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COLONIZATION OF SOUTH AMERICA FROM CARIBBEAN ISLANDS CONFIRMED BY MOLECULAR PHYLOGENY WITH INCREASED TAXON SAMPLING

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Abstract. A previous phylogeny of New World orioles (*Icterus*) suggested a possible example of island-to-mainland colonization. Using two mitochondrial genes (cytochrome *b* and ND2), that study showed that 43 of the recognized species/subspecies are divided into three clades (A, B, C). Because of a lack of fresh tissue, however, two key taxa—the South American Orange-crowned Oriole (*I. auricapillus*) and the Caribbean Hispaniola Oriole (*I. dominicensis dominicensis*)—were missing from that analysis. To complete the phylogeny, we sequenced both genes for these taxa and reconstructed a well-supported phylogeny via parsimony and maximum-likelihood analyses. The addition of *I. d. dominicensis* to the phylogeny confirms that the Greater Antillean Oriole (*I. dominicensis*) is polyphyletic, and taxonomic revision of this species complex is warranted. Also, the placement of *I. auricapillus* and *I. d. dominicensis* within clade A has important implications for biogeography. The revised phylogeny implies that clade A orioles colonized mainland South America from Caribbean islands. Orioles thus provide a striking example of reverse colonization that contradicts the traditional assumption in island biogeography of mainland-to-island colonization.

Key words: island biogeography, Icterus, phylogeny, mtDNA, cytochrome b, ND2, polyphyly.

Colonización de América del Sur desde las Islas del Caribe Confirmada por Filogenia Molecular con Muestreo Taxonómico Incrementado

Resumen. Una filogenia previa de *Icterus* sugirió un posible ejemplo de colonización de islas a continente. Usando dos genes mitocondriales (citocromo *b* y ND2), este estudio mostró que 43 de las especies/subespecies reconocidas están divididas en tres clados (A, B, C). Sin embargo, debido a la falta de tejido fresco, dos taxones clave—*I. auricapillus* y *I. dominicensis dominicensis*—faltaron del análisis. Para completar la filogenia, secuenciamos ambos genes para estos taxones y reconstruimos una filogenia con buen soporte vía análisis de parsimonia y de máxima verosimilitud. La adición de *I. d. dominicensis* a la filogenia confirma que *I. dominicensis* es polifilético y la revisión taxonómica de este complejo de especies está justificada. Además, la ubicación de *I. auricapillus* e *I. d. dominicensis* dentro del clado A tiene implicancias importantes para la biogeografía. La filogenia revisada implica que el clado A de *Icterus* colonizó el continente de América del Sur desde las islas del Caribe. Los *Icterus* brindan así un ejemplo sorprendente de colonización revertida que contradice la presunción tradicional en biogeografía de islas de colonización desde los continentes a las islas.

The equilibrium theory of island biogeography has been a central concept in evolution and ecology (MacArthur and Wilson 1967, Emerson and Kolm 2005). According to this theory, the number of species on an island is a function of the island's size and its distance from the nearest mainlands (MacArthur and Wilson 1967, Emerson and Kolm 2005). By including this measure of distance, the model assumes that species originate from mainlands and immigrate to islands, a phenomenon for which there is much evidence. Island populations, however, can also act as sources for other islands, even for far distant islands such as the Galapagos (Hedges et al. 1992, Burns et al. 2002). Several new studies have shown that islands can act as sources for mainlands as well (Raxworthy et al. 2002, Filardi and Moyle 2005, Nicholson et al. 2005, Bellemain and Ricklefs 2008, Fuchs et al. 2008). Thus, there is a growing recognition that the implicit assumption that mainlands are always the source of species, and that islands are always the recipients, may not be correct (Bellemain and Ricklefs 2008).

Previous phylogenetic work on New World orioles hinted at such island-to-mainland colonization in some Caribbean and mainland South American orioles (Omland et al. 1999). There are roughly 30 recognized species of New World oriole (*Icterus*) (Clements 2007), ranging from southern Canada to northern Argentina (Jaramillo and Burke 1999). For this genus, Omland et al. (1999) constructed a molecular phylogeny based on cytochrome *b* and ND2 sequences of 43 taxa, including most of the species. The phylogeny showed that *Icterus* is composed of three monophyletic groups, which Omland et al. (1999) named clades A, B, and C. Clade A is of particular interest in terms of island biogeography because it includes many Caribbean island species, as well as some mainland species from North, Central, and South America.

One South American species, the Orange-crowned Oriole (*I. auricapillus*), was placed within this clade on the basis of a short sequence of about 300 base pairs of cytochrome *b*, which, because of a lack of fresh tissue, was the only information available (Omland et al. 1999). Also missing from the phylogeny was a potentially informative subspecies, the Hispaniola Oriole (*I. dominicensis dominicensis*), for which Omland et al. (1999) had sequenced only cytochrome *b*, again because of a lack of fresh

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tissue. The oriole phylogeny has been used as a basis for a series of studies of plumage pattern, pigment, migration, and song evolution (Omland and Lanyon 2000, Hofmann et al. 2006, Kondo and Omland 2007, Price et al. 2007). More complete taxon sampling, such as the addition of *I. auricapillus* and *I. d. dominicensis* to the phylogeny, should provide a better understanding of the evolutionary history of this genus.

Our goals for this study were as follows: (1) To determine the position of these two taxa within the oriole phylogeny by using fresh tissue samples, (2) to test whether model-based maximum-likelihood analysis of these data with current techniques produced results consistent with the equally weighted parsimony analysis used by Omland et al. (1999), and (3) to determine if the newly constructed phylogeny confirms that Caribbean orioles of clade A colonized mainland South America from the Caribbean.

METHODS

To complete the phylogeny, we sequenced both cytochrome *b* and ND2 for *I. auricapillus* and *I. d. dominicensis* by using the same primer sets as did Omland et al. (1999) and analyzed the phylogeny by using PAUP* (Swofford 2003) and GARLI. With PAUP*, we analyzed the data by using equally weighted parsimony, the main method used by Omland et al. (1999). For maximum-likelihood analysis, we first ran Modeltest (Posada and Crandall 1998), which selected the GTR + I + G model as the one that best fit the data. GARLI implements new genetic algorithms that allow rapid heuristic maximum-likelihood searches (Zwickle 2006). We changed GARLI's threshold precision values to 0.0005 and 0.0001, respectively, to make the output trees more precise. To determine nodal support from bootstrap analyses using both maximum parsimony and maximum likelihood, we ran 1000 pseudoreplicates by using PAUP* and GARLI, respectively. We were interested in seeing how closely the model-based results from this new algorithm compared to results based on parsimony. We reconstructed the area of origin for the orioles of clade A by using equally weighted parsimony in MacClade (Maddison and Maddison 2002). The fit of our mtDNA data to competing hypotheses relating to the colonization history of South America was assessed by likelihood-based Shimodaira–Hasegawa (1999) and Templeton (1983) tests.

RESULTS

There is strong agreement between the results produced by the two different phylogenetic analyses (Fig. 1). Both *I. auricapillus* and *I. d. dominicensis* were placed in clade A, as suggested by the previous partial data. The new tree shows the same three clades, with no major differences from the previously published tree. Bootstrap percentages of the two methods are highly correlated (Fig. 1). Furthermore, there are no nodes that received >50% bootstrap support by one method that were contradicted by nodes with >50% support from the other method (parsimony and likelihood). Several aspects of the earlier parsimony tree that were only weakly supported (e.g., *I. maculialatus* as sister to clade A, with clade B in turn sister to that group) are again present in the maximum-likelihood tree. The clade comprising *I. laudabilis*, *I. oberi*, *I. d. portoricensis*, and *I. d. dominicensis* (Fig. 2) lacks strong support by either method, as can be seen in Fig. 1, which indicates less than 50% bootstrap support by each method.

The South American taxa in clade A form a strongly supported clade, with *I. auricapillus* sister to the *I. cayanensis* complex (including *chrysocephalus*). The most parsimonious reconstruction of the historical biogeography of clade A indicates that South America was colonized by ancestors from the Caribbean (Fig. 2). The node separating *I. d. northropi* and *I. d. melanopsis* from the rest of the Caribbean clade A orioles (along with the South American clade, which is nested within the Caribbean clade) has 83% bootstrap support (Fig. 1). The internodes separating the species in the clade of *I. laudabilis, I. oberi, I. d. portoricensis*, and *I. d. dominicensis* are short (Fig. 2), a pattern implying that the speciation generating these taxa was rapid and accounting for the lack of resolution in Fig. 1.

We also used PAUP* to determine genetic distances. The sequence of *I. auricapillus* differed by ~3% on average from that of the the *I. cayanensis* complex, and these two South American taxa differed from Caribbean Island species by about 4–6%. Distances among the subspecies of *I. dominicensis* generally ranged from 4.8% to 5.4%, although *I. d. melanopsis* and *I. d. northropi* differed by only 0.7%.

DISCUSSION

COMPARING THE TWO MODELS

The strong agreement between the tree produced by GARLI model-based maximum likelihood and the tree produced by equally weighted parsimony (Omland et al. 1999) provides further confidence in the basic structure of the mitochondrial phylogeny of the orioles. The only nodes in the likelihood and parsimony trees that differed were those weakly supported in both. For example, 41.0% of the nodes had 100% bootstrap support from both methods, and 30.8% of the nodes were within 5% of the support of their counterparts on the other tree. In the majority (66.7%) of the cases where the difference between the nodes was >5%, the newer method provided increased bootstrap support for nodes. We are currently sequencing multiple nuclear introns that continue to support the major oriole clades (see Allen and Omland 2003; F. Jacobsen, unpublished data).

POLYPHYLY OF THE GREATER ANTILLEAN ORIOLE

Our results provide increased support for considering each of the four Greater Antillean orioles in the *I. dominicensis* group as separate species (also see Garrido et al. 2005, Price and Hayes 2009). With cytochrome *b* and ND2 sequences for *I. d. dominicensis* completed, there is strong evidence that *I. dominicensis* as currently classified is polyphyletic (in Fig. 1, there is 83% bootstrap support for the node uniting *I. d. dominicensis* and *I. d. portoricensis* with eight other Caribbean and South American taxa.) This is a convincing case of polyphyly caused by incorrect taxonomy rather than by hybridization or incomplete lineage sorting (Bond 1956; see review by Funk and Omland 2003). Also, most of these taxa diverge by 4–6% from each other, implying long independent evolutionary histories. Although *I. d. melanopsis* and *I. d. northropi* are quite close in mtDNA sequence (0.7% divergence), they are well separated geographically and have distinct adult plumages (Raffaele et al. 1998, Jaramillo and Burke 1999, Omland and Lanyon 2000). Although comparisons of more individuals and additional loci should provide interesting insights into the details of evolution and speciation in this complex, the mtDNA differences, along with well documented differences in song, morphometrics (Garrido et al. 2005), and plumage (Omland and Lanyon 2000, Price and Hayes 2009), provide strong support for recognizing nominate *dominicensis, portoricensis, melanopsis*, and *northropi* as four distinct species.

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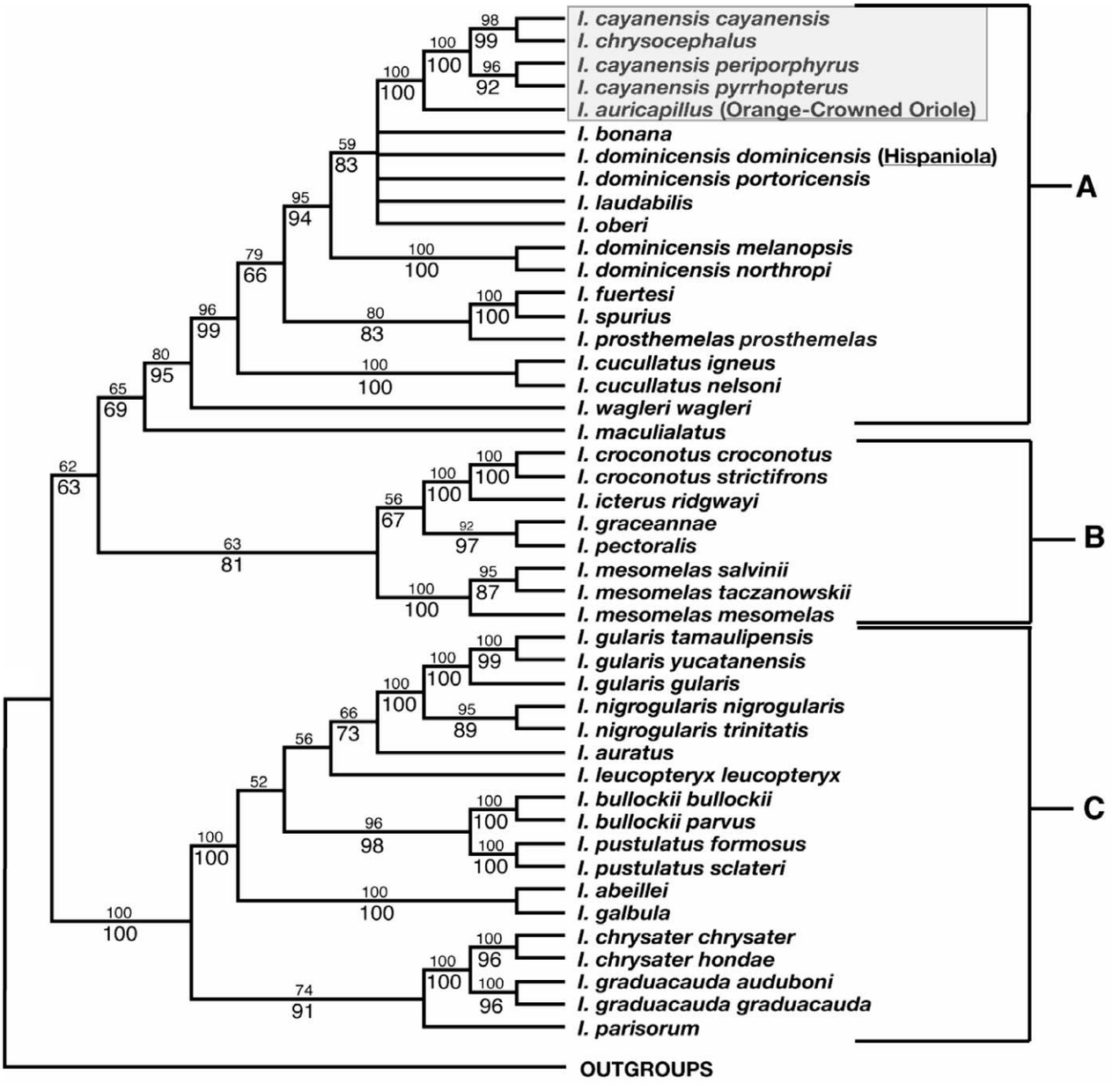


FIGURE 1. Bootstrap tree for *Icterus* phylogeny. Parsimony values are shown above branches (small text from PAUP*), and maximum-likelihood values are shown below (large text from GARLI). One thousand pseudoreplicates were conducted for each method. Note the strong correlation between the bootstrap-support values for the two different methods. Designations of clades A, B, and C follow Omland et al. (1999). Shaded area indicates South American clade A orioles.

COLONIZATION OF SOUTH AMERICA FROM THE CARIBBEAN

A number of recent studies have provided evidence of dispersal from islands to mainland Central/South America, India, Africa, Australia and New Guinea (Burns et al. 2002, Filardi and Moyle 2005, Yoder and Nowak 2006, Bellemain and Ricklefs 2008). Our study indicates that dispersal from Caribbean islands to South America is necessary to explain the distribution of orioles in the region. Parsimony and maximum-likelihood analyses of cytochrome *b* and ND2 place *I. auricapillus* and *I. d. dominicensis* within clade A. *Icterus auricapillus*, ranging from eastern Panama to northern Colombia and Venezuela, is sister to the Epaulet Oriole complex (*I. cayanensis*), also endemic to South America (Clements 2007). *Icterus d. dominicensis* is part of a group of closely related orioles all found on islands in the

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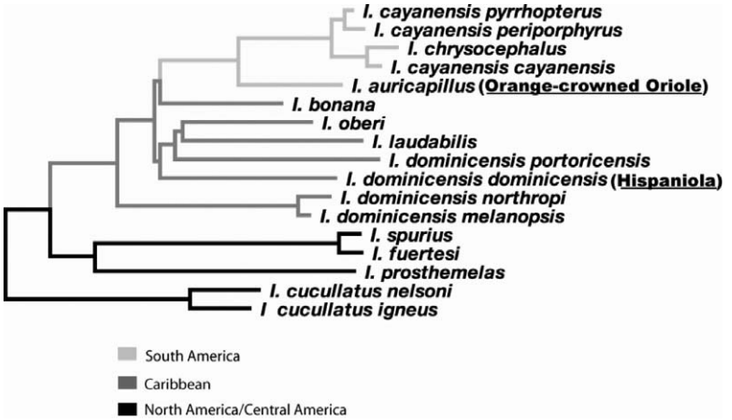


FIGURE 2. Maximum-likelihood topology of clade A biogeography. Biogeographic reconstruction shows evidence of colonization of the South American mainland by clade A orioles from Caribbean islands. Reconstruction conducted with MacClade 4.0 using equally weighed parsimony (Maddison and Maddison 2002).

Caribbean (Clements 2007). Both the position of these two taxa within clade A and bootstrap values produced by maximum-likelihood methods support a Caribbean islands-to-mainland South America colonization (Fig. 2). The South American clade (*I. auricapillus*, *I. cayanensis*, and *I. chrysocephalus*) is nested deeply within the Caribbean group. In particular, there is 83% maximum-likelihood support for a node placing five Caribbean taxa (including *I. d. dominicensis*) closer to the South American clade than to the two remaining Caribbean taxa (*I. d. melanopsis* of Cuba and *I. d. northropi* of the Bahamas). An alternative maximum-likelihood reconstruction under the constraint of Caribbean monophyly (all island taxa more closely related to each other than any is to either North or South American mainland taxa) was not a significantly worse fit, though the results were consistent with reverse colonization (Shimodaira–Hasegawa test, $P = 0.06$). A Templeton test provided no evidence of a difference in fit between the constrained tree and the best maximum-likelihood tree. Independent work on the oriole phylogeny with multiple nuclear introns clearly supports the core of clade A. Furthermore, preliminary intron analyses agree with the placement of *I. bonana* as sister to the *I. auricapillus*/*I. cayanensis* clade, also supporting colonization of South America from Caribbean islands (F. Jacobsen, unpublished data). The Greater Antilles and South America were last connected by land at least 33–35 million years ago (Iturralde-Vinent and MacPhee 1999; also see Hedges 2001). In contrast, the speciation that separated the *I. auricapillus*/*I. cayanensis* clade from island taxa likely occurred within the last 2–4 million years, given the sequence divergence between these South American and Caribbean taxa (assuming roughly 1.6%–2.0% sequence divergence per million years) (Fleischer et al. 1998, Lovette 2004). Although the date of the last land connection is uncertain (Hedges 2001), the most recent possible land bridge is at least an order of magnitude older than the split between the taxa of interest. On this basis, it seems that dispersal from Caribbