Phylogenetic relationships of the mockingbirds and thrashers (Aves: Mimidae)

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ABSTRACT

The mockingbirds, thrashers and allied birds in the family Mimidae are broadly distributed across the Americas. Many aspects of their phylogenetic history are well established, but there has been no previous phylogenetic study that included all species in this radiation. Our reconstructions based on mitochondrial and nuclear DNA sequence markers show that an early bifurcation separated the Mimidae into two clades, the first of which includes North and Middle American taxa (*Melanotis*, *Melanoptila*, *Dumetella*) plus a small radiation that likely occurred largely within the West Indies (*Ramphocinclus*, *Allenia*, *Margarops*, *Cinclocerthia*). The second and larger radiation includes the *Toxostoma* thrasher clade, along with the monotypic Sage Thrasher (*Oreoscoptes*) and the phenotypically diverse and broadly distributed *Mimus* mockingbirds. This mockingbird group is biogeographically notable for including several lineages that colonized and diverged on isolated islands, including the Socorro Mockingbird (*Mimus graysoni,* formerly *Mimodes*) and the diverse and historically important Galapagos mockingbirds (formerly *Nesomimus*). Our reconstructions support a sister relationship between the Galapagos mockingbird lineage and the Bahama Mockingbird (*M. gundlachi*) of the West Indies, rather than the Long-tailed Mockingbird (*M. longicaudatus*) or other species presently found on the South American mainland. Relationships within the genus *Toxostoma* conflict with traditional arrangements but support a tree based on a preivous mtDNA study. For instance, the southern Mexican endemic Ocellated Thrasher (*T. ocellatum*) is not an isolated sister species of the Curve-billed thrasher (*T. curvirostre*).

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1. Introduction

The mockingbirds, thrashers and allied birds that comprise the avian family Mimidae are well-known models in evolutionary biology and behavioral ecology. The Galapagos mockingbirds inspired Charles Darwin when he noted the morphological differences among forms from several islands and their differentiation from related species that occur on the South American mainland (Darwin, 1845, 1859). Other species of mockingbirds and thrashers have some of the most extensive song repertoires known in all birds (e.g., Kroodsma and Parker, 1977; Derrickson, 1987; Read and Weary, 1992), and many functional and behavioral aspects of their vocal and learning abilities have been characterized (e.g., Kroodsma

et al., 1997; Derrickson, 1988; Botero et al., 2009a); the group as a whole shows extensive variation in the extent and use of acoustic signals, and this behavioral diversity has informed comparative studies of how complex song traits evolve (Botero et al., 2009b). The group is likewise notable for its high interspecific variation in social and mating systems (Curry, 1989; Curry and Grant, 1990), as even within the mockingbirds breeding groups vary across a sociality spectrum from socially monogamous pairs, to parents with helpers who are previous offspring, to plural breeding groups that contain multiple reproducing pairs (Curry, 1988).

No previous phylogenetic survey has included a full sample of mimid species, and this lack of a completely inclusive phylogenetic hypothesis has hindered some comparative analyses of trait variation in this group. Nonetheless, many aspects of the phylogenetic history of the Mimidae radiation are well established. The mimid clade is sister to the more diverse Old World starlings (Sturnidae;

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Beecher, 1953; Stallcup, 1961; Sibley and Ahlquist, 1984, 1990; Malcarney et al., 1994; Voelker and Spellman, 2004; Ericson and Johansson, 2003; Cibois and Cracraft, 2004; Barker et al., 2004; Zuccon et al., 2006; Lovette and Rubenstein, 2007). The Mimidae + Sturnidae are in turn sister to the lineage comprising the two species of Oxpeckers (Buphagidae), and fall within a broader songbird radiation that includes the thrushes and dippers (Cibois and Cracraft, 2004; Zuccon et al., 2006; Lovette and Rubenstein, 2007). Several phenotypically odd New World taxa (e.g., *Donacobius, Rhodinocichla*) have at times been suggested to be allied to the Mimidae, but phylogenetic evidence has since shown that they fall elsewhere within the Passeriformes (Seutin and Bermingham, 1997; Alström et al., 2006; Johansson et al., 2008; Gelang et al., 2009). In reconstructions based on molecular data, a long and highly supported branch separates the Sturnidae from the earliest node within the Mimidae (Zuccon et al., 2006; Lovette and Rubenstein, 2007), thereby strongly supporting the monophyly of the Mimidae as it is currently classified (e.g., A.O.U., 1998).

The broad outline of phylogenetic relationships within the Mimidae is also well established (Hunt et al., 2001; Lovette and Rubenstein, 2007). Species in the family fall into two clades, the first of which comprises three species found in Mexico and northern Central America (*Melanoptila* and *Melanotis*), plus a group that has radiated mostly within the West Indian archipelago (*Cinclocerthia, Margarops, Allenia, Ramphocinclus*). The migratory and monotypic Gray Catbird (*Dumatella carolinensis*) which breeds in North America is embedded within this otherwise West Indian clade (Hunt et al., 2001; Lovette and Rubenstein, 2007). At the intraspecific level, the phylogeography of all endemic West Indian species found on more than one island (*Cinclocerthia ruficada, C. gutturalis, Margarops fuscatus, Allenia fusca*) has been explored using mitochondrial markers (Hunt et al., 2001).

The second and larger of the two subclades within the Mimidae comprises the continental thrashers (*Toxostoma* and *Oreoscoptes*) and the mockingbirds (*Mimus*, plus the species formerly assigned to *Nesomimus* and *Mimodes*). Relationships among *Toxostoma* populations and species have been reconstructed in an extensive series of studies using allozyme, mitochondrial DNA, morphological, and behavioral characters (Zink et al., 1997, 1999; Zink and Blackwell-Rago, 2000; Zink et al., 2001; Rojas-Soto, 2003; Sgariglia and Burns, 2003; Rojas-Soto et al., 2007). Collectively, these studies have supported the monophyly of the species assigned to *Toxostoma*, clarified the relationships among many of their populations, and identified some populations that might warrant future recognition as full species (e.g., Rojas-Soto et al., 2007). At a slightly deeper phylogenetic level, the *Toxostoma* clade is sister to the remaining taxa in this thrasher/mockingbird group. The monotypic Sage Thrasher (*Oreoscoptes montanus*) is in turn sister to a group that includes all of the *Mimus* mockingbirds (Lovette and Rubenstein, 2007).

