feeding morphologies (Fig. 5). For example, some species (*Coereba*, *Euneornis*) have thin bills and are specialized to feed on nectar. Other species (*Tiaris*, *Melopyrrha*, *Melanospiza*, *Loxigilla*, and *Loxipasser*) have more conical bills of various sizes and feed on seeds. In contrast to the substantial differences in morphol-

ogy, levels of sequence divergence among Darwin's finches and their close relatives are surprisingly low, indicating they all share a very recent common ancestry.

Much of the literature about bill evolution within Darwin's finches and potential close relatives has focused on whether or not the ancestor to Darwin's finches had a ''warbler-type'' or ''finch-type'' bill. We feel that characterization of bill types into one of these two categories is overly simplistic as the nature of variation among these species is much more continuous than such a classification indicates (Fig. 5). Instead of focusing on the specific ancestor to Darwin's finches, a more useful approach to understanding the history of morphological change within this group is to consider the pattern of change across all the nodes in the phylogeny of Darwin's finches and their close relatives. Our study shows that the entire domed nest clade has undergone extensive bill evolution in a relatively short time frame (Fig. 5) compared to other lineages of tanager-finches. We propose two possible explanations for this pattern that are not necessarily mutually exclusive of each other. One possibility is that since many of these species are island taxa, there may have been strong selection for different bill types as these birds colonized new islands with vacant niches. An alternative, more structuralist interpretation is that the ancestor to all of these birds possessed a developmental-genetic architecture (passed on to its descendents) that included a greater variety of regulatory genes controlling nasiocranial development.

Darwin's finches are often cited as the classic example of an adaptive radiation. However, given the phylogenetic context from which Darwin's finches evolved (Figs. 1–3), whether or not Darwin's finches should be considered an adaptive radiation depends on how this concept is defined. If a definition that incorporates speciation rate as its sole criterion (Guyer and Slowinski 1993) is used, Darwin's finches would not qualify as an adaptive radiation. Their immediate sister taxon contains six species (Fig. 2, 3), while Darwin's finches themselves contain 13 species. Thus, a topology such as this is not so unbalanced that it could arise by chance alone. Whether or not the entire domed nest clade could be considered an adaptive radiation under this definition requires further study as the sister taxon to the domed nest clade can not be determined definitively with the current dataset (Fig. 1). Alternatively, if more traditional definitions of adaptive radiation are used (e.g., Simpson 1953; Grant 1963; Givnish 1997), Darwin's finches themselves, as well as the entire domed nest clade, would probably qualify as an adaptive radiation. These more traditional definitions incorporate diversity of ecological role and rapid speciation rate. Darwin's finches and other members of the domed nest clade have clearly undergone rapid morphological divergence in a relatively short time frame. The adaptive nature of this change has been well studied within Darwin's finches, but remains unexplored among their close relatives as identified in this study. Although these species are known to specialize on a diversity of food items, detailed experimental, observational, and comparative studies should be pursued in the future to better characterize correlations between trophic (bill) morphology and dietary specialization. Recent studies (Vincek et al. 1997; Freeland and Boag 1999; Sato et al. 1999) have shown that adaptive evolution in Darwin's finches occurred

over a short time span. Our data show that among the relatives of Darwin's finches, the evolution of bill diversity was also rapid and extensive. Thus, the adaptive evolution of bill size and shape in Darwin's finches was preceeded and paralleled by the evolution of diverse feeding morphologies among their close relatives, most of which occur in the Caribbean.

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Corresponding Editor: S. Edwards