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Molecular phylogenetics of Trogon: Exploring patterns of diversification in a widespread neotropical avian genus

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MOLECULAR PHYLOGENETICS OF *TROGON*: EXPLORING PATTERNS OF DIVERSIFICATION IN A WIDESPREAD NEOTROPICAL AVIAN GENUS

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ABSTRACT

Molecular Phylegenetic of *Trogon*: Exploring Patterns of Diversification in a Widespread Neotropical Avian Genus

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Study of Neotropical avian biodiversity have generally been focused on South American taxa. As a result, the contribution of Central America to overall Neotropical diversity remains under-studied. The Great American Interchange (GAI) between North and South America is a biogeographic event known to impact biodiversity throughout the Neotropics, linking the evolutionary history of these land masses. Here I show that genetic diversity in the well-known and widespread Neotropical avian genus *Trogon* greatly exceeds previously recognized biodiversity in this group. Results also invoke a Central American center of origin for the genus, with multiple independent dispersals into and subsequent diversification within South America. This has created non-monophyly in the current taxonomy, which has been masked by the use of misleading plumage characters in historical classification of the genus.

Recovered patterns can be used in comparative studies with other Neotropical groups, providing insights into the evolutionary past of this diversity rich region.

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CHAPTER 1

INTRODUCTION

The avian order Trogoniformes is comprised of a single family, Trogonidae. Members of the family share a number of morphological, osteological, and anatomical characters (Collar 2001; Espinosa de los Monteros 1998; Johnsgard 2000). The most distinctive feature of Trogonidae is the arrangement of the toes. Trogonids are the only birds that have heterodactyl feet, where digits one and two are oriented backward, whereas three and four are pointed forward. Support for the monophyly of Trogonidae appears strong, but its phylogenetic relationships to other families are poorly understood (Sibley and Alquist 1990). The difficulty in elucidating these relationships stems from the lack of extant, closely related families. The lack of recent common ancestors with other families creates long branches in phylogenetic analyses, and makes relationships more difficult to reconstruct due to homoplasy. Trogonidae is currently comprised of six genera: *Apaloderma* (African trogons), *Harpactes* (Asian trogons), *Priotelus* (Caribbean trogons), *Euptilotis* (Eared Quetzal), *Pharomachrus* (Neotropical quetzals), and *Trogon* (Neotropical trogons). The focus of this study is the molecular phylogenetics of *Trogon*, which are currently comprised of 17 species (Sibley and Monroe 1990).

Past molecular phylogenetic studies of *Trogon* (Espinosa de los Monteros 1998; Johansson and Ericson 2005; Moyle 2005) were unable to fully explore the evolution of the group due to sampling limitations. Taxon sampling at the species level was incomplete in each study, ranging from only five (Johansson and Ericson 2005) to 14 (Moyle 2005) of the 17 currently recognized species. Also, each study used only one individual per species in the analyses, making intraspecific diversity and non-monophyly of species impossible to assess. This incomplete sampling at both the species and intraspecific level can lead to a simplified and/or false phylogenetic reconstruction (Omland et al. 1999), which can fail to fully elucidate the evolutionary history of the group.

In this study I improved past phylogenetic analyses by greatly increasing the sampling of *Trogon* at the species and intraspecific level. All 17 of the currently recognized species were included in the study, and multiple samples (n = 2-18) were analyzed from each species. This sampling produced a more robust hypotheses of relationships among, and genetic diversity within, recognized species.

This robust *Trogon* phylogeny was then used to explore the impact of the Great American Interchange (GAI) on its historic diversification (Chapter 2), and the evolution of some of its external morphological characters (Chapter 3). The GAI is the exchange of biotia between North and South America after the completion of the Isthmus of Panama ca. 3 mya (Simpson 1940; Stehli and Webb 1985). Patterns in the phylogeny were used to infer the direction of *Trogon* dispersal between these continents, and the GAI's impact on its diversification.

The phylogeny was also used to explore the evolution of *Trogon* morphology, with character reconstruction at ancestral nodes and an analysis of how traits track the molecular phylogeny.

This study offers great insight into the evolution of *Trogon*. The relationships among species are described in more detail than in previous studies. The analysis of multiple individuals per species allows greater resolution at the tips of the tree, revealing marked genetic diversity and suggesting incorrect taxonomy in a number of species. The resulting phylogeny offers the best tool available to explore complex patterns in the biogeography and character evolution of *Trogon*. The recovered patterns can serve as a model of comparison for future studies of other Neotropical groups.

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CHAPTER 2

THE GREAT AMERICAN INTERCHANGE IN BIRDS: A PHYLOGENETIC PERSPECTIVE WITH THE GENUS *TROGON*

Introduction

The "Great American Interchange" (GAI) is the exchange of biota between North and South America after the completion of the Isthmus of Panama, and is recognized as having a dramatic effect on biodiversity in both continents (Simpson 1940; Stehli and Webb 1985; Vrba 1992; Wallace 1876). Before the GAI the biota of North America had general Holarctic affinities due to historic connections with Europe and Asia, while the biota of South America formed a distinct assemblage due to its "splendid isolation" since the breakup of Gandwanaland (Marshall 1988; Morley 2003; Simpson 1980; Stehli and Webb 1985). This isolation was disrupted by the completion of the Isthmus of Panama, a protracted geological event that culminated in a complete land bridge between North and South America ca. 3 mya (Coates and Obando 1996). The impact of the GAI on mammalian biodiversity throughout North and South America is well documented in the fossil record (Marshall 1988; Simpson 1980; Stehli and Webb 1985). The mammalian exchange was asymmetrical, with more North American groups able to establish and diversify in South America. Hypothesized proximate factors for the asymmetry include a combination of demographic, climatic,

competitive, and dispersal variables. The impact of the GAI on other vertebrate groups, including birds, are less understood due to a comparatively poor fossil record.

Most hypotheses regarding the evolution of avian biodiversity in the Neotropics have focused on South America (Haffer 1997), and in general do not assess the impact of the GAI. These hypotheses evoke the effects of paleogeography, river barriers, climate change, and ecotones to explain South American avian biodiversity, particularly among areas of endemism in the Amazon Basin. Cracraft and Prum (1988) were the first to investigate relationships among these areas within a phylogenetic framework through a cladistic analysis of morphological characters in three genera. More recent studies used DNA sequence data to elucidate phylogeographic patterns in the Amazon (Aleixo 2004; Cheviron et al. 2005; Eberhard and Bermingham 2005; Marks et al. 2002; Ribas et al. 2005). These studies provided important incites regarding the evolutionary history of birds in South America. However, the role of the GAI in large-scale Neotropical avian biodiversity patterns remains unclear due to limited sampling in Central America. Additional studies with comprehensive geographic and taxonomic sampling of groups occurring in both Central and South America are needed to assess the impact of the GAI on historical diversification in birds. Robust phylogenies for such groups can be used to infer the direction and timing of movement across the Isthmus of Panama, and the location of phylogenetic breaks beyond the Amazon Basin.

The avian genus *Trogon* (Family Trogonidae) is a good model for study of the GAI and biogeographic patterns across the entire Neotropics. It contains 17 species that are collectively distributed from the southwestern United States to northern Argentina, with many species occurring in both continents. All species of *Trogon* are non-migratory, and regarded as relatively weak fliers that move only short distances (Collar 2001). Therefore, biogeographic patterns are not likely to be blurred by long-distance dispersal. Past phylogenetic research on the genus has been unable to explore intercontinental evolutionary patterns due to either incomplete sampling or a focus on the pantropical distribution of the entire family (Espinosa de los Monteros 1998; Johansson and Ericson 2005; Moyle 2005). Also, all three studies used one exemplar per species. This sampling scheme makes the assessment of intraspecific diversity and species monophyly impossible, and could produce a misleading phylogeny of the group (Omland et al. 1999). Additional sampling of each species will produce a more robust phylogeny better equipped to evaluate the GAI and diversification patterns across Central and South America.

The goals of this study are: i) to produce a robust molecular phylogeny of *Trogon* with broad geographic sampling of each species, ii) to use the phylogeny to detect intercontinental biogeographic patterns and reconstruct the ancestral areas of lineages, and iii) to evaluate the impact of the GAI on the evolutionary history of the genus.

Materials and Methods

Sampling

I analyzed 160 *Trogon* samples representing all 17 species to produce a phylogeny of the group. Multiple samples from each species (n = 2-19) were analyzed with a focus on maximizing geographic coverage, and allowed the evaluation of intraspecific genetic diversity for most species. Representatives (n = 29) of all other genera in the family (*Apaloderma*, *Euptilotis*, *Harpactes*, *Pharomachrus*, and *Priotelus*) were used as outgroups. Samples were acquired through scientific collecting, loans from ornithology holdings at research institutions, or available sequences in GenBank (Table 2.1).

Sequencing techniques

Total genomic DNA was extracted from tissue, blood, or toepads using a DNeasy Tissue Kit (Qiagen Inc.). The mitochondrial DNA (mtDNA) NADH dehydrogenase 2 (ND2) gene was amplified via polymerase chain reaction using the following primers: L5215 (Hackett 1996), L5758, H5766 (Johnson and Sorenson 1998), and HTrpC (Smithsonian Tropical Research Institute). Amplified products were purified with ExoSAP-IT (USB Corp.). Sequencing reactions were performed using a Big Dye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems), purified using CleanSEQ (Agencourt Bioscience Corp.), and analyzed with an ABI 3100-avant automated sequencer (Applied Biosystems). Sequences were aligned, verified by eye, and checked for the absence of internal stop codons using the program SEQUENCHER (Gene Codes Corp.).

Phylogenetic inference

I used maximum likelihood (ML) and Bayesian inference methods to construct phylogenetic hypotheses of relationships among samples. Both methods produced similar topologies and identified the same nodes as well supported. I used MODELTEST 3.7 (Posada and Crandall 1998) and the Akaike Information Criterion (Posada and Buckley 2004) to determine the model of molecular evolution for the sequence data. I then used the program TREEFINDER (Jobb et al. 2004) to construct a ML phylogeny of the complete dataset. This program uses a fast sampling algorithm to estimate all parameters and construct a phylogeny. I used this phylogeny to delimit *Trogon* lineages based on taxonomy, geography, or genetic distance. One sample from each such lineage was chosen to create a truncated dataset which fully captures the genetic diversity of the group. MODELTEST 3.7 was used (see above) to select the appropriate model of sequence evolution for the truncated dataset. I used PAUP* 4.0b10 (Swofford 2002) and a successive approximations approach (Swofford et al. 1996) to construct the best ML approximation of phylogeny. ML nodal support was assessed in TREEFINDER with 100 non-parametric bootstrap replicates.

I performed Bayesian inference analyses using the program MRBAYES 3.1.2 (Ronquist and Huelsenbeck 2003). Trial runs (ngen = 1,000,000, samplefreq = 100, and burnin = 2000) were performed with and without partitions (by codon position). Although the partitioned analysis produced a posterior distribution with higher likelihood scores, the relationships among lineages were identical and the nodal support was very similar between analyses. Therefore, a longer analysis was completed without partitions to reduce the number of parameters and to

maximize the amount of characters per partition. Two long runs (ngen = 10,000,000, samplefreq = 100, and burnin = 50,000) were joined to produce a posterior distribution of 100,000 trees.

Character mapping

Character mapping, or ancestral character reconstruction, is a useful tool for investigating history of the GAI in this study. The isolation of Central and South America before the formation of the Isthmus of Panama devalues vicariance as a means of explaining the Central and South American distribution of *Trogon*. The sedentary nature of this genus also de-emphasizes the role of long-distance dispersal between continents prior to the completion of the isthmus. Finally, the dense taxonomic and geographic sampling of the study ensures that most *Trogon* lineages are included in the phylogeny, which is a basic assumption of the analysis (Omland 1999).

I assessed the area of origin and intercontinental dispersals in *Trogon* using character mapping and the phylogeny of the truncated dataset. I used simple parsimony (Fitch 1971) and stochastic mapping (Huelsenbeck et al. 2003) to hypothesize the biogeography of each node in the phylogeny. Four character states were used in the analysis: Central America, Chocó-Darién, Andes Mountains, and *cis*-Andes. Simple parsimony reconstruction was done using MESQUITE 1.06 (Maddison and Maddison 2005). Stochastic mapping was done using SIMMAP 1.0 (Bollback 2006) with the last 5000 trees of the posterior distribution from the two long Bayesian runs for a total of 10,000 trees. Ten draws were simulated from each tree to create a posterior probability for each

state at each node. The program does not use a bias parameter prior when characters have more than one state, and two different rate parameter priors were tested ($\alpha = 3$, $\beta = 2$ and $\alpha = 5$, $\beta = 5$).

Date estimates

I estimated the timing of dispersal events between Central and South America to evaluate their relation to the completion of the Isthmus of Panama. Estimates were calculated using the truncated dataset and molecular clock methodology. Phylogenies of the ingroup were constructed in PAUP* 4.0b10 with and without the constraint of a molecular clock. The constrained phylogeny was statistically inferior at $\alpha = 0.05$ (likelihood ratio test, $\chi^2_{39} = 55.10$, $P = 0.045$). I identified samples that were deviating from clocklike behavior using the program LINTREE (Takezaki et al. 1995). Two samples were removed from the dataset [*clathratus* (USNM B02029) and *curucui* (LSU B25715)], and the above procedure was repeated. Resulting phylogenies with and without the constraint of a molecular clock were not statistically different at $\alpha = 0.05$ (likelihood ratio test, $\chi^2_{37} = 51.73$, $P = 0.055$). I then applied a calibrated molecular clock to this clock-like phylogeny. The rate for Hawaiian honeycreeper cytrochrome-*b* (cyt-*b*) evolution was estimated at 1.6%/my (Fleischer *et al.* 1998). This rate was calibrated using ages of Hawaiian islands and Kimura 2-Parameter corrected cyt-*b* sequence data. This rate was later calibrated as 2.2%/my for the more complex GTR + Γ model of molecular evolution (Weir and Schluter 2004). Since this calibrated rate is for a different mitochondrial gene, the relative rates of cyt-*b* and ND2 in *Trogon* was calculated. For a subset of samples (n = 14) GTR + Γ corrected pairwise

distances were calculated for cyt-*b* and ND2. The rate of evolution for ND2 was 1.55 times the rate of cyt-*b*, and the molecular clock was calibrated at 3.41% divergence/my and applied to the phylogeny.

Results

Phylogenetic inference

The resulting phylogeny splits *Trogon* into two major clades, and most nodes are well-supported (Figure 2.1). Relationships among species generally correspond to a previous study that used mitochondrial and nuclear data and fourteen of seventeen *Trogon* species (Moyle 2005). The 160 samples fall within 41 distinct mitochondrial lineages that characterize the diversity within *Trogon* (Figure 2.2). Intraspecific diversity was high in many species, with multiple independent lineages inhabiting distinct geographic areas. The observed intraspecific diversity among lineages revealed four cases of non-monophyly in the current taxonomy (*collaris, melanurus, viridis*, and *violaceus*).

Intercontinental phylogeography

violaceus-surrucura-curucui complex (Figure 2.3A) – The polyphyletic *violaceus* has a fragmented and widespread distribution from Mexico to the eastern Brazil. The basal phylogenetic break in this species corresponds to the Andes Mountains. West of the Andes (*trans*-Andes), there is a shallow divergence between samples from the Chocó-Darién and Central America. East of the Andes (*cis*-Andes), two distinct *violaceus* lineages are embedded in a clade with *surrucura* and *curucui*, which both occur only in the *cis*-Andes.

viridis-bairdii complex (Figure 2.3B) – The paraphyletic *viridis* has a fragmented distribution from western Panama to eastern Brazil. The basal phylogenetic break in this species also corresponds to the Andes Mountains. Samples in the *trans*-Andes are most closely related to *bairdii*, which has a norrow distribution in Costa Rica and Panama. Samples of *viridis* from throughout the *cis*-Andes form a clade with shallow divergence and no geographic structure (Figure 2.1).

melanurus-massena-comptus complex (Figure 2.3C) – The polyphyletic *melanurus* also has a fragmented distribution ranging from western Panama to eastern Brazil. Again, the basal phylogenetic break in this species corresponds to the Andes Mountains. Samples in the *trans*-Andes are most closely related to *massena*, which has a distribution from Mexico to northern Ecuador. There are two distinct lineages of *melanurus* in the *cis*-Andes. These lineages form a clade with *comptus*, which has a narrow distribution in the western foothills of the Andes in Colombia and Ecuador.

rufus (Figure 2.3D) – This monophyletic species has a fragmented and widespread distribution from Honduras to eastern Brazil. As in the clades described above, the Andes Mountains is aligned with the basal phylogenetic break. In the *trans*-Andes there is a relatively shallow divergence between samples from the Chocó-Darién and Central America. In the *cis*-Andes there are at least four distinct lineages distributed in the Guianan Shield, Amazon Basin and Chaco regions of South America.

collaris-aurantiiventris complex (Figure 2.3E) – The paraphyletic species *collaris* has a fragmented distribution from Mexico to eastern Brazil. In contrast to the previous groups, the basal phylogenetic break in this species corresponds to the Isthmus of Panama. There are two *collaris* lineages in Central America, with a phylogenetic break between them associated with the Isthmus of Tehauntepec in Mexico. The lineage distributed in lower Central America is most closely related to *aurantiiventris*, which has a narrow distribution in Costa Rica and Panama. There was discordance between phenotype and mtDNA genotype in one *collaris* and one *aurantiiventris* samples (Figure 2.1), indicating introgression between these species in western Panama. Samples of *collaris* from east Isthmus of Panama form three lineages corresponding to the Chocó-Darién, Guianan highlands, and southwestern Amazon Basin.

Character mapping and date estimates

Both simple parsimony and stochastic mapping converged on the same result in the area cladogram (Figure 2.4). The basal node, corresponding to the common ancestor of *Trogon*, was coded as Central American in parsimony and stochastic mapping (100% posterior probability) analyses. Despite more lineages being distributed in South America (27 versus 14 in Central America), these results invoke a Central American origin for the genus. Shifts from Central to South America map onto the phylogeny in six separate clades, supporting multiple independent dispersal events between the two continents.

The earliest dispersal event in each of these six clades was dated to test its association with the completion of the Isthmus of Panama ca. 3 mya. The earliest

event was characterized as the most basal node before a step change from Central to South America in the area cladogram. Although there is variability in results, date estimates of these nodes generally cluster at about 3-2 mya (Table 2.2). One notable exception is node 4 (ca. 6-9 mya), which was estimated to be considerably older.

Discussion

Thorough taxonomic and geographic sampling within *Trogon* produced a robust phylogeny that confidently describes the relationships among, and the genetic diversity within, most species. The application of character mapping, molecular clock dating, and phylogeography were used with this phylogeny to reveal the significant impact of the GAI on the evolutionary history of *Trogon*.

Character mapping demonstrates that *Trogon* is Central American in origin, despite higher lineage diversity in South America. This result is in contrast to a hypothesis that the area of greatest differentiation is an indicator of the area of origin (Adams 1902), and supports the need for more complex analyses to answer this question (Cain 1944; Lomolino et al. 2006). The high extant lineage diversity in South America is the result of relatively recent diversification driven by the GAI and multiple, uni-directional dispersals into a previously unoccupied area. The asymmetrical dispersal and South American diversification recovered in *Trogon* parallels the general pattern recovered in the mammalian GAI (Marshall 1988; Stehli and Webb 1985). This recurring pattern enforces the need for systematic and biogeographic studies to include Central American forms to

gain a full understanding of evolutionary history and historic diversification patterns in South American biota.

The timing of dispersal events from Central to South America highlights the importance of the Isthmus of Panama in intercontinental movements in *Trogon*. Using molecular clocks to date divergence times has many possible sources of error, including rate variation among lineages, clock calibration, saturation, and genetic polymorphism in ancestral populations (Arbogast et al. 2002; Edwards and Beerli 2000). These sources of error could be particularly troublesome with a single-locus study. Given these caveats, the time estimates of dispersal events from Central to South America should be considered coarse approximations. Nonetheless, time estimates for five of six events cluster around 2-3 mya. These estimates provide support that, despite their ability to fly, these sedentary birds did not disperse between continents until the completion of the isthmus. Aside from the methodological problems with molecular clocks, the variation in estimates is likely due to stochastic, habitat, climatic, and ecological parameters associated with the dispersal and establishment of a population. The estimate that greatly precedes the isthmus (ca. 6-9 mya) could be associated with long distance dispersal or a proposed earlier land bridge (Bermingham and Martin 1998). It is interesting to note that this pre-isthmus dispersal involved an ancestor of the *personatus-collaris-aurantiiventris* complex, which is generally comprised of highland lineages.

Dense sampling of widespread clades was able to reveal intercontinental phylogeographic patterns in *Trogon*. In most cases the basal phylogenetic break

was associated with the Andes Mountains. The northern Andes Mountains rapidly uplifted 5-2 mya (Gregory-Wodzicki 2000), making them both geographically and temporally associated with the Isthmus of Panama. These rising mountains likely created a semi-permeable barrier to organisms moving from Central to South America across the isthmus. The basal position of this phylogeographic break in multiple clades provides evidence that *Trogon* ancestors were able to cross or circumvent the northern Andes soon after crossing the isthmus.

More recent dispersal events in the area cladogram reveal underlying complexity in the roles of the Isthmus of Panama and Andes Mountains in biogeographic patterns. At the tips of the cladogram there are multiple sister relationships between lineages distributed in Central America and the Chocó-Darién. There are no secondary crossings of the Andes Mountains, and levels of sequence divergence between these lineages correspond to ca. 0.2-1.5 mya. This phylogeographic pattern has been observed in other birds and types of organisms (Brower 1994; Brumfield and Capparella 1996; Cracraft and Prum 1988; Hoffmann and Baker 2003; Perdices et al. 2002). This suggests that the Andes Mountains have become an increasingly selective barrier for *Trogon* in the more recent evolutionary past. The phylogenetic break in these sister lineages corresponding to the isthmus highlights its duel role in biogeography as a corridor or a barrier for gene flow.

Prominent morphological characters and cryptic geographic genetic structure has misled traditional taxonomy of *Trogon*. Characters such as belly color, tail

patterns, the presence of a pectoral line, and colors of soft parts (e.g. iris, orbital ring, bill) have been used in the taxonomy of *Trogon* (Gould 1875; Ridgway 1911; Wetmore 1972). Plumage patterns on the tail and wingpanel are hypothesized to play a role in species recognition (Collar 2001), but empirical evidence supporting these ideas is lacking. Three non-monophyletic species (*melanurus*, *viridis*, and *violaceus*) have relatively conserved morphologies across distinct lineages separated by the Andes Mountains and the Isthmus of Panama. In each case one or more of these lineages is most closely related to another species with pronounced, diagnosable differences in morphological characters. This demonstrates that some morphological characters are labile with respect to phylogeny, which is a recurring theme in avian phylogenetic studies (Burns et al. 2003; Kennedy et al. 2000; Omland and Lanyon 2000; Pereira and Baker 2005; Weckstein 2005). A more thorough review of character evolution in this genus is needed to fully evaluate the relationship between morphology and phylogeny.

Collectively, these results demonstrate that the GAI was an important mechanism in the recent and relatively rapid historical diversification of *Trogon* in South America. The significant impact of the GAI on the evolution of the genus was masked by incomplete molecular phylogenetic study and incorrect taxonomy. The New World latitudinal diversity gradient is one of the longest recognized and most debated biological patterns (Willig et al. 2003). Hypotheses explaining high rates of diversification in South America have focused on the role of barriers as mechanisms (Haffer 1997). These barriers are hypothesized to

have formed through sea-level fluctuations (Emsley 1965), development of rivers (Ayres and Clutton-Brock 1992; Capparella 1991), climatic changes (Haffer 1969), or suture zones across ecotones (Endler 1982). The most commonly evoked mechanism is allopatric divergence in refugia created by the contraction of tropical habitats during cycles of climatic cooling in the late Pliocene and Pleistocene (Haffer 1969). However, support for the contraction of rain forests during this time has been criticized (Colinvaux 2005; Colinvaux et al. 2001). The temporal proximity of the GAI and climatic cycles associated with the refuge model make their roles in recent South American diversification difficult to differentiate. The high rates of diversification in South American biota is likely driven by a combination of multiple mechanisms (Bush 1994), and the reliance on refugia in explaining these high rates has likely overshadowed the role of the GAI. Results of this study reveal that the GAI was a driving force in creating the high levels of South American diversity in *Trogon*, and suggest it may play a larger role in Neotropical diversification than has been recognized.

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Tables

Table 2.1. Genetic samples used in the study.

Genus	Species	Museum*	Tissue††	Country
Trogon	*aurantiiventris*1	STRI	PA-TAU145	Panama
Trogon	*aurantiiventris*2	STRI	PA-TAU194	Panama
Trogon	*aurantiiventris*3	MBM	GMS1012	Panama
Trogon	*aurantiiventris*4†	MBM	GMS1034	Panama
Trogon	*aurantiiventris*5	LSUMNS	B26405-a	Panama
Trogon	*bairdii*1†	STRI	PA-TBA383	Panama
Trogon	*bairdii*2	STRI	PA-TBA384	Panama
Trogon	*bairdii*3	STRI	PA-TBA385	Panama
Trogon	*citreolus*1	CNAV	P002919	Mexico
Trogon	*citreolus*2†	CNAV	PE25988	Mexico
Trogon	*clathratus*1†	USNM	B02029	Panama
Trogon	*clathratus*2	USNM	B02304	Panama
Trogon	*collaris*1†	LSUMNS	B22827	Bolivia
Trogon	*collaris*2	LSUMNS	B12471	Bolivia
Trogon	*collaris*3	LSUMNS	B9341-a	Bolivia
Trogon	*collaris*4	LSUMNS	B35769	Costa Rica
Trogon	*collaris*5†	ANSP	2032	Ecuador
Trogon	*collaris*6†	USNM	B10636	Guyana
Trogon	*collaris*7	USNM	B10733	Guyana
Trogon	*collaris*8	USNM	B10782	Guyana
Trogon	*collaris*9†	MBM	GAV1965	Honduras
Trogon	*collaris*10†	FMNH	394271	Mexico
Trogon	*collaris*11	MZFC	HGO-SLP140	Mexico
Trogon	*collaris*12	FMNH	394272	Mexico
Trogon	*collaris*13	FMNH	394273	Mexico
Trogon	*collaris*14	MZFC	OVMP0703	Mexico
Trogon	*collaris*15	FMNH	393987	Mexico
Trogon	*collaris*16	MBM	DAB1316	Nicaragua
Trogon	*collaris*17	USNM	B01545	Panama
Trogon	*collaris*18	LSUMNS	B2141	Panama
Trogon	*collaris*19	FMNH	397885	Peru
Trogon	*comptus*1	LSUMNS	B29953-a	Ecuador
Trogon	*comptus*2†	ANSP	2297	Ecuador
Trogon	*comptus*3	ANSP	2349	Ecuador
Trogon	*comptus*4	ZMUC	132166	Ecuador
Trogon	*comptus*5	ZMUC	132167	Ecuador

Table 2.1 continued.

Genus	Species	Museum*	Tissue††	Country
Trogon	*curucui*1	FMNH	394463	Bolivia
Trogon	*curucui*2	FMNH	394464	Bolivia
Trogon	*curucui*3	AMNH	JJW266-a	Bolivia
Trogon	*curucui*4	ANSP	2733	Ecuador
Trogon	*curucui*5†	LSUMNS	B25715	Paraguay
Trogon	*curucui*6	UMMZ	227501-b	Paraguay
Trogon	*curucui*7	FMNH	320981	Peru
Trogon	*curucui*8†	FMNH	433225	Peru
Trogon	*curucui*9	LSUMNS	B10564	Peru
Trogon	*elegans*1	FMNH	434015	El Salvador
Trogon	*elegans*2	FMNH	434013-a	El Salvador
Trogon	*elegans*3†	FMNH	434014	El Salvador
Trogon	*elegans*4	MZFC	DEUT042	Mexico
Trogon	*elegans*5	MZFC	QRO189	Mexico
Trogon	*elegans*6	MZFC	QRO486	Mexico
Trogon	*elegans*7†	MBM	JK03280	Mexico
Trogon	*massena*1†	MBM	JK01022	Honduras
Trogon	*massena*2	MZFC	B1935	Mexico
Trogon	*massena*3	MZFC	B2073	Mexico
Trogon	*massena*4	MZFC	CHIIMA221	Mexico
Trogon	*massena*5	STRI	PA-TMS315	Panama
Trogon	*massena*6	STRI	PA-TMS84	Panama
Trogon	*massena*7	STRI	PA-TMS273	Panama
Trogon	*massena*8	MBM	JK04273	Panama
Trogon	*massena*9	LSUMNS	B28530-a	Panama
Trogon	*melanocephalus*1	MBM	JK01020	Honduras
Trogon	*melanocephalus*2†	MBM	JK01035	Honduras
Trogon	*melanocephalus*3	MBM	JK01041	Honduras
Trogon	*melanocephalus*4	MZFC	B2014	Mexico
Trogon	*melanocephalus*5	MZFC	CONA99-009	Mexico
Trogon	*melanocephalus*6	KU	547-a	Mexico
Trogon	*melanocephalus*7	MBM	DAB1854	Nicaragua
Trogon	*melanurus*1	LSUMNS	B14826	Bolivia
Trogon	*melanurus*2†	FMNH	391999	Brazil
Trogon	*melanurus*3	FMNH	392000	Brazil
Trogon	*melanurus*4	FMNH	389729	Brazil

Table 2.1 continued.

Genus	Species	Museum*	Tissue††	Country
Trogon	*melanurus*5	LSUMNS	B31379-a	Brazil
Trogon	*melanurus*6	ANSP	3263	Ecuador
Trogon	*melanurus*7	ANSP	4634	Ecuador
Trogon	*melanurus*8†	ANSP	4683	Ecuador
Trogon	*melanurus*9†	ANSP	8244	Guyana
Trogon	*melanurus*10	ANSP	8642	Guyana
Trogon	*melanurus*11	LSUMNS	B2500	Peru
Trogon	*melanurus*12	FMNH	397887	Peru
Trogon	*melanurus*13	FMNH	433226	Peru
Trogon	*mexicanus*1	MZFC	BMM656	Mexico
Trogon	*mexicanus*2	MZFC	HGO-SLP027	Mexico
Trogon	*mexicanus*3	FMNH	343219	Mexico
Trogon	*mexicanus*4	FMNH	393988	Mexico
Trogon	*mexicanus*5†	FMNH	394275	Mexico
Trogon	*mexicanus*6	MZFC	OMVP0319	Mexico
Trogon	*mexicanus*7	MZFC	OMVP0436	Mexico
Trogon	*mexicanus*8	MZFC	OMVP0463	Mexico
Trogon	*mexicanus*9	MZFC	QRO280	Mexico
Trogon	*mexicanus*10	MZFC	QRO467	Mexico
Trogon	*mexicanus*11	MZFC	CONACYT450	Mexico
Trogon	*mexicanus*12	MZFC	HGO-SLP424	Mexico
Trogon	*mexicanus*13†	MBM	JK03279	Mexico
Trogon	*mexicanus*14	FMNH	343220-a	Mexico
Trogon	*personatus*1†	ZMUC	115519	Bolivia
Trogon	*personatus*2†	ZMUC	134954	Colombia
Trogon	*personatus*3	ZMUC	134972	Colombia
Trogon	*personatus*4	USNM	B03099	Ecuador
Trogon	*personatus*5†	ANSP	3791	Ecuador
Trogon	*personatus*6†	ANSP	506	Ecuador
Trogon	*personatus*7	ANSP	559	Ecuador
Trogon	*personatus*8†	USNM	B15882	Guyana
Trogon	*personatus*9	LSUMNS	B48503	Guyana
Trogon	*personatus*10	FMNH	397889	Peru
Trogon	*personatus*11	LSUMNS	B421	Peru
Trogon	*personatus*12†	LSUMNS	B7596	Venezuela
Trogon	*personatus*13	AMNH	GFB2125-a	Venezuela

Table 2.1 continued.

Genus	Species	Museum*	Tissue††	Country
Trogon	*rufus*1†	FMNH	389730	Brazil
Trogon	*rufus*2	FMNH	389731	Brazil
Trogon	*rufus*3†	ANSP	2216	Ecuador
Trogon	*rufus*4†	ANSP	8471	Guyana
Trogon	*rufus*5	ANSP	8477	Guyana
Trogon	*rufus*6	STRI	HA-TRR-HA74	Honduras
Trogon	*rufus*7	STRI	PA-TRR252	Panama
Trogon	*rufus*8	LSUMNS	B2109	Panama
Trogon	*rufus*9†	MBM	GMS975	Panama
Trogon	*rufus*10	MBM	JK04197	Panama
Trogon	*rufus*11	LSUMNS	B26564-a	Panama
Trogon	*rufus*12†	ZMUC	115780	Paraguay
Trogon	*rufus*13	ZMUC	115779	Paraguay
Trogon	*rufus*14†	LSUMNS	B27391	Peru
Trogon	*surrucura*1†	USNM	B05982	Argentina
Trogon	*surrucura*2	USNM	B05987	Argentina
Trogon	*suracurra*3	USP	X7	Brazil
Trogon	*suracurra*4	USP	X9	Brazil
Trogon	*surrucura*5	LSUMNS	B35558-a	Brazil
Trogon	*violaceus*1†	LSUMNS	B18257	Bolivia
Trogon	*violaceus*2	FMNH	393038	Costa Rica
Trogon	*violaceus*3	ANSP	3289	Ecuador
Trogon	*violaceus*4†	ZMUC	113903	Ecuador
Trogon	*violaceus*5†	ANSP	5154	Ecuador
Trogon	*violaceus*6	USNM	B04344	Guyana
Trogon	*violaceus*7†	ANSP	8664	Guyana
Trogon	*violaceus*8†	MBM	GAV1688	Honduras
Trogon	*violaceus*9	MBM	JK01036	Honduras
Trogon	*violaceus*10	MZFC	HGO-SLP166	Mexico
Trogon	*violaceus*11	MZFC	QRO338	Mexico
Trogon	*violaceus*12	MZFC	CONACYT297	Mexico
Trogon	*violaceus*13	LSUMNS	B26531	Panama
Trogon	*violaceus*14	STRI	PA-TVI654	Panama
Trogon	*violaceus*15	LSUMNS	B27592	Peru
Trogon	*violaceus*16	LSUMNS	B7561	Venezuela
Trogon	*violaceus*17	AMNH	ROP258-a	Venezuela

Table 2.1 continued.

Genus	Species	Museum*	Tissue††	Country
Trogon	*viridis*1	FMNH	391274	Brazil
Trogon	*viridis*2	FMNH	391275	Brazil
Trogon	*viridis*3	FMNH	392704	Brazil
Trogon	*viridis*4	FMNH	389732	Brazil
Trogon	*viridis*5	FMNH	389733	Brazil
Trogon	*viridis*6	ZMUC	114931	Ecuador
Trogon	*viridis*7†	ANSP	4659	Ecuador
Trogon	*viridis*8	ANSP	8463	Guyana
Trogon	*viridis*9	ANSP	8576	Guyana
Trogon	*viridis*10	USNM	B11315	Guyana
Trogon	*viridis*11†	USNM	B11332	Guyana
Trogon	*viridis*12	LSUMNS	B28774	Panama
Trogon	*viridis*13	STRI	PA-TVI630	Panama
Trogon	*viridis*14	LSUMNS	B4209	Peru
Trogon	*viridis*15	LSUMNS	B7385	Venezuela
Trogon	*viridis*16	AMNH	SC931-a	Venezuela
Apaloderma	*aequatoriale*1†	ANSP	11460	Equatorial Guinea
Apaloderma	*narina*1	FMNH	434493	Dem. Rep. Congo
Apaloderma	*narina*2	AMNH	RWD21159-a	Liberia
Apaloderma	*narina*3†	MBM	JK01506	Malawi
Apaloderma	*narina*4	FMNH	390084	South Africa
Apaloderma	*vittatum*1	FMNH	439090	Malawi
Apaloderma	*vittatum*2	FMNH	439094	Malawi
Apaloderma	*vittatum*3†	FMNH	438534	Mozambique
Apaloderma	*vittatum*4	FMNH	384820-a	Uganda
Euptilotis	*neoxenus*1†	AMNH	PRS2606-a	USA
Harpactes	*ardens*1†	FMNH	429208	Philippines
Harpactes	*diardii*1†	ANSP	1128-a	Malaysia
Harpactes	*duvaucelii*1†	LSUMNS	B38592-a	Malaysia
Harpactes	*erythocephalus*1†	AMNH	PRS2170-a	Vietnam
Harpactes	*oreskios*1†	ANSP	1316-a	Malaysia
Harpactes	*orrhophaeus*1†	LSUMNS	B38633-a	Malaysia
Pharomachrus	*antisianus*1	LSUMNS	B22820-a	Bolivia
Pharomachrus	*antisianus*2†	FMNH	397882	Peru
Pharomachrus	*auriceps*1	FMNH	397883	Peru
Pharomachrus	*auriceps*2†	LSUMNS	B3533-a	Peru

Table 2.1 continued.

Genus	Species	Museum*	Tissue††	Country
Pharomachrus	*fulgidus*1	ZMUC	115750	
Pharomachrus	*moccino*1†	MBM	DAB1262	Nicaragua
Pharomachrus	*pavoninus*1	ANSP	2689	Ecuador
Pharomachrus	*pavoninus*2†	FMNH	397884	Peru
Pharomachrus	*pavoninus*3	LSUMNS	B5033-a	Peru
Priotelus	*roseigaster*1†	KU	6363-a	Dominican Republic
Priotelus	*roseigaster*2	STRI	RD-TRO1	Dominican Republic
Priotelus	*temnurus*1	ANSP	5564-a	Cuba
Priotelus	*temnurus*2†	ANSP	5565-a	Cuba

† samples selected for the truncated dataset

* AMNH = American Museum of Natural History, ANSP = Academy of Natural Sciences Philadelphia, CNAV = Colección Nacional de Aves, Universidad Nacional Autónoma de México, FMNH = Field Museum of Natural History, KU = University of Kansas Natural History Museum, LSUMNS = Louisiana State University Museum of Natural Sciences, MBM = Marjorie Barrick Museum of Natural History, MZFC = Museo de Zoología "Alfonso L. Herrera", STRI = Smithsonian Tropical Research Institute, UMMZ = Museum of Zoology, Univeristy of Michigan, USP = Universidade de São Paulo, Brazil, ZMUC = Zoological Museum University of Copenhagen

†† a = Moyle 2005, b = Sorenson et al. 2003

Table 2.2. Date estimations for nodes representing dispersal from Central to South America.

Node	Estimated Age (mya)	
	ML distance*	ML branch lengths
1	3.06 ± 0.49	2.51
2	2.44 ± 0.12	2.29
3	2.51 ± 0.35	2.02
4	9.18 ± 0.46	6.44
5	1.80 ± 0.20	1.58
6	3.52 ± 0.28	2.90

* mean ± SD

Figure Legends

Figure 2.1. Bayesian phylogeny of the complete dataset. The phylogeny is rooted with representatives of *Pharomachrus, Euptilotis, Priotelus, Apaloderma,* and *Harpactes* (not shown). Numbers following taxa labels refer to sample numbers in Table 2.1. Samples marked by † were selected for the truncated dataset. Numbers on nodes correspond to maximum likelihood bootstrap percentages, with asterisks representing values ≥90. Bold branches represent nodes with posterior probabilities ≥95% in the Bayesian analysis.

Figure 2.2. Bayesian phylogeny of the truncated dataset. The phylogeny is rooted with representatives of *Pharomachrus, Euptilotis, Priotelus, Apaloderma,* and *Harpactes* (not shown). Nodal support as in Figure 2.1. Numbers after taxon labels refer to general biogeographic areas (displayed on map) of samples contained in each lineage.

Figure 2.3. Detailed biogeographic patterns in the A) *violaceus*, B) *viridis*, C) *melanurus*, D) *rufus*, and E) *collaris* clades. Symbols correspond to sampling localities from the complete dataset represented in that lineage. Species plates (Collar 2001; Hilty 2003) represent approximate plumage patterns for lineages. The two subspecies of *surrucura* have different belly colors, but both were recovered in a single clade (A). Introgression between *collaris* and *aurantiiventris* lineages was recovered in western Panama (E). Nodal support as in Figure 2.1.

Figure 2.4. Area cladogram of *Trogon* under parsimony (A) and stochastic (B) models. Area was mapped onto the phylogeny with four possible states (Central America, Chocó-Darién, Andes Mountains, and *cis*-Andes), with current states displayed in middle column. Pie charts refer to the confidence of each state at each node. Nodes labeled with numbers referred to in Table 2.2.

Figure 2.1

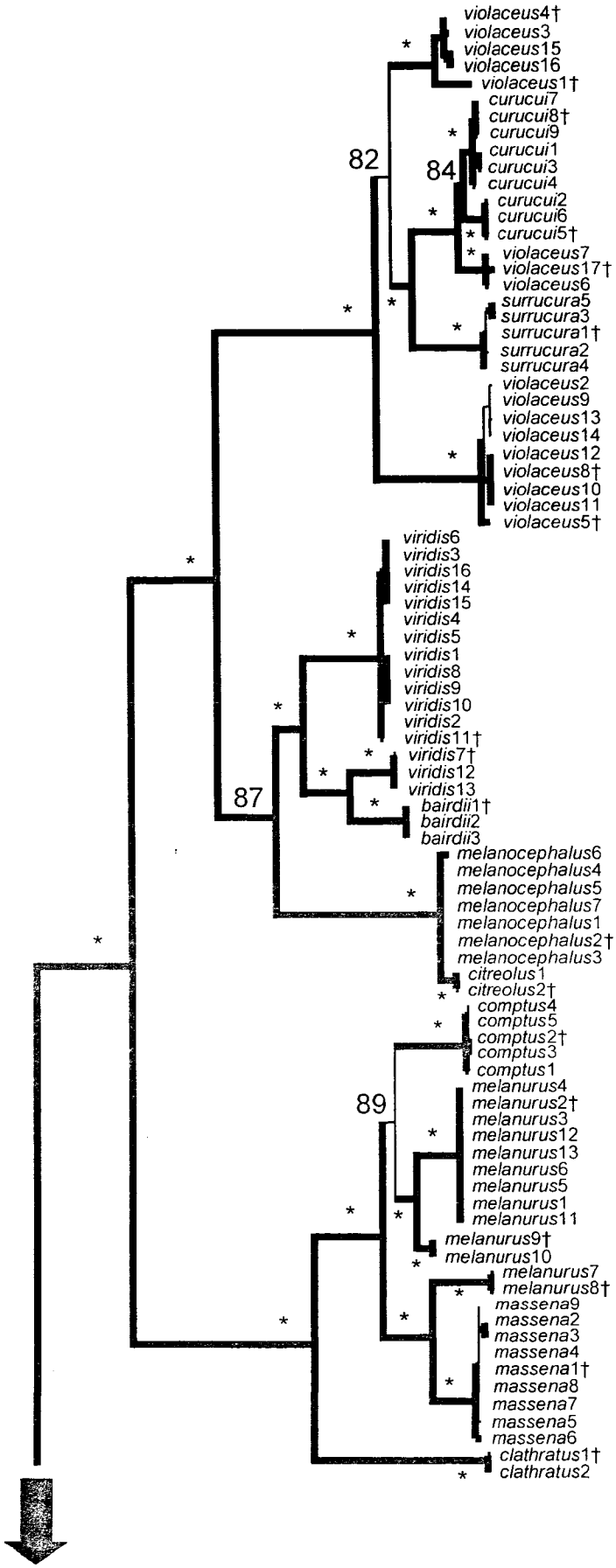


Figure 2.1. continued

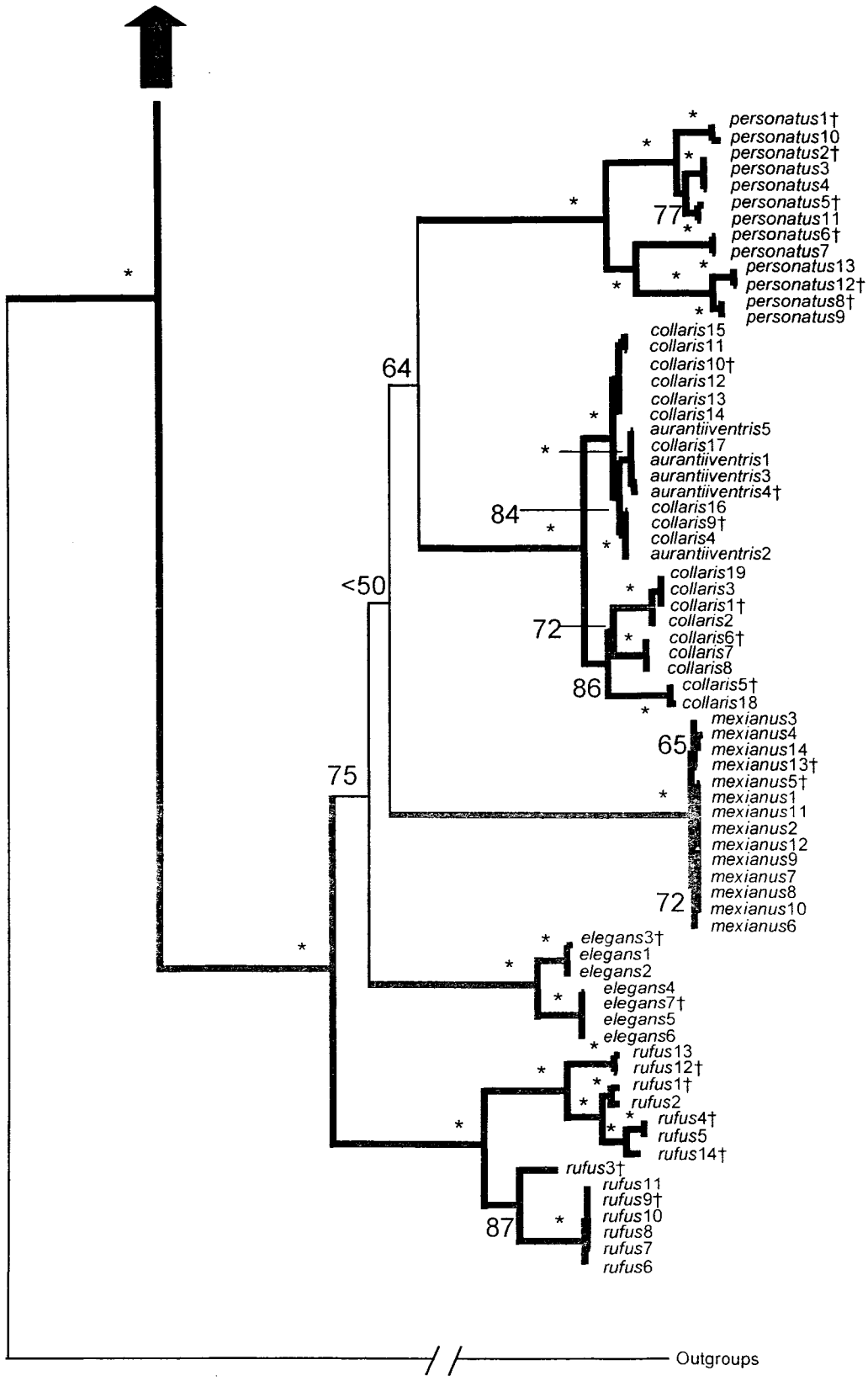


Figure 2.2

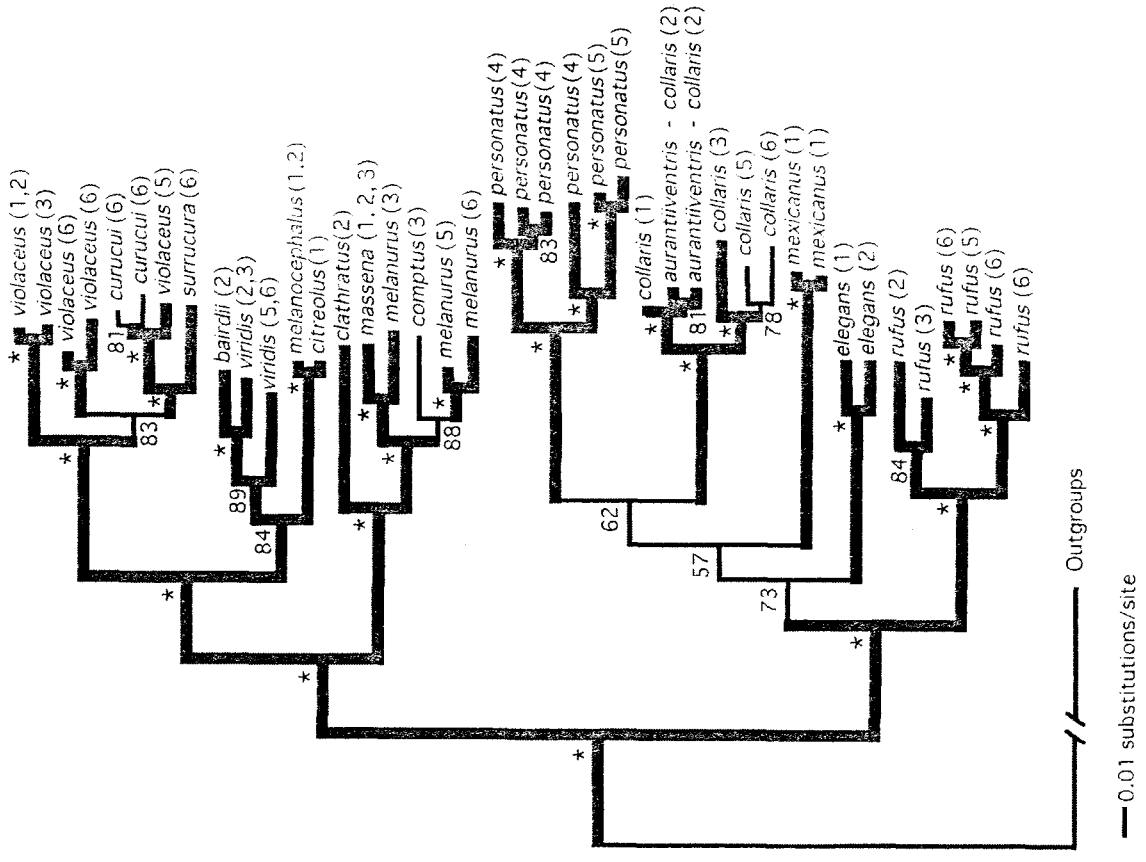


Figure 2.3

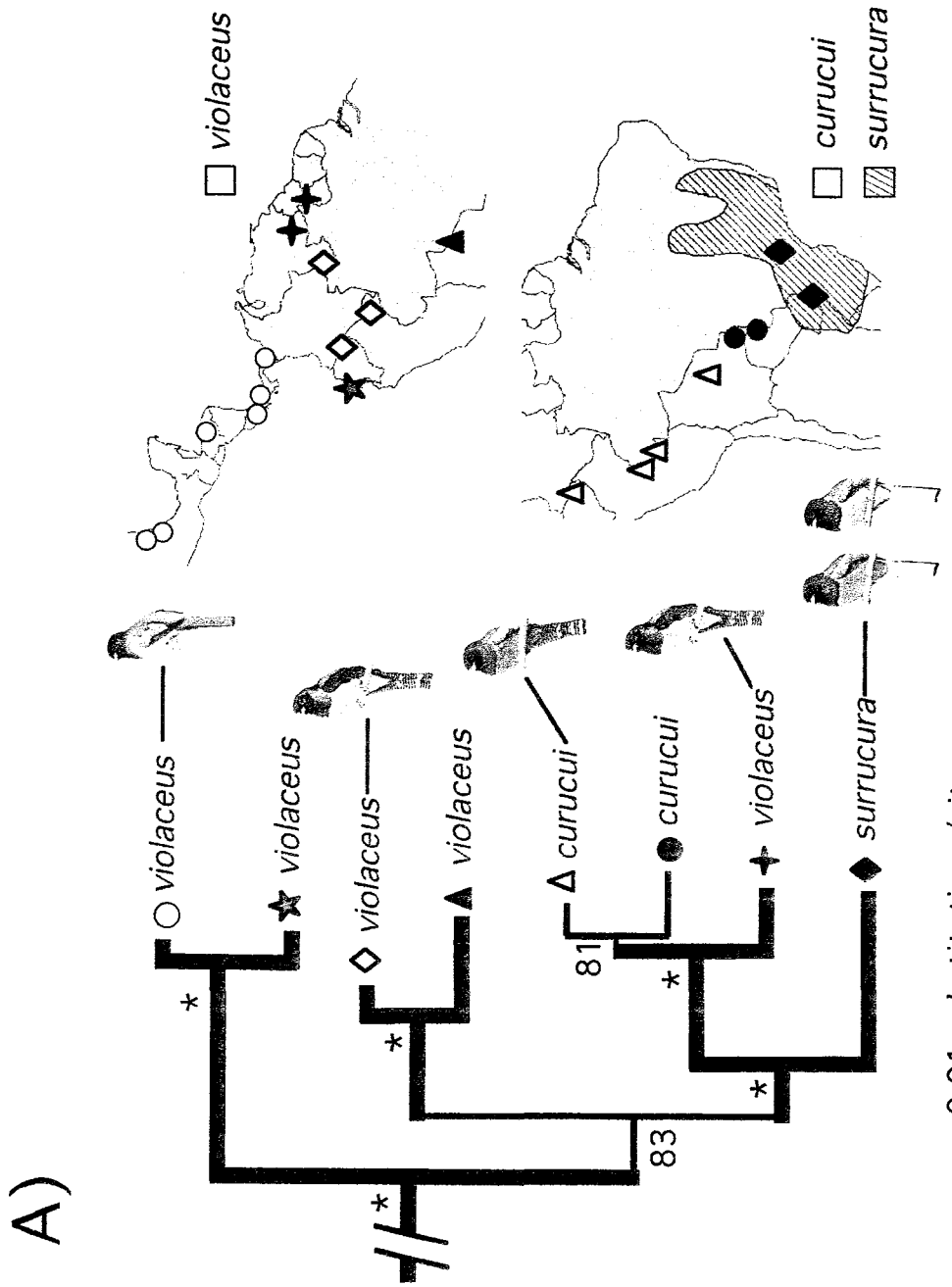


Figure 2.3 continued.

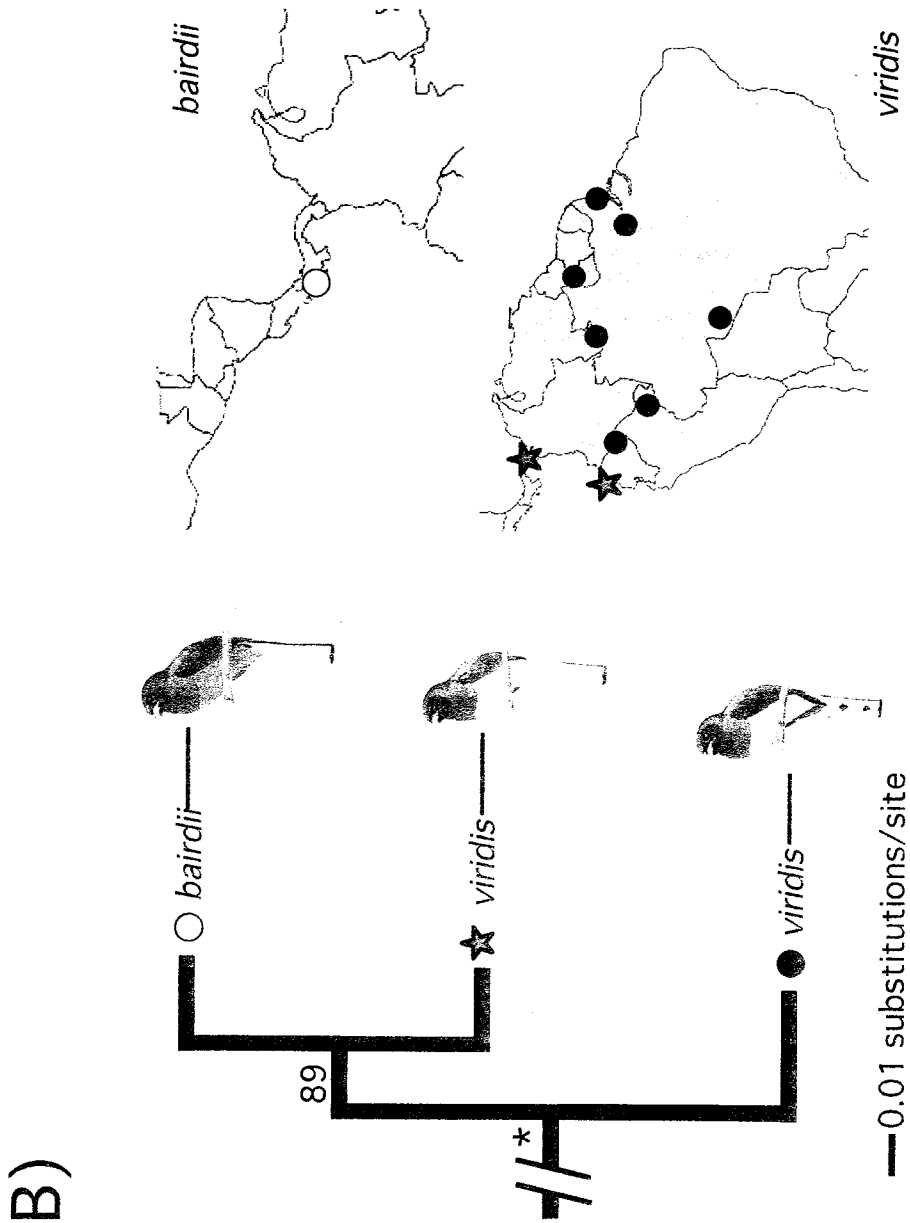


Figure 2.3 continued.

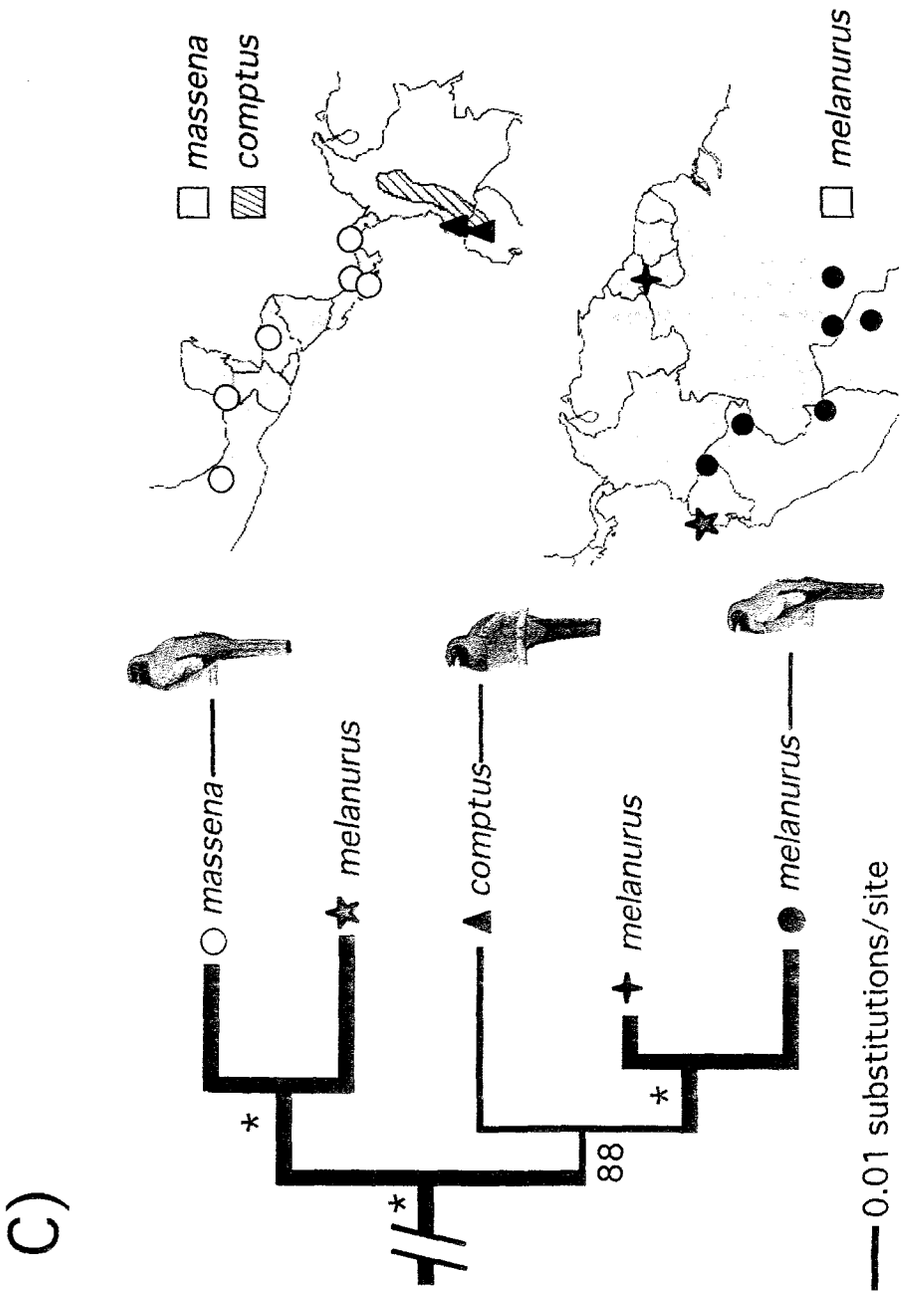


Figure 2.3 continued.

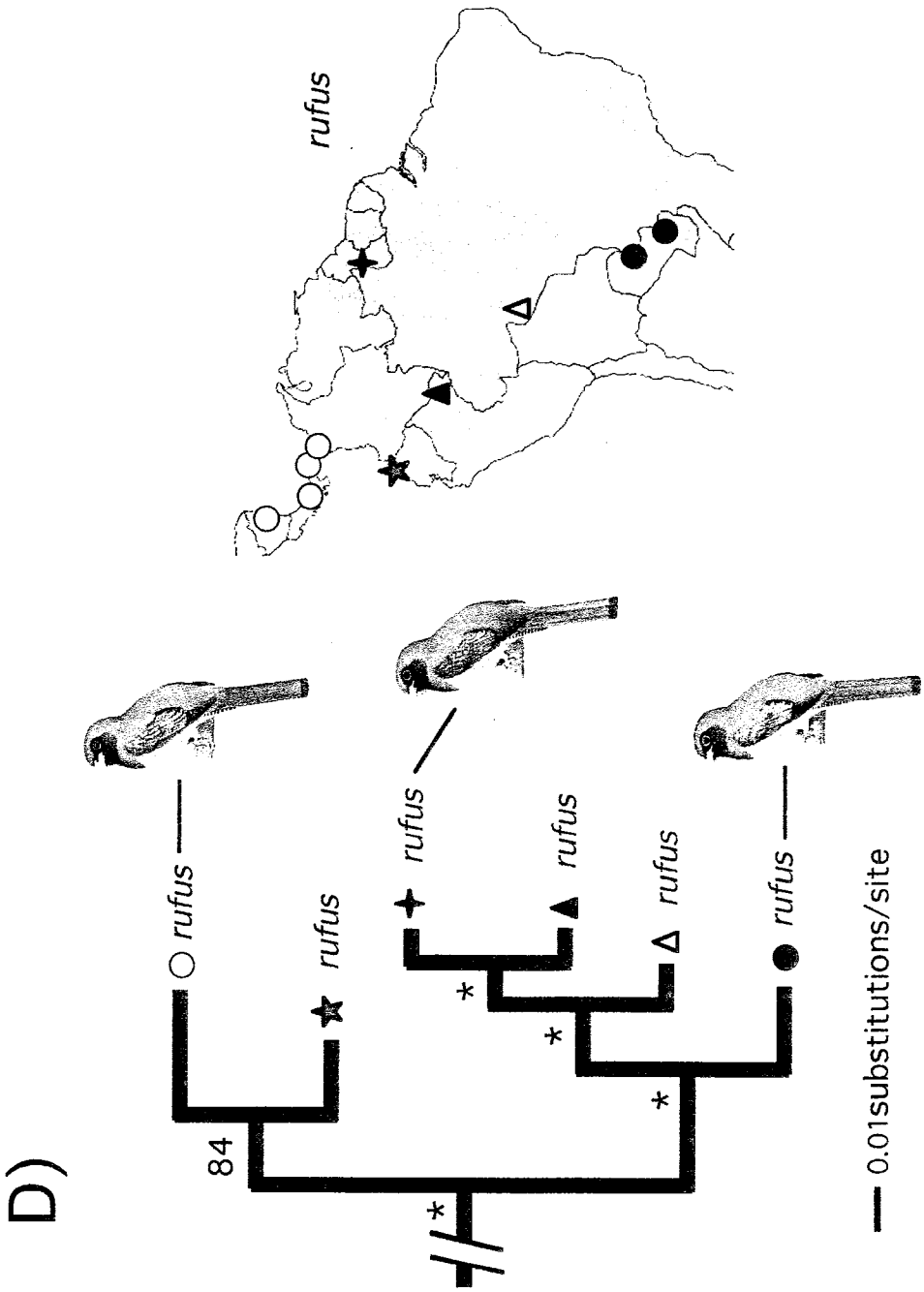


Figure 2.3 continued.

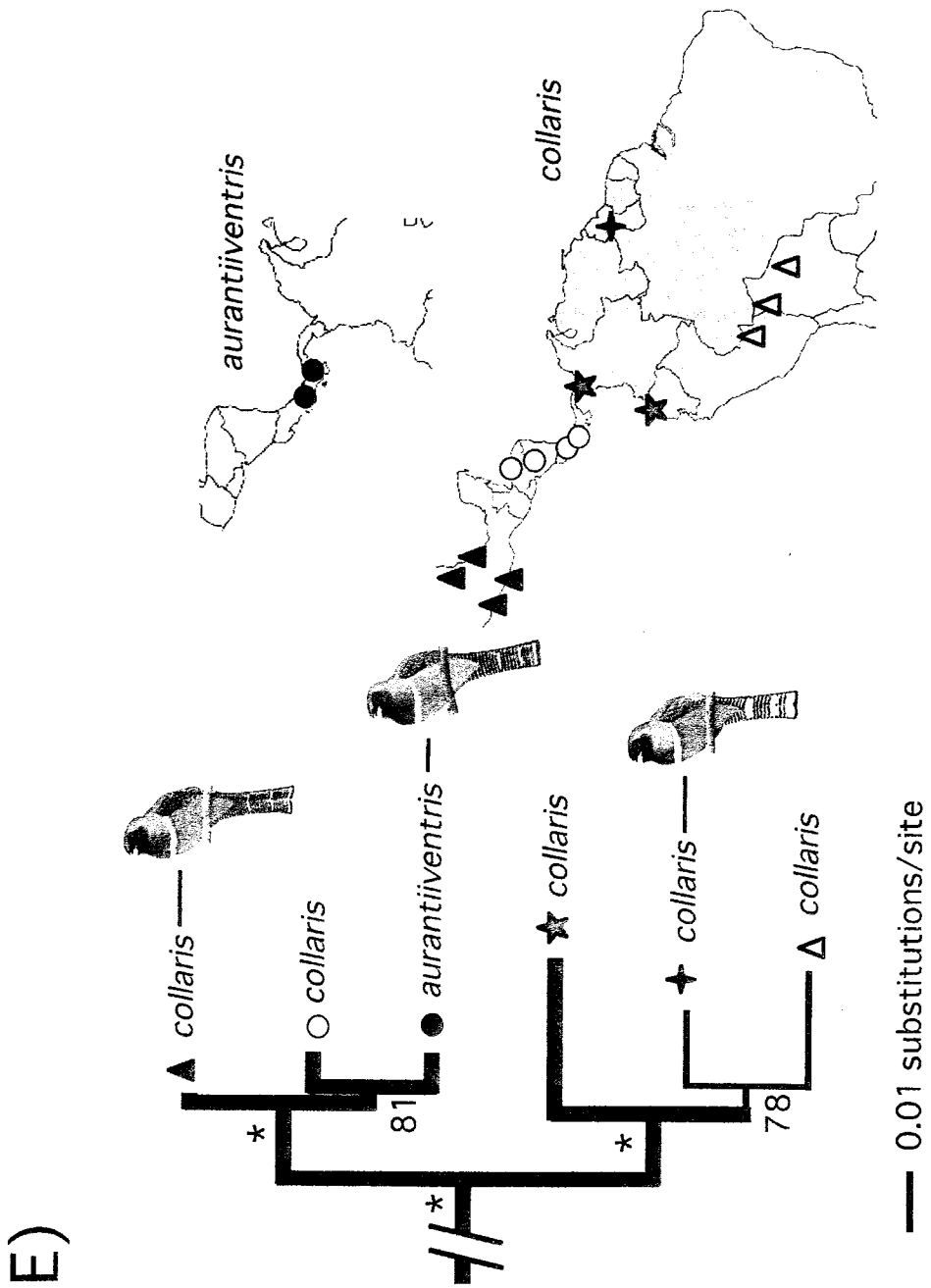
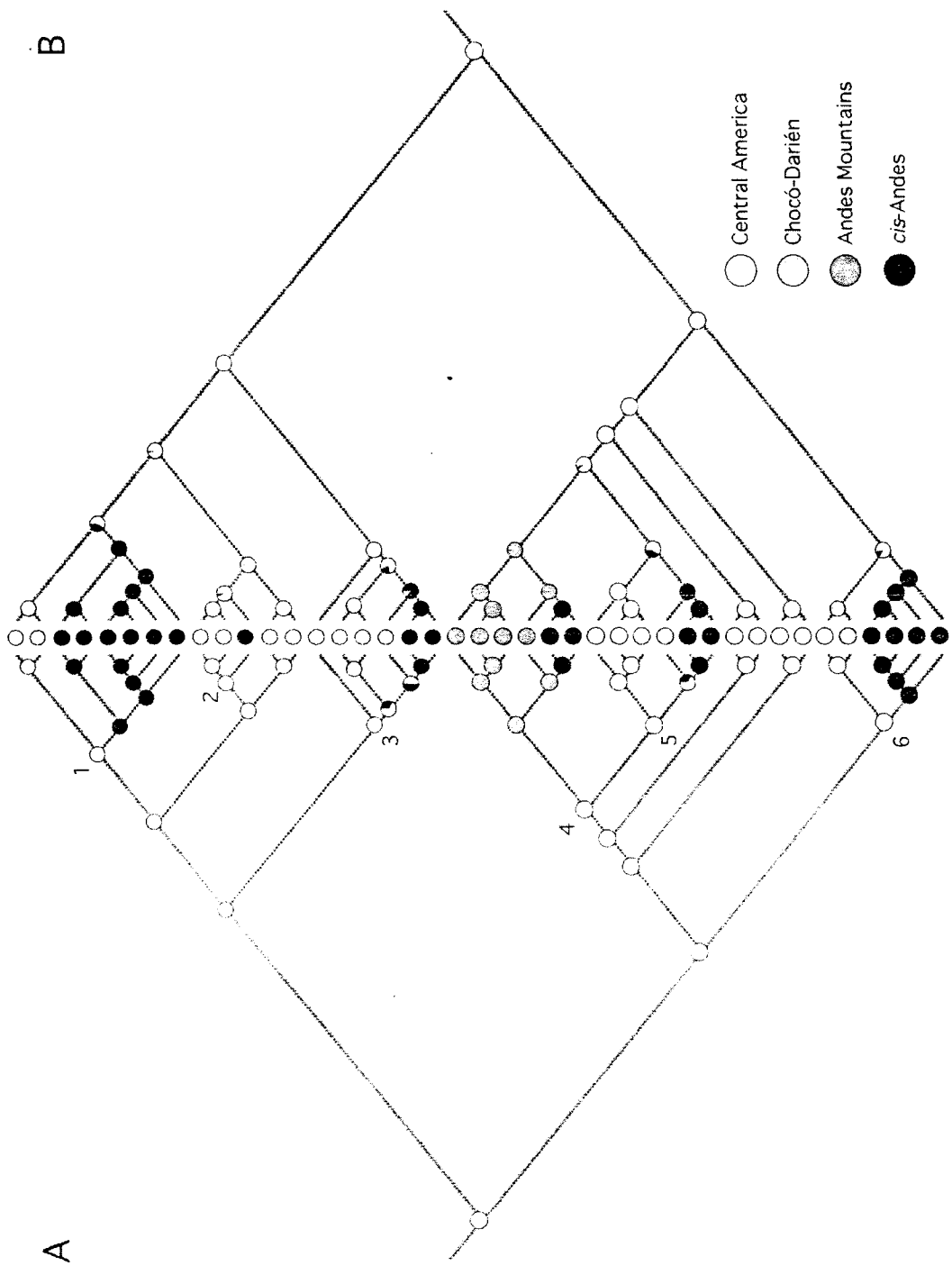


Figure 2.4



CHAPTER 3

THE PHYLOGENETIC UTILITY OF PROMINENT EXTERNAL MORPHOLOGICAL CHARACTERS IN *TROGON*

Introduction

The utility of external morphology in avian phylogenetics is a longstanding debate (Lowe 1915; Stone 1912). Patterns and colors of plumage and soft parts are believed to be particularly useful in groups with conserved and specialized morphology (Bock 1963; Short 1974). However, plumage and soft parts characters are also believed to be labile due to selection (Andersson 1994; Omland and Lanyon 2000; Prum 1997) or fixation of genetic mutations (Mundy et al. 2004; Theron et al. 2001) . This lability increases homoplasy, which weakens their usefulness as phylogenetic characters (Felsenstein 1973).

Several recent studies have used molecular phylogenies and ancestral character reconstruction to assess the evolution of plumage (Dumbacher and Fleischer 2001; Hill and Mcgraw 2004; Hofmann et al. 2006; Omland and Lanyon 2000; Price and Pavelka 1996; Weckstein 2005) or soft part characters (Johnson 1999; Kennedy et al. 2000; Pereira and Baker 2005; Weckstein 2005). In general, these studies have mapped the evolution of a small set of prominent morphological characters on a phylogeny derived from DNA sequences. Results

indicate that these morphological characters are often evolutionary labile and provide poor phylogenetic signal.

Species in the genus *Trogon* have a relatively conserved morphology, but are recognized as among the most colorful of all birds (Collar 2001; Johnsgard 2000). *Trogon* species have prominent, brightly colored plumage patches and soft parts (bill, iris, and eye-ring). Males and females both have brightly colored red or yellow bellies. Aside from the belly, females are drab compared to males and have a generally muted brown or grey plumage. Males have metallic green backs and green, blue, or black heads and breasts. Some species have a thin white or black pectoral line between the breast and belly patches. Males also have striking black and white pied tail patterns that are species specific. These tail patterns are hypothesized to play a role in species recognition (Collar 2001), but empirical evidence supporting this idea is lacking.

I studied the evolution of a set of these external morphological traits in a phylogenetic context using ancestral state reconstruction. A previous study that analyzed character evolution in *Trogon* used a molecular phylogeny which included only 10 of the 17 recognized species (Espinosa de los Monteros 1998). This lack of taxonomic sampling can produce a misleading phylogenetic hypothesis (Omland et al. 1999), which can compromise the results of ancestral state reconstructions since one of the primary assumptions is that the phylogeny used is a robust hypothesis of relationships among taxa (Omland 1999). For the fist time there exists a comprehensive molecular phylogeny of *Trogon*, which includes intraspecific sampling of all recognized species (Chapter 2). I used this

molecular phylogeny and three methods (parsimony, maximum-likelihood, and stochastic mapping) of ancestral state reconstruction to explore the evolution and phylogenetic utility of a set of external morphological characters.

Materials and Methods

Phylogenic inference

The phylogeny used for character mapping was taken from a previous study, which analyzed mitochondrial DNA from 160 *Trogon* individuals (Chapter 2). A subset of 41 *Trogon* individuals captured the genetic diversity within the group, and maximum-likelihood (ML) and Bayesian methods were used to construct a robust phylogenetic hypothesis of these 41 samples (Chapter 2, Figure 3.1).

Character matrix and properties

I coded eight morphological characters (Table 3.1) for each of the 41 *Trogon* units. Characters were coded with the aid of study skins at the Barrick Museum of Natural History, as well as the text and plates in Johnsgard (2000) and Collar (2001). The number of states per character ranged from two to four (Table 3.1). I used the program MACCLADE 4.03 (Maddison and Maddison 2000) to calculate the overall number of steps, retention index (RI), and consistency index (CI) for each character.

The putative sister genus to *Trogon* remains unclear (Johansson and Ericson 2005; Moyle 2005), and the coded characters are highly polymorphic in other trogonid genera (Collar 2001). The phylogenetic uncertainty and polymorphisms in pool of possible *Trogon* outgroups can lead to a misleading polarization of

characters (Grandcolas et al. 2004), and therefore outgroups were neither coded nor used in subsequent analyses.

Ancestral state reconstruction

I reconstructed the ancestral states of all characters at all nodes using parsimony, ML, and Bayesian stochastic methods. Parsimony and ML analyses were performed in the program MESQUITE 1.06 (Maddison and Maddison 2005) using the ML phylogeny. Simple, unordered parsimony criteria were used, which assumes equiprobable character states and rates of change throughout the phylogeny (Fitch 1971). ML reconstructions were done using a Markov k-state 1 parameter model (Lewis 2001), which follows a Jukes-Cantor model of evolution with a rate of change parameter. Bayesian stochastic mapping (Huelsenbeck et al. 2003; Nielsen 2002) analyses were performed in SIMMAP 1.0 (Bollback 2006) using the posterior distribution of 10,000 trees (the last 5,000 trees from two separate Bayesian runs). The analysis was run with two different prior settings. In both runs the bias prior was set at α = 100, which correlates to equiprobable character states. The rate prior sets the substitution rate of the character, and was adjusted to different settings for each run (α = 3, β = 2 and α = 5, β = 5).

Results

Character properties and ancestral state reconstruction

There was variation in the number of steps, RI, and CI among the characters (Table 3.2). Female back color, male head color, and bill color tracked the phylogeny relatively well across all measurements (low number of steps, high RI

and CI). Tail pattern and iris color had intermediate values. Belly color, pectoral line, and orbital ring color tracked the phylogeny poorly by comparison (high number of steps, low RI and CI).

Parsimony, ML, and Bayesian stochastic methods produced similar results for the reconstruction of states on ancestral nodes. Figure 3.2 illustrates example reconstructions for a relatively phylogenetically robust (male head color) and labile (orbital ring color) character. All three methods of reconstruction produced consistent results for character states of the common ancestor of *Trogon* (Table 3.2). Characters that were confidently traced back to the basal node include male head color (green), bill color (yellow), tail pattern (multiple bands), iris color (dark), and pectoral line (present).

Distribution of step changes in characters

Step changes in characters were not randomly distributed across the phylogeny. There was variation in the exact placement of step changes due to different but equally parsimonious reconstructions, and uncertainty of branch lengths and rates of character change. However, the position of step changes could confidently be mapped onto subclade A or B for all characters except female back color (Table 3.3). A disproportionate amount of step changes in characters mapped onto branches in subclade A of the phylogeny. All characters except for female back color had at least three changes in subclade A. Only three of the characters (tail pattern, belly color, and orbital ring color) changed in subclade B, with a single step in each case.

Discussion

The results reveal that most of the prominent external characters were labile with respect to the molecular phylogeny. This finding is in agreement with other studies that used molecular phylogenies and ancestral state reconstruction to investigate character evolution (see introduction). The characters examined have all been used as tools in traditional taxonomy *Trogon* (Gould 1875; Ridgway 1911; Wetmore 1972; Zimmer 1948). The non-monophyly of four *Trogon* species (*violaceus*, *viridis*, *melanurus*, and *collaris*) in the phylogeny suggests that traditional taxonomy has led to an incorrect hypothesis of the evolutionary history of the genus. However, the small sampling of characters in this study cannot serve as a thorough examination of the utility of morphology in *Trogon* taxonomy. Many more characters of different types (e.g. additional plumage, osteological, and physiological) would be needed for a comprehensive non-molecular estimate of phylogeny to compare or combine with the molecular phylogeny.

Most step changes mapped onto subclade A, which makes the characters more labile and subject to homoplasy in this section of the phylogeny. This subclade contains all lowland species (generally occur below 2000 m), and three of the four non-monophyletic species. In some cases, the distribution of sister species (or lineages) within subclade A are parapatric or partly sympatric. These sympatric lineages are in general phenotypically similar, but with changes in a few prominent characters. For example, the species *massena* and *melanurus* are sympatric in central Panama through the Chocó-Darién. These species have very similar morphologies, with the exception of differences in bill color, iris color,

and the presence/absence of a pectoral line. It is plausible that these traits play a role in recognition and reinforcement isolation in these species, but rigorous study of the underlying mechanisms and behavioral impacts of these trait changes are needed to test this hypothesis.

Subclade B has relatively few step changes in these external characters. The basal node in this subclade separates the lowland species *rufus* from a clade of generally highland species (*elegans, mexicanus, personatus, collaris,* and *aurantiiventris*). The characters studied here were notably conserved in the highland clade, with the only step change being a switch in the tail pattern of *mexicanus*. Characters in the highland clade and *rufus* were scored the same with two exceptions. *Trogon rufus* has a yellow belly and blue orbital ring, and the highland species have red bellies and red orbital rings. Again, if sympatric reinforcement isolation is playing a role in *Trogon* character evolution then the generally allopatric (geographically or altitudinally) distribution of the lineages in subclade B may contribute to its morphological conservatism.

This study provides insight of the evolution of some of the more conspicuous and polymorphic characters in *Trogon*. The use of ancestral character reconstruction in this study has created an opportunity to re-assess traditional views and provide future direction in the study of these characters. The lability of the characters in subclade A decreases their utility in the phylogenetics of this genus. This finding echoes the results of other studies that used similar methods to investigate the lability of external characters in different avian groups. These

results confirm that caution should be used when relying on prominent, external characters when forming phylogenetic hypotheses in birds.

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Tables

Table 3.1. Data matrix of *Trogon* characters.

	Character*							
Taxon	A	B	C	D	E	F	G	H
violaceus (Mesoamerica)	1	2	0	2	0	1	1	1
violaceus (Chocó)	1	2	0	2	0	1	1	1
violaceus (Amazon)	1	1	0	2	0	1	1	1
violaceus (Chaco)	1	1	0	2	0	1	1	1
surrucura	1	1	0	1	0	0	1	2
violaceus (Guiana Shield)	1	1	0	2	0	1	1	1
curucui (Amazon)	1	1	1	2	0	0	1	2
curucui (Chaco)	1	1	1	2	0	0	1	2
melanocephalus	1	2	0	1	2	1	1	3
citreolus	1	2	0	1	0	1	1	0
viridis (trans-Andes)	1	1	0	1	0	1	0	0
bairdii	1	1	0	1	0	0	0	0
viridis (cis-Andes)	1	1	0	1	0	1	0	0
clathratus	1	0	1	2	1	0	0	3
massena	1	0	2	0	3	0	0	2
melanurus (trans-Andes)	1	0	1	0	1	0	1	2
comptus	1	0	1	0	1	0	0	3
melanurus (Guiana Shield)	1	0	1	0	0	0	1	2
melanurus (Amazon)	1	0	1	0	0	0	1	2
personatus (Bolivia)	0	0	1	2	0	0	1	2
personatus (Colombia)	0	0	1	2	0	0	1	2
personatus (S Ecuador)	0	0	1	2	0	0	1	2
personatus (W Ecuador)	0	0	1	2	0	0	1	2
personatus (Guyana)	0	0	1	2	0	0	1	2
personatus (Venezuela)	0	0	1	2	0	0	1	2
collaris (Mexico)	0	0	1	2	0	0	1	2
collaris (Cen. America)	0	0	1	2	0	0	1	2
aurantiiventris	0	0	1	2	0	0	1	2
collaris (Chocó)	0	0	1	2	0	0	1	2
collaris (Guiana Shield)	0	0	1	2	0	0	1	2
collaris (S Amazon)	0	0	1	2	0	0	1	2

Table 3.1. Continued.

Taxon	Character*							
	A	B	C	D	E	F	G	H
mexicanus (W Mexico)	0	0	1	1	0	0	1	2
mexicanus (E Mexico)	0	0	1	1	0	0	1	2
elegans (Mexico)	0	0	1	2	0	0	1	2
elegans (Cen. America)	0	0	1	2	0	0	1	2
rufus (Cen. America)	0	0	1	2	0	1	1	0
rufus (Chocó)	0	0	1	2	0	1	1	0
rufus (Chaco)	0	0	1	2	0	1	1	0
rufus (Amazon)	0	0	1	2	0	1	1	0
rufus (Guiana Shield)	0	0	1	2	0	1	1	0
rufus (W Amazon)	0	0	1	2	0	1	1	0

*Character codes:

A-Female back color: 0=brown, 1=grey

B-Head color: 0=green, 1=violet, 2=black

C-Bill color: 0=blue, 1=yellow, 2=red

D-Tail pattern: 0=no white, 1=one white band at tip, 2=multiple white bands

E-Iris color: 0=dark, 1=white, 2=yellow, 3=red

F-Belly color: 0=reddish, 1=yellow

G-Pectoral line: 0=absent, 1=present

H-Orbital ring color: 0=bluish, 1=yellow, 2=reddish, 3=black

Table 3.3. Character reconstruction for *Trogon* common ancestor.

	Character*							
Method	A	B	C	D	E	F	G	H
Parsimony **	e	0	1	2	0	e	1	e
Maximum likelihood †	1 (0.64)	0 (0.87)	1 (0.87)	2 (0.84)	0 (0.96)	0 (0.57)	1 (0.77)	2 (0.52)
Bayesian stochastic §	0 (0.51)	0 (0.98)	1 (0.98)	2 (0.99)	0 (0.99)	0 (0.51)	1 (0.96)	2 (0.49)

* Character codes as in Table 3.1.

** e=equivocal

† most likely state (likelihood probability)

§ most likely state (Bayesian probability)

Table 3.2. Summary statistics of data matrix.

	# steps				
Character	Total	Subclade A	Subclade B	RI	CI
Female back	1	equivocal	equivocal	1.00	1.00
Male Head color	3	3	0	0.91	0.67
Bill color	3	3	0	0.90	0.67
Tail pattern	5	4	1	0.80	0.60
Iris color	4	4	0	0.50	0.75
Belly color	5	4	1	0.71	0.20
Pectoral line	4	4	0	0.40	0.25
Orbital ring color	8	7	1	0.67	0.38

Figure Legends

Figure 3.1. Maximum likelihood phylogeny of *Trogon* genetic diversity. The phylogeny is rooted with representatives of *Pharomachrus, Euptilotis, Priotelus, Apaloderma,* and *Harpactes* (not shown). Grey lines on branches represent one of many equally parsimonious mappings of step changes in characters (except female back color). Subclades A and B are referred to in the text.

Figure 3.2. Ancestral character reconstruction for male head color (A) and orbital ring color (B). Character reconstructions were done using parsimony (left) and maximum likelihood (right) methods. Branch lengths are drawn to scale, and circles on nodes are shaded according to illustrate probability of each state. Taxon order is the same as Figure 3.1.

Figure 1

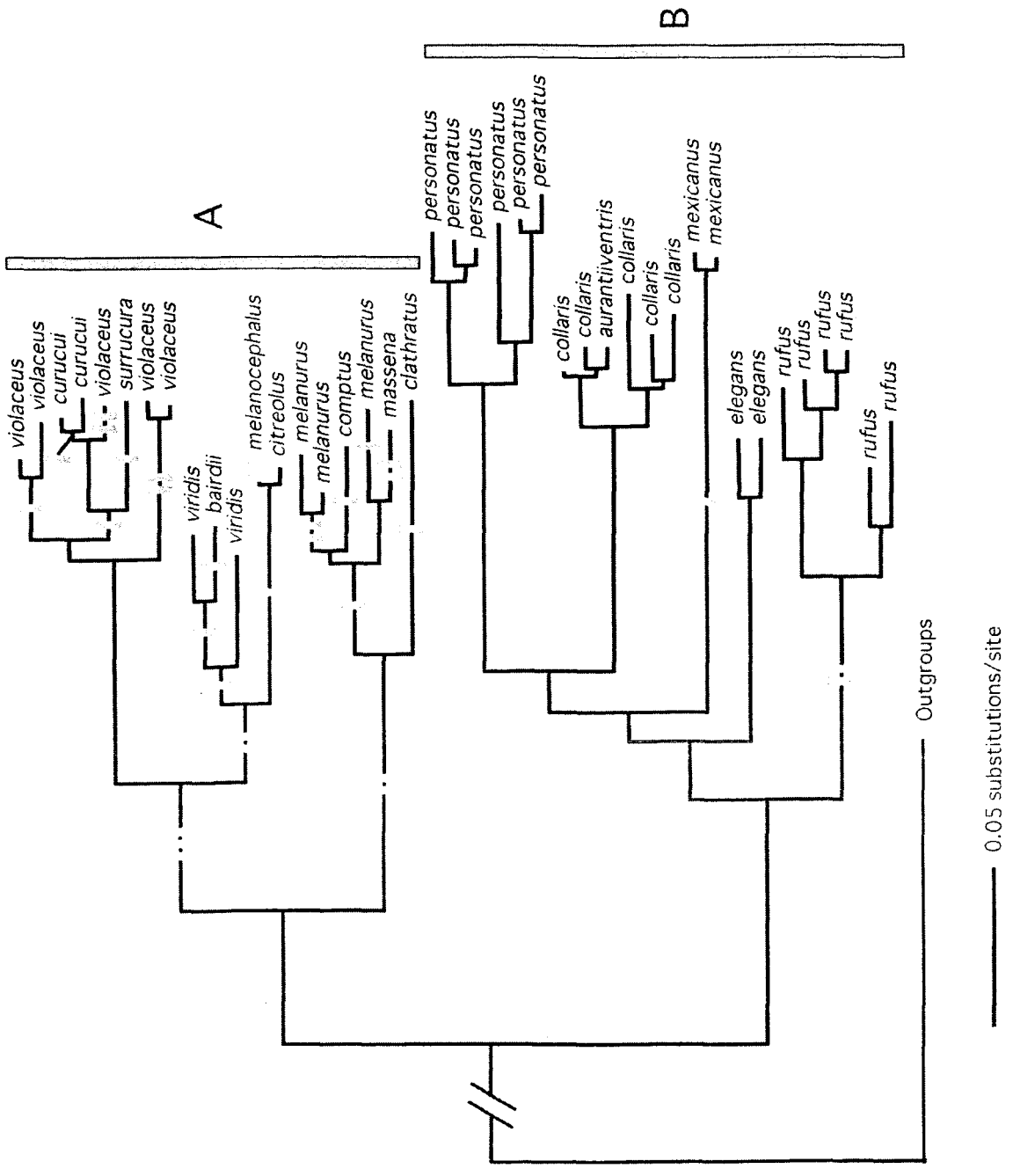
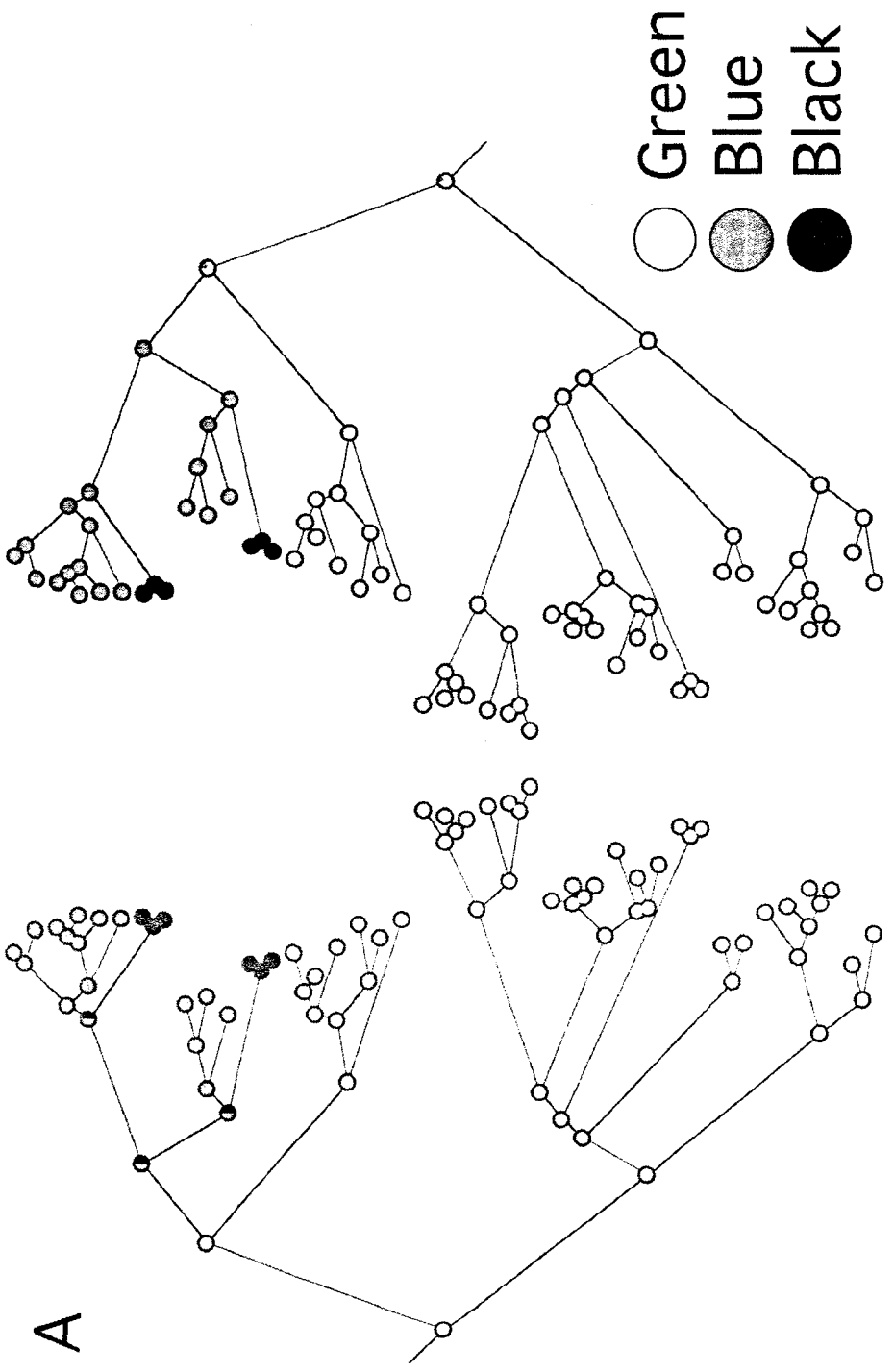


Figure 3.2.



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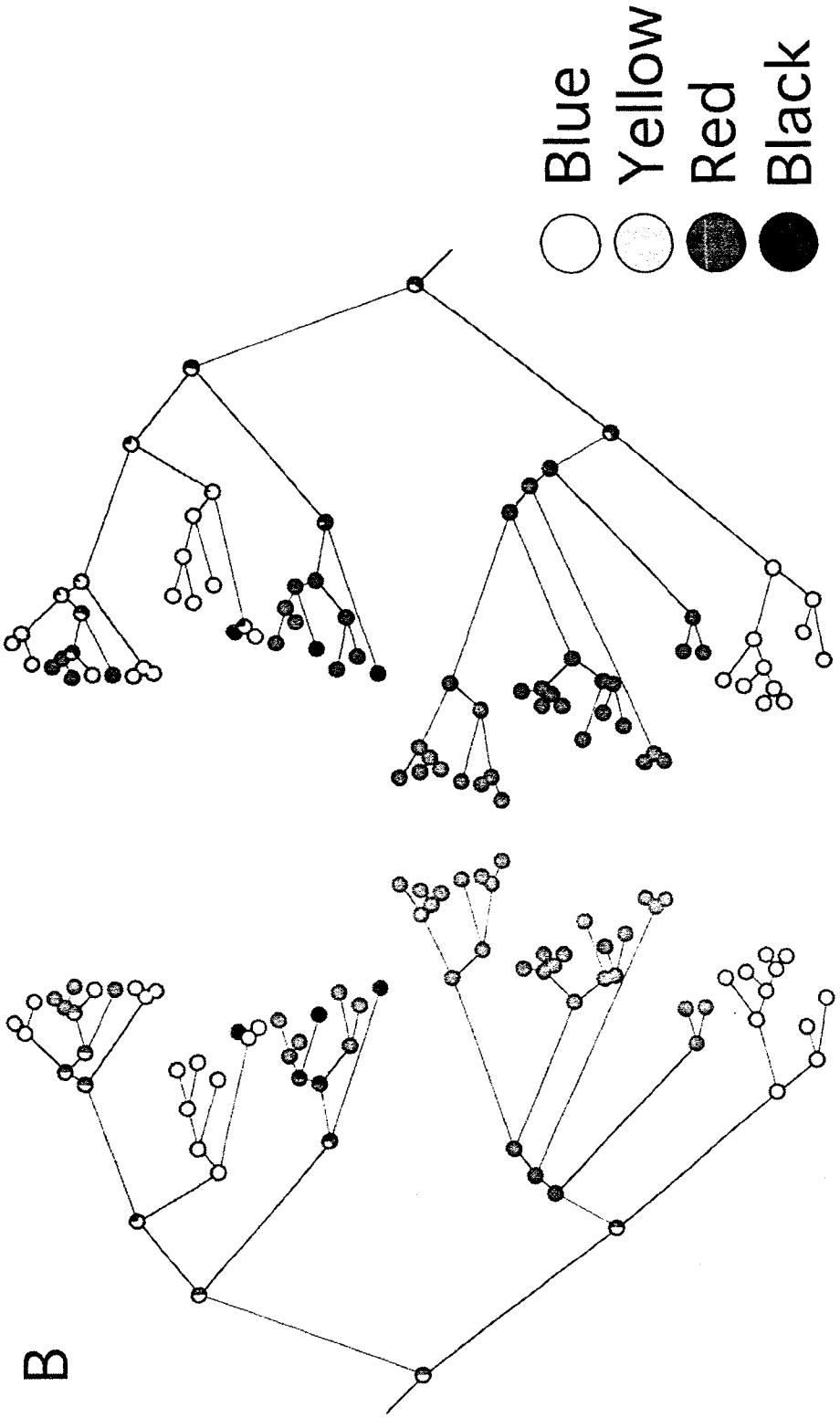

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