The *Mimus* mockingbird radiation is relatively recent and presents a number of phylogenetic and systematic challenges. Mockingbird species are distributed throughout much of North, Central, and South America, and different lineages have colonized both archipelagos (the West Indies and the Galapagos) and continental satellite islands (Isla Socorro in the Pacific Ocean off of Mexico; the Islas San Andrés in the Caribbean off of southern Central America). As is often the case for insular birds, many of the island mockingbird lineages have differentiated substantially in morphological and behavioral traits. This differentiation is pronounced within the Galapagos, where the four generally recognized species have evolved differences in bill shape and size, plumage pattern, body size, song, and mating systems, among other traits (Gulledge, 1975; Abbott and Abbott, 1978; Curry, 1989). Phylogeographic surveys of the Galapagos populations using mitochondrial (Arbogast et al., 2006) and microsatellite (Hoeck et al., 2010) markers have

shown that the historical population structure within the *Nesomimus* group does not fully track the traditional species boundaries that were defined based on phenotypic traits, suggesting instead that this radiation has a complex within-archipelago history of dispersal, gene flow, and phenotypic differentiation (Arbogast et al., 2006; Hoeck et al., 2010). Several studies have found the *Nesomimus* group to be embedded within the broader *Mimus* clade (Arbogast et al., 2006; Lovette and Rubenstein, 2007) and taxonomically this group is now merged into *Mimus* (Remsen et al., 2010), but precisely where the *Nesomimus* lineage falls in relation to these other mockingbirds remains uncertain.

A somewhat analogous situation involves the Socorro Mockingbird (*Mimus graysoni*), a morphologically distinct endangered species endemic to its remote namesake island. This species was separated into the monotypic genus *Mimodes* until analyses of mitochondrial DNA characters revealed that it falls well within the *Mimus* mockingbird group (Barber et al., 2004).

Relationships within the Tropical (*M. gilvus*) and Northern (*M. polyglottos*) Mockingbird complex are complex and not fully resolved. These taxa hybridize in their zone of contact in central Mexico (Wetmore, 1943), and they have sometimes been considered conspecific. They are generally classified as separate species (e.g., Davis and Miller, 1960; Mayr and Short, 1970; A.O.U., 1998) and mitochondrial DNA-based phylogenetic reconstructions suggest that some populations of these taxa are well differentiated (Hunt et al., 2001). Morphological traits suggest this complex further includes the San Andrés Mockingbird, a distinctively large-billed population found only on its namesake islands in the western Caribbean that has most often been considered a subspecies of *gilvus* (e.g., Davis and Miller, 1960; A.O.U., 1998; Dickinson, 2003), but which is sometimes treated as the full species *M. magnirostris* (e.g., Bond, 1956).

Here we use mitochondrial and nuclear intron DNA sequence markers to reconstruct the phylogenetic relationships among all Mimidae species, which we hope will aid in future comparative analyses of morphological, ecological, and behavioral trait variation in this group.

2. Materials and methods

2.1. Taxonomic and molecular marker sampling

We included in our analyses sequences from all 34 currently recognized species of Mimidae (A.O.U., 1998; Dickinson, 2003), including multiple representatives of most species (Appendix A). The majority of the samples obtained for this study allowed the extraction of high-quality DNA, and from these we generally obtained sequences of five protein-coding mtDNA genes (ND2, CO1, CO2, ATPase8, and ATPase6) with a combined length of 4118 nucleotides, and sequences from three autosomal nuclear intron loci, beta-fibrinogen introns 5 (*FGB-5*; Kimball et al., 2009) and 7 (*FGB-7*; Prychitko and Moore, 1997), transforming growth factor beta-2 intron 5 (*TGFB2–5*; Primmer et al., 2002), and rhodopsin intron 1 (*RHO-1*; Primmer et al., 2002). The combined length of these nuclear loci is 2963 aligned nucleotides (not including regions of ambiguous alignment). Our laboratory methods for the generation of these sequences have been detailed elsewhere (Lovette and Rubenstein, 2007; Lovette et al., 2010). In some cases (see Appendix A) we did not obtain the full set of loci from a sample, as was also true in the few cases when the sequences were obtained from studies conducted in other laboratories (Appendix A; Barber et al., 2004; Arbogast et al., 2006).

We generated sequences from three species (*Mimus graysoni, Toxostoma ocellatum, Toxostoma guttatum*) and four Mexican *Mimus*

gilvus individuals (a species from which we also included high-quality samples from other locations) from toe-pads taken from museum skin samples. Toe-pad samples were extracted and amplified in a dedicated ancient-DNA laboratory facility using stringent protocols as described in Lovette and Rubenstein (2007). From the *M. graysoni* and *T. guttatum* samples we sequenced nearly the entire set of mtDNA coding genes; from the *T. occellatum* and *M. gilvus* samples we sequenced only the mtDNA ND2 gene.

Preliminary analyses showed that in all cases, sequences from conspecific samples had very high similarity. Because we are primarily concerned here with interspecific relationships, and to reduce computation times, we selected a single representative of each species to include in some phylogenetic analyses (Appendix A), although we report additional analyses (see below) with all samples included.

Previous studies have provided robust evidence that the Mimidae species included here form a monophyletic group that is the sister-group of the starlings (Sturnidae; e.g., Sibley and Ahlquist, 1990; Barker et al., 2004; Cibois and Cracraft, 2004; Zuccon et al., 2006; Voelker and Spellman, 2004; Lovette and Rubenstein, 2007). We included single representatives of five Sturnidae subclades (see Lovette and Rubenstein, 2007; *Lamprotornis superbus, Onychognathus morio, Aplonis panayensis, Sturnus vulgaris, Rhabdornis inornatus*) as outgroups, along with one representative (*Buphagus africanus*) of the sister group to the Mimidae + Sturnidae, and one more distant outgroup taxon (*Catharus guttatus*).

2.2. Bayesian phylogenetic methods

We based all phylogenetic reconstructions on Markov chain Monte Carlo (MCMC) analyses conducted using MrBayes 3.1.2. (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The number of MCMC generations, number of concurrent chains, and number of separate runs varied among analyses, as described below. All MCMC runs were sampled every 1×10^4 generations and were run using the parallel computing resources of the Computational Biology Service Unit at the Cornell University Theory Center.

For each set of MCMC analyses, we evaluated the 'burn-in' period by plotting variation in log likelihood scores and individual parameter values across the duration of the run, and by evaluating variation in the posterior probability scores of the most variable nodes using the web-based program AWTY (Wilgenbusch et al., 2004). We then discarded the pre-stationarity output, and to be conservative at least the initial 25% of the apparently stationary samples, based on the slowest-converging metric. We evaluated convergence among runs by comparing the resulting consensus topologies, and by plotting the posterior probability scores of individual nodes using AWTY. The retained post-stationarity samples from separate but convergent runs were then combined to calculate majority-rule consensus trees, posterior probability values for each node, mean branch lengths, and parameter estimates.

In addition to the phylogenetic analyses covered in detail below, we also ran a variety of preliminary analyses using other phylogenetic methods (maximum likelihood and maximum parsimony), alternative data partitioning schemes, and subsets of the overall dataset. Those results were highly consistent with the results of the comprehensive Bayesian analyses reported here.

2.3. Data partitions and model selection

Our dataset comprised a heterogeneous mix of mtDNA protein-coding and nuclear non-coding loci, and hence we used six data partitions in our likelihood analyses, assigning single partitions to each of the three independent nuclear loci (*FGB-5* and *FGB-7* are linked and were grouped into a single partition) and separate partitions for each codon position in the mtDNA sequences. Likewise, the four mtDNA genes are a single linkage group and were analyzed together. For each partition (mtDNA1stcodon, mtDNA2ndcodon, mtDNA3rdcodon, *FGB-5* + *FGB-7*, *TGFB2–5*, *RHO-1*), we used the program MrModeltest v2 (Nylander, 2004) to identify the best-fitting model under the Bayesian information criterion (BIC; Akaike, 1973; Kass and Raftery, 1995; Posada and Buckley, 2004). The preferred model for all mtDNA partitions was GTR + G + I and the preferred model for the Fib 5&7, TGFB5 and Rho1 partitions was HKY + G. These two models were applied respectively to all analyses involving these data partitions.

2.4. Gene tree analyses

To assess congruence among independent gene trees, we ran separate Bayesian MCMC phylogenetic analyses on each of the four unlinked data partitions (mtDNA, *FGB-5* + *FGB-7*, *TGFB2–5*, *RHO-1*). To facilitate comparisons across datasets, these analyses included only single representatives of 30 Mimidae species from which we sampled all loci (Mimidae species entirely missing from these nuclear gene trees are *M. graysoni, T. guttatum, T. ocellatum,* and *T. curvirostre*). Each gene-tree analysis was run in MrBayes for 1×10^7 generations sampled every 1×10^4 generation, with five replicated runs of four chains with default heating. Plots of –ln likelihood scores, parameter values, and posterior probability scores for individual nodes suggested that each analysis had converged before (usually well before) the 5×10^6 generation. The topologies of all well-supported nodes of the two independent runs also converged by the 5×10^6 generation, as did the posterior probability scores of individual nodes as assessed graphically using AWTY. We discarded the first 9×10 generations as 'burn-in' and combined the remaining 100 samples from each run to calculate 90% majority-rule consensus topologies for each gene tree. The .con file created by MrBayes was visualized in FigTree v.1.2.2. This consensus tree was confirmed in PAUP by combining the last 90% of each .t file into one .t file. A majority-rule consensus tree was then visualized.

We used a similar approach to analyze the mitochondrial sequences alone.

2.5. Combined data analyses

We conducted further MCMC analyses that included all loci sampled from all samples listed in Appendix A. These more comprehensive analyses were run with six partitions, three for the mitochondrial codon positions and one each for the three unlinked nuclear intron loci. Five independent runs, each with four concurrent chains, were run for 1.3×10^7 generations. The first 1×10^6 generations were discarded as burn-in; the remaining samples from the independent runs were highly congruent, and the combined post-burn-in samples from all five runs were used to derive a 50% majority rule consensus tree and to calculate mean branch lengths.

3. Results

All sequences new to this study have been deposited in Gen-Bank; Appendix A gives accession numbers for both these and all previously reported sequences.

The Bayesian analyses of all concatenated loci from all samples produced a topology (Fig. 1) in which nearly all nodes are highly supported, and which is largely consistent with the relationships found in previous studies that included subsets of these taxa as
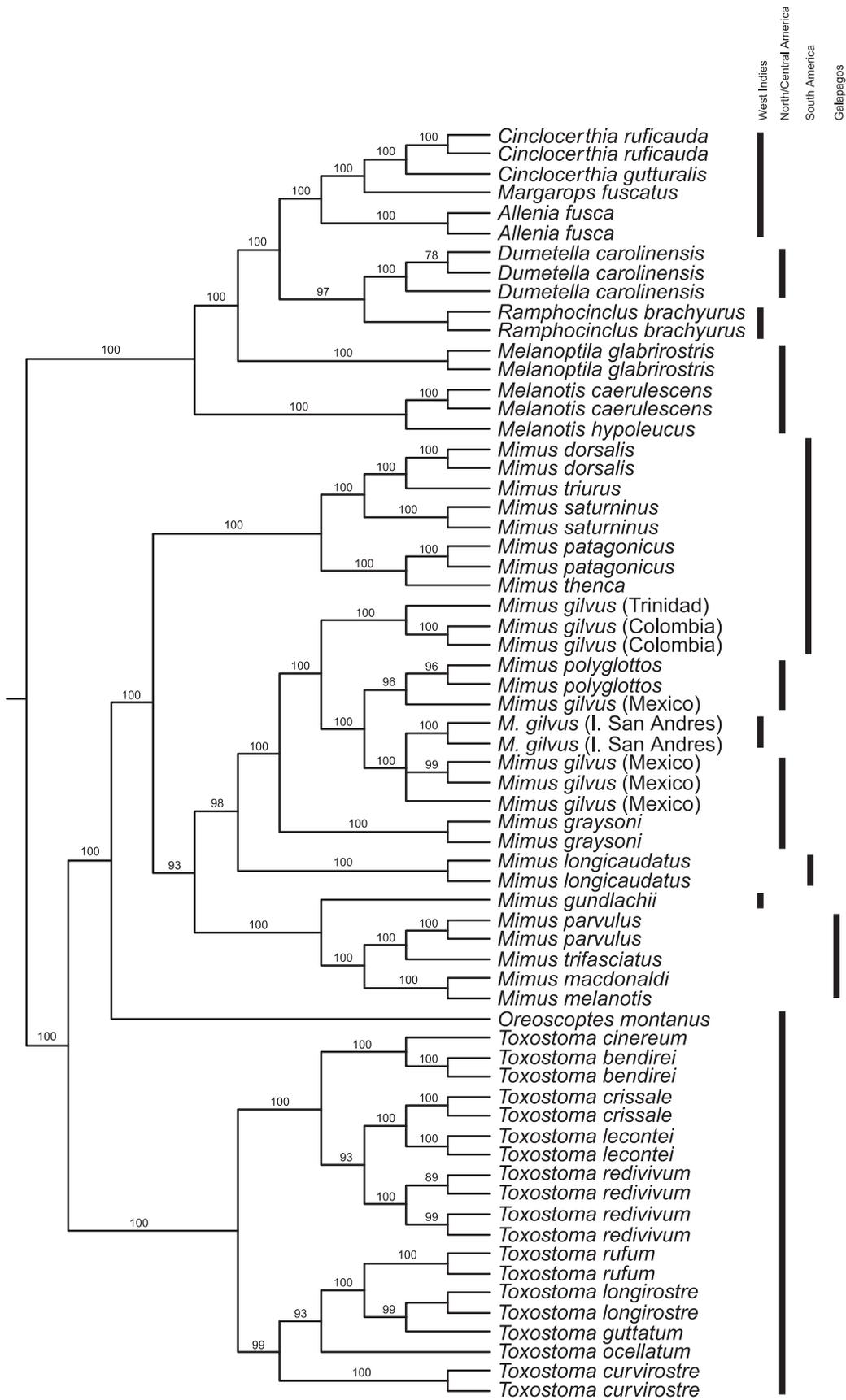
Fig. 1. Relationships among species of Mimidae estimated by Bayesian MCMC analyses of concatenated mitochondrial and nuclear intron sequences subdivided into six partitions (three mitochondrial partitions by codon position; nuclear locus partitions *FGB-5 + FGB-7, TGFB2-5, RHO-1*). The topology shown here is a 50% majority rule consensus of post-burn-in trees. Numbers adjacent to nodes indicate posterior probability values >75. Topology is rooted to outgroup taxa (not shown) in the sister family Sturnidae as described in the text. Geographic descriptors at right indicate primary area of breeding distribution.

described above. Novel or potentially important aspects of this tree include the placement of the Galapagos mockingbird lineage as sister to the Bahama mockingbird (*Mimus gundlachi*) with a posterior probability score of 100; this relationship was found with lower support in previous studies (Arbogast et al., 2006). As has been found previously, both the Galapagos Mockingbird group (previously separated as *Nesomimus*) and the Socorro Mockingbird (previously in *Mimodes*) are embedded within a shallow clade that also includes all *Mimus* mockingbird taxa. Taxa that have not been included in earlier molecular phylogenetic reconstructions include the Brown-backed Mockingbird (*Mimus dorsalis*) of the southwestern Andes which falls within a clade of other continental South American mockingbirds, and the San Andrés Mockingbird (*M. [gilvus] magnirostris*) which falls within the Northern/Tropical (*M. polyglottos/gilvus*) mockingbird complex.

As expected at this level of divergence, all phylogenetic analyses based on single nuclear loci had low resolution (Fig. 2), although each provided some support for relationships that receive higher support in the in the concatenated analysis. In contrast, the analyses based on mitochondrial sequences alone (Fig. 3) produced a strongly supported topology that was identical at the species and higher level to that of the concatenated analysis (Fig. 1). Considered together, these results indicate that the topology in the

concatenated analysis is driven overwhelmingly by the signal in the mitochondrial data partition.

4. Discussion

4.1. Phylogenetic relationships within the Mimidae

Fig. 1 presents our most comprehensive summary of the phylogenetic relationships within the Mimdae based on our analyses of mitochondrial and nuclear DNA sequence markers. Under this phylogenenetic hypothesis, the Mimidae can be subdivided by a basal split into two daughter clades, one of which comprises the 'blue' mockingbirds, New World catbirds, and Antillean thrashers, the other containing the *Mimus* mockingbirds and the continental thrashers.

4.1.1. Blue mockingbirds, new world catbirds, and antillean thrashers

The blue mockingbird/catbird/antillean thrasher clade contains nine species that are currently assigned to seven genera (*Melanotis, Melanoptila, Dumetella, Ramphocinclus, Allenia, Margarops, Cinclocerthia*; A.O.U., 1998). Relationships within this group were explored by Hunt et al. (2001) using mitochondrial markers and by Lovette and Rubenstein (2007) using both mitochondrial and
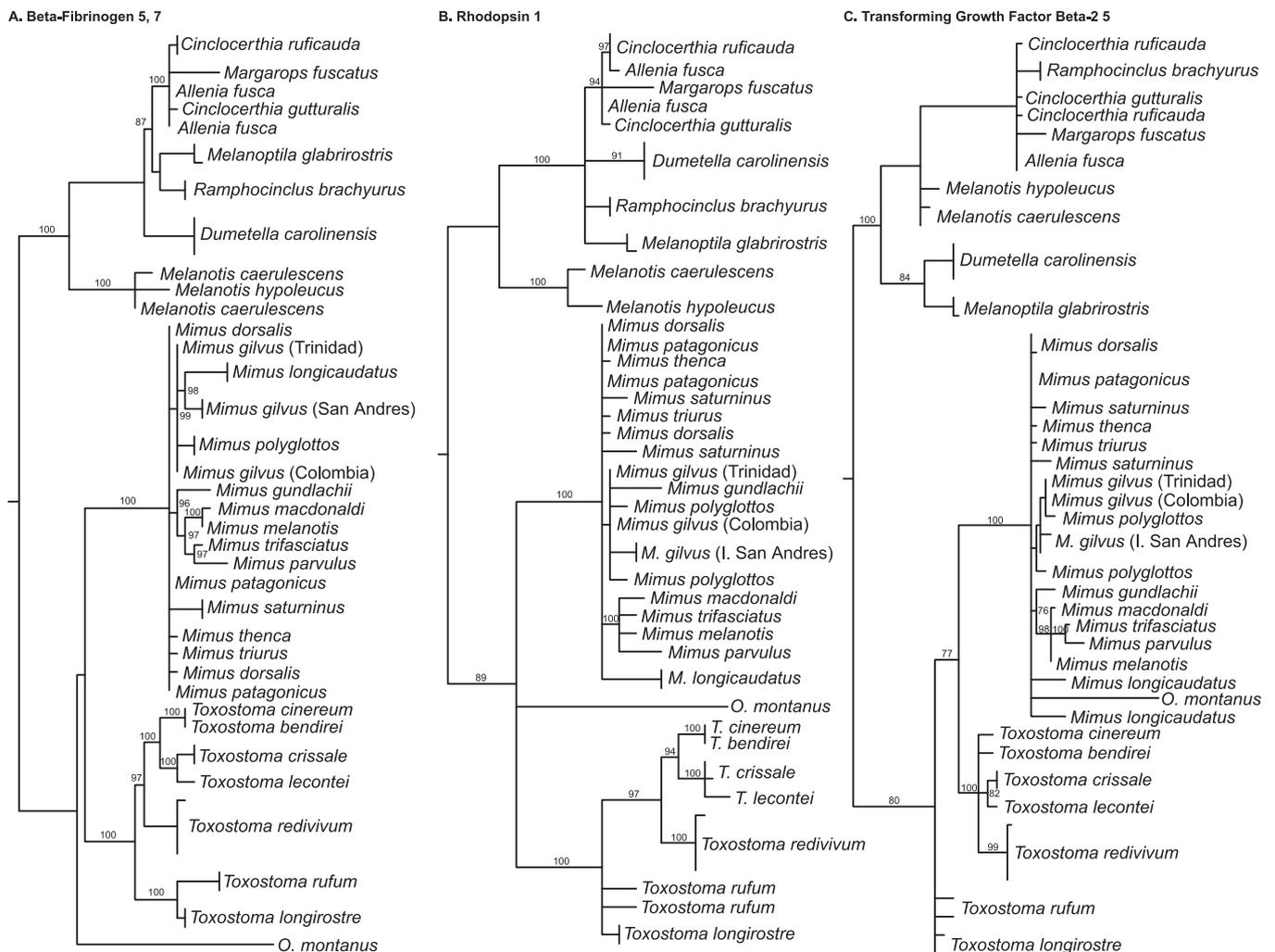
Fig. 2. Three single-locus gene tree hypotheses based on nuclear intron sequences. Topologies represent 50% majority rule consensus of post-burn-in trees. Numbers adjacent to nodes indicate posterior probability values >75%. All reconstructions were rooted using Sturnidae outgroup taxa (not shown).
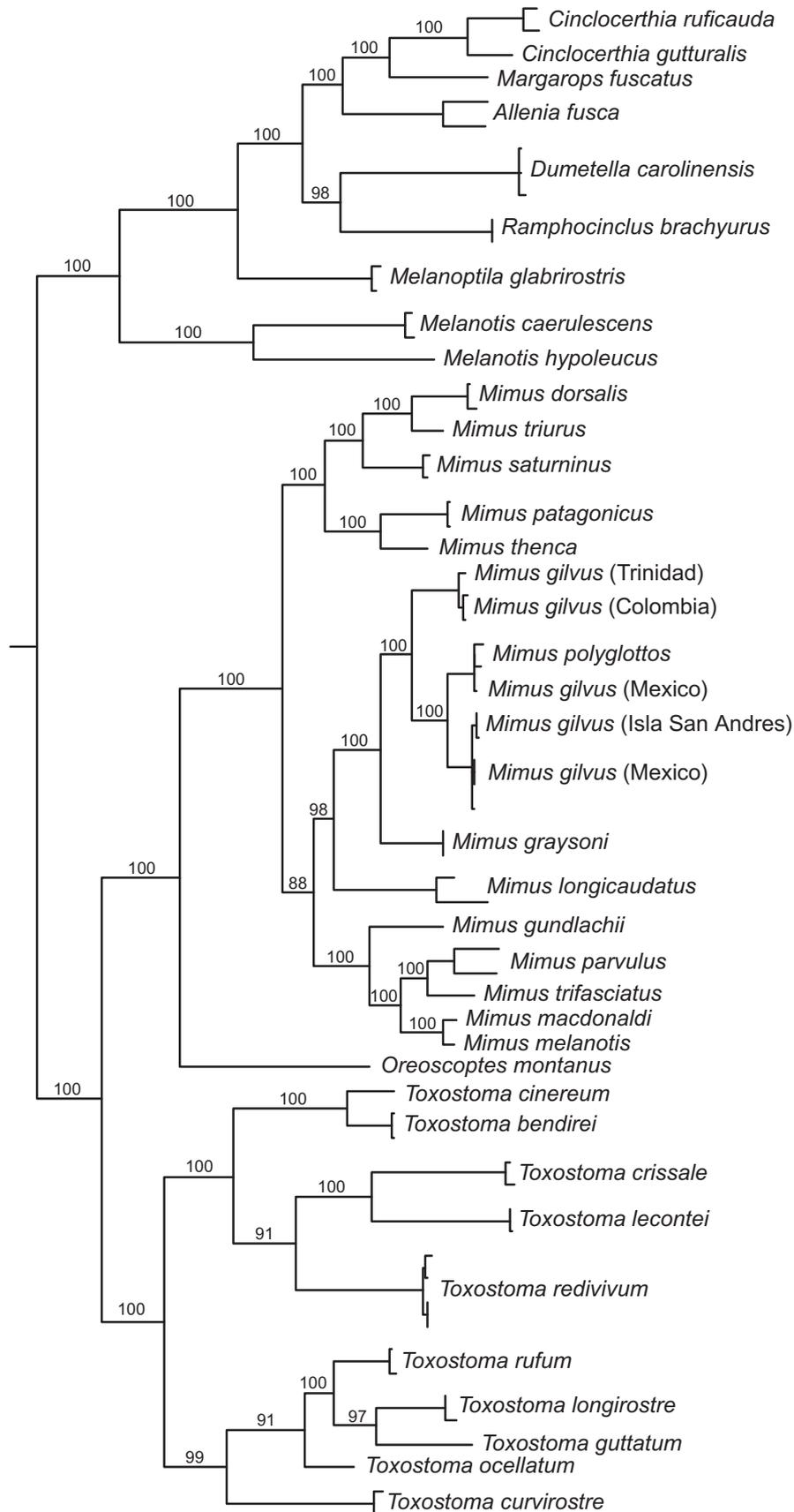
Fig. 3. Bayesian likelihood reconstruction of relationships among Mimidae species based on mitochondrial sequences alone. Numbers adjacent to nodes indicate posterior probability values >75%. All reconstructions were rooted using Sturnidae outgroup taxa (not shown).

nuclear DNA data; our topologies here are consistent with those earlier results and the historical interpretations based on them. An early split within this clade separates the blue mockingbird lineage from a clade containing the remaining catbirds and Antillean thrashers. The two *Melanotis* blue mockingbirds have allopatric distributions in Mexico and northern Central America, and they are clearly sister taxa although they are separated by substantial genetic divergence in comparison to many other sister species pairs within the Mimidae (Fig. 3).

All but one of the remaining taxa in the catbird/antillean thrasher group have distributions within the Caribbean basin. The basal split within this clade separates the Black Catbird (*Melanoptila glabrirostris*) of the Yucatan peninsula from the remaining species. This general topology, with two successive early-splitting lineages now found on the Central American mainland, may hint at the route of colonization into the West Indies taken by the ancestor of the radiation now found in that island system. The sister-clade to *Melanotis* comprises five species of thrashers resident within the West Indies, plus the Gray Catbird (*Dumetella carolinensis*), a migratory species with a broad breeding range that spans much of the United States and southern Canada, and which winters in the continental regions surrounding the Gulf of Mexico and on the western islands in the Greater Antilles. As found previously (Hunt et al., 2001; Lovette and Rubenstein, 2007), *Dumetella* is embedded within the Antillean thrasher radiation as the sister taxon of *Ramphocinclus brachyurus*, the White-breasted Thrasher, a highly endangered species found only on the Lesser Antillean islands of Martinique and St. Lucia. Based on the phylogenetic evidence, it seems most likely that the ancestral *Dumetella* lineage recolonized North America from the West Indies, adding to the growing list of avian examples of such 'reverse colonization' of continental areas from island source populations that have been identified from phylogenetic evidence (Bellemain and Ricklefs, 2008; Sheldon et al., 2009; Sturge et al., 2009). The *Dumetella* lineage likewise probably transitioned to long-distance migration from a sedentary ancestor, a change consistent with predictions that avian migratory behaviors have high evolutionary lability despite the complex suite of traits necessary to sustain successful migration (Berthold, 1999; Zink, 2002).

The five species of resident Antillean thrashers are all found in the Lesser Antilles, with one (*Margarops fuscatus*) extending its range to Puerto Rico and the Bahamian archipelago. These birds have a complex pattern of island occupancy, with some Lesser Antillean islands supporting all five species. The morphological and behavioral variation within this shallow clade of thrashers is correspondingly high, and this group may represent the sole avian example of a Lesser Antillean adaptive radiation (Ricklefs and Bermingham, 2008).

The high morphological distinctiveness of the Antillean thrasher species has resulted in all but *Cinclocerthia* being currently classified into monotypic genera (A.O.U., 1998; Banks et al., 2002). Although many of these taxa are morphologically divergent from the other species in this clade, it could be argued that this group is generically over-split, as this Antillean thrasher clade is likely no older than the *Mimus* or *Toxostoma* clades which similarly contain a range of species with high phenotypic variation, including some island forms that have differentiated notably from their continental allies. There is no intermediate generic reassignment that recognizes monophyletic subgroups within this clade while also reflecting the major phenotypic differences among these taxa. If the genera we currently recognize as *Melanoptila, Dumetella, Ramphocinclus, Allenia, Margarops,* and *Cinclocerthia* were grouped into a single genus, *Dumetella* Wood, 1837 would have nomenclatural priority.

4.1.2. Toxostoma thrashers

Our reconstructions of species-level relationships of the *Toxostoma* thrashers are highly consistent with previous phylogenetic hypotheses for this group (Zink et al., 1999; Lovette and Rubenstein, 2007). We found these birds to be subdivided into two clades (Fig. 1), each comprised of five currently recognized species (A.O.U., 1998, and later supplements). Within the first of these groups, the Gray (*T. cinereum*) and Bendire's (*T. bendirei*) thrashers are sister species separated by relatively low genetic divergence, consistent with the expectation that these taxa are closely allied (e.g., Mayr and Short, 1970; A.O.U., 1998; Zink et al., 1999). This group also contains the more divergent sister-species pair formed by the Crissal (*T. crissale*) and Le Conte's (*T. lecontei*) thrashers, which together are in turn sister to the California Thrasher (*T. redivivium*).

The second *Toxostoma* clade includes the Curve-billed Thrasher (*T. curvirostre*) as sister to the remaining four species; this topology is not consistent with the suggestion (Sibley and Monroe, 1990) that *T. curvirostre* is most closely allied to the Ocellated Thrasher (*T. ocellatum*). However, the clade formed by the Brown (*T. rufum*), Long-billed (*T. longirostre*), and Cozumel (*T. guttatum*) thrashers matches previous predictions about their close affinities (Mayr and Short, 1970; A.O.U., 1998; Zink et al., 1999; Sibley and Monroe, 1990).

4.1.3. Mimus mockingbirds

The *Mimus* mockingbirds form a shallow clade of 14 or 15 species that collectively are sister to the Sage Thrasher (*Oreoscoptes montanus*) lineage (Fig. 1). Subgroups within this relatively recent radiation include a clade of five species endemic to South America. Within this South American group, the two southernmost species (the Chilean Mockingbird *M. thenca* and Patagonian Mockingbird *M. patagonicus*) are allopatric sister taxa separated by the heights of the southern Andes. The range-restricted Brown-backed Mockingbird (*M. dorsalis*), which has not been included in previous phylogenetic surveys of this genus, is sister to the White-banded Mockingbird (*M. triurus*), and these two species are in turn sister to the broadly distributed Chalk-browed Mockingbird (*M. saturninus*).

A second group within Mimus comprises the Northern (*M. polyglottos*) and Tropical (*M. gilvus*) Mockingbirds along with two island forms, the Socorro Mockingbird (*Mimus [Mimodes] graysoni*) and the San Andrés Mockingbird (*M. [gilvus] magnirostris*). As found previously (Barber et al., 2004), *M. graysoni* is embedded within the larger *Mimus* clade, where it sister to the remaining members of the *M. polyglottos/gilvus* group. Relationships among the *polyglottos/gilvus* group are complicated, as both *M. magnirostris* and *M. polyglottos* fall within the *M. gilvus* cluster, thereby rendering *M. gilvus* paraphyletic. At this level of divergence, nearly all of the phylogenetic signal in our analyses derives from the mitochondrial loci (see Fig. 2), so this paraphyly reflects the history of the associated mitochondrial gene tree. In the absence of new behavioral and genetic information from the *M. polyglottos/gilvus* hybrid zone in Central Mexico, we recommend retaining the current species-level taxonomy for these groups, recognizing both *M. gilvus* and *M. polyglottos* but considering *M. magnirostris* a subspecies of *M. gilvus*.

A final group within Mimus comprises the Galapagos mockingbird clade, and their apparent sister taxon, the Bahama Mockingbird (*M. gundlachii*).

4.2. Historical biogeography of oceanic island mockingbirds

The current distribution of *Mimus* mockingbirds suggests that these birds (or their recent ancestors) are accomplished

over-water dispersers, as at least five *Mimus* lineages have independently colonized one or more oceanic islands. In addition to being found across much of North America, the Northern Mockingbird (*M. polyglottos*) is resident through the Bahamas, the large islands of the Greater Antilles except for Jamaica, and the Cayman Islands; phylogeographic studies have shown that these West Indian populations are closely allied to the more northerly continental populations, implying a recent set of island colonizations (Hunt et al., 2001). The Tropical Mockingbird (*M. gilvus*) has similarly colonized the most of the Lesser Antillean island chain from South America (Hunt et al., 2001). In the western Caribbean, a separate colonization by a lineage in the *M. polyglottos/gilvus* group gave rise to the unusually large-billed population (species/subspecies *M. magnirostris*) on San Andrés Island; the mitochondrial evidence suggests that the San Andrés population is allied to *M. gilvus* lineages from southern Mexico (Fig. 1), thereby suggesting its likely colonization source. The more divergent mockingbird population (*M. graysonii*) endemic to Isla Socorro–a small, arid island in the Pacific Ocean located about 600 km west of the central Mexican coast – is apparently derived from the lineage that is also ancestral to the entire *M. polyglottos/gilvus* group, implying a substantially earlier colonization of that remote island along with a substantial period of isolation of *M. graysonii*. (Fig. 1).

The mockingbird dispersal event with the most notable evolutionary consequences was the colonization of the Galapagos by the ancestor of the lineages that then radiated in that archipelago. Darwin noted the affinities of the Galapagos mockingbirds to species of *Mimus* from the South American continent (Darwin, 1859), and it was long assumed that the Galapagos lineage was most closely related to species found on that relatively nearby source. Mitochondrial sequence-based analyses by Arbogast et al. (2006) instead identified the Bahama Mockingbird (*M. gundlachii*) as the sister lineage to the Galapagos clade, a finding mirrored in our phylogenetic results presented here (Fig. 1) based on somewhat more extensive sampling of DNA markers. In addition to being recovered in our phylogenetic analyses of mitochondrial sequences (Fig. 3), the sister relationship between the Bahama Mockingbird and the Galapagos Mockingbird group was notably recovered in the independent topologies from two of our three nuclear loci (Fig. 2). Several other Galapagos vertebrates are allied to West Indian taxa (reviewed in Parent et al., 2008), suggesting that in each case the common ancestor of these island forms was prone to over-water dispersal.

Acknowledgments

Appendix A

Taxa included in this study, tissue types, collecting localities, institutional sources, and GenBank accession numbers.

Taxon	Museum source[a] & sample No.	Type[b]	Locality	Mitochondrial coding genes				Nuclear intron loci			
				ND2[d]	CO1	CO2	ATPases[e]	Fib-5	Fib-7	Rho-1	TGFB2-4
Dumetella carolinensis	STRI-BHDCA4	T	Bahamas, Grand Bahama I.	EF468192	EF484216	EF484317	EF486776	EF468323	EF471844	EF472856	EF484115
Dumetella carolinensis	CUMV-50343	T	USA, New York, Tompkins Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Dumetella carolinensis	CUMV-50532	T	USA, New York, Tompkins Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Melanoptila glabrirostris	LSUMNS-B0081	T	Mexico, Quintana Roo, Isla Cozumel	EF468197	EF484221	EF484322	EF486781	EF468328	EF471849	EF472861	EF484120
Melanoptila glabrirostris	CUMV-50356	T	Mexico	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus polyglottos	LSUMNS-B21369	T	USA, California, San Bernardino	EF468202	EF484226	EF484327	EF486786	EF468333	EF471854	EF472866	EF484125
Mimus polyglottos	CUMV-50469	T	USA, New York, Tompkins Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus gilvus	STRI-CCMGI1	T	Trinidad, Chacachacare I.	EF468196	EF484220	EF484321	EF486780	EF468327	EF471848	EF472860	EF484119
Mimus gilvus	CAB110[c]	B	Colombia	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus gilvus	CAB111[c]	B	Colombia	Pending	Pending	Pending	Pending	Pending	Pending	Pending	–
Mimus gilvus	CUMV-33468	S	Mexico, Quintana Roo	Pending	–	–	–	–	–	–	–

Species	Voucher		Location								
Mimus gilvus	CUMV-33466	S	Mexico, Campeche	Pending	—	—	—	—	—	—	—	—
Mimus gilvus	CUMV-33464	S	Mexico, Yucatan	Pending	—	—	—	—	—	—	—	—
Mimus gilvus	CUMV-33465	S	Mexico, Yucatan	Pending	—	—	—	—	—	—	—	—
Mimus magnirostris	CAB-MMAG1[c]	B	Colombia, San Andres I.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus magnirostris	CAB-MMAG2[c]	B	Colombia, San Andres I.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus gundlachi	STRI-JAMGU1	T	Jamaica, Portland Ridge	EF468198	EF484222	EF484323	EF486782	EF468329	EF471850	EF472862	EF484121
Mimus thenca	MNHN-2676	T	Chile	EF468204	EF484228	EF484329	EF486788	EF468335	EF471856	EF472868	EF484127
Mimus longicaudatus	LSUMNS-B5229	T	Peru, Lambayeque	EF468200	EF484224	EF484325	EF486784	EF468331	EF471852	EF472864	EF484123
Mimus longicaudatus	LSUMNS-B3810	T	Peru, Ica	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus saturninus	CUMV-50582[009]	T	Argentina, Buenos Aires Prov.	EF468203	EF484227	EF484328	EF486787	EF468334	EF471855	EF472867	EF484126
Mimus saturninus	CUMV-50581[008]	T	Argentina, Buenos Aires Prov.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus patagonicus	CUMV-50577[004]	T	Argentina, Jujuy Prov.	EF468201	EF484225	EF484326	EF486785	EF468332	EF471853	EF472865	EF484124
Mimus patagonicus	CUMV-50578[001]	T	Argentina, Jujuy Prov.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus triurus	CUMV-MACH14	T	Argentina, Buenos Aires Prov.	EF468205	EF484229	EF484330	EF486789	EF468336	EF471857	EF472869	EF484128
Mimus dorsalis	CUMV-50579[002]	T	Argentina, Jujuy Prov.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus dorsalis	CUMV-50580[006]	T	Argentina, Jujuy Prov.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Mimus parvulus	WFU-Isab02[d]	B	Ecuador, Galapagos, Isabella I.	AY311553	DQ083935	—	DQ087201	Pending	Pending	Pending	Pending
Mimus parvulus	WFU-Scz2[d]	B	Ecuador, Galapagos, Santa Cruz I.	AY311553	DQ083934	—	DQ087200	Pending	Pending	Pending	Pending
Mimus trifasciatus	WFU-Ntr03[d]	B	Ecuador, Galapagos, Champion I.	AY311544	DQ083929	—	DQ087195	Pending	Pending	Pending	Pending
Mimus macdonaldi	WFU-Nma002[d]	B	Ecuador, Galapagos, Española I.	AY311555	DQ083930	—	DQ087196	Pending	Pending	Pending	Pending
Nesomimus melanotis	WFU-Scr01[d]	B	Ecuador, Galapagos, San Cristóbal I.	AY311576	DQ083931	—	DQ087197	Pending	Pending	Pending	Pending
Oreoscoptes montanus	LSUMNS-B19513	T	USA, California, San Bernardino Co.	EF468206	EF484230	EF484331	EF486790	EF468337	EF471858	EF472870	EF484129
Mimus graysoni	Barber et al., 2004		Mexico, Isla Socorro	AY758199	—	—	—	—	—	—	—
Mimus graysoni	CUMV-24114	S	Mexico, Isla Socorro	Pending	Pending	Pending	Pending	—	—	—	—
Toxostoma rufum	LSUMNS-B0490	T	USA, Louisiana, Cameron Parish	EF468209	EF484233	EF484334	EF486793	EF468340	EF471861	EF472873	EF484132
Toxostoma rufum	CUMV-50815	T	USA, New York, Tompkins Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma cinereum	LSUMNS-B6745	T	Mexico, Baja California	EF468208	EF484232	EF484333	EF486792	EF468339	EF471860	EF472872	EF484131
Toxostoma curvirostre	BMNH-CBTH024	T	Mexico, San Lius Potosi	Pending	Pending	Pending	Pending	—	—	—	—
Toxostoma curvirostre	BMNH-CBTH051	T	Mexico, Chihuahua	Pending	Pending	Pending	Pending	—	—	—	—
Toxostoma longirostre	BMNH-BTH2TX	T	USA, Texas, Atascosa Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma longirostre	BMNH-BTH4TX	T	USA, Texas, Atascosa Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma guttatum	CUMV-30516	S	Mexico, Quintana Roo, Cozumel I.	Pending	Pending	Pending	Pending	—	—	—	—
Toxostoma ocellatum	CUMV-29035	S	Mexico, Quintana Roo, Cozumel I.	Pending	—	—	—	—	—	—	—
Toxostoma bendirei	BMNH-BETH4	T	USA, Arizona, Pima Co.	Pending	Pending	Pending	Pending	Pending	—	Pending	Pending
Toxostoma bendirei	BMNH-BETH5	T	USA, Arizona, Pima Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma crissale	BMNH-CRTH2AZ	T	USA, Arizona, Cochise Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma crissale	BMNH-CRTH6CA	T	USA, California, San Bernardino Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma lecontei	BMNH-LETH7AZ	T	USA, Arizona, La Paz Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma lecontei	BMNH-LETH8AZ	T	USA, Arizona, La Paz Co.	Pending	Pending	Pending	Pending	Pending	—	Pending	Pending
Toxostoma redivivium	SDSU-2311	T	USA, California, Lake Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma redivivium	SDSU-2318	T	USA, California, Tuolumne Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma redivivium	SDSU-2375	T	USA, California, San Diego Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Toxostoma redivivium	SDSU-2378	T	USA, California, San Diego Co.	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Ramphocinclus brachyurus	STRI-SLRBR2	T	St. Lucia	EF468207	EF484231	EF484332	EF486791	EF468338	EF471859	EF472871	EF484130
Ramphocinclus brachyurus	STRI-SLRBR1	T	St. Lucia	Pending	—	—	—	—	—	—	—
Melanotis caerulescens	LSUMNS-B0022	T	Mexico, Puebla	EF468193	EF484217	EF484318	EF486777	EF468324	EF471845	EF472857	EF484116
Melanotis caerulescens	LSUMNS-B0048[18]	T	Mexico, Puebla	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Melanotis hypoleucus	CUMV-44026	T	Mexico, Chiapas	EF468199	EF484223	EF484324	EF486783	EF468330	EF471851	EF472863	EF484122

a (continued)

Taxon	Museum source[a] & sample No.	Type[b]	Locality	Mitochondrial coding genes				Nuclear intron loci			
				ND2[d]	CO1	CO2	ATPases[e]	Fib-5	Fib-7	Rho-1	TGFB2-4
Allenia fusca	STRI-DOMFU3	T	Dominica, Springfield	EF468195	EF484219	EF484320	EF486779	EF468326	EF471847	EF472859	EF484118
Allenia fusca	STRI-SLMFU4	T	St. Lucia	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Margarops fuscatus	STRI-BUMFT1	T	Antigua and Barbuda, Barbuda	EF468194	EF484218	EF484319	EF486778	EF468325	EF471846	EF472858	EF484117
Cinclocerthia ruficauda	STRI-GUCRU1	T	Guadaloupe	EF468191	–	–	–	–	–	–	–
Cinclocerthia ruficauda	ANSP-B2134	T	St. Vincent, St. Andrew Parish	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending
Cinclocerthia gutturalis	STRI-SLCRU2	T	St. Lucia	Pending	Pending	Pending	Pending	Pending	Pending	Pending	Pending

[a] Institutional sources of samples: ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; BMNH: Bell Museum of Natural History, University of Minnesota, Minneapolis, Minnesota, USA; CUMV: Cornell University Museum of Vertebrates, Ithaca, New York, USA; LSUMNS: Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana, USA; MNHN: Museo Nacional de Historia Natural, Santiago, Chile; SDSU: San Diego State University Museum of Biodiversity, San Diego, CA, USA; WFU: Wake Forest University, Winston-Salem, NC, USA.
[b] Sample types: B = blood; T = frozen or buffer-preserved tissue; S = toe-pad shaving from museum skin.
[c] Sequences courtesy of C. Botero/D. Cadena.
[d] Sequences courtesy of B. Arbogast and collaborators (see Arbogast et al., 2006).

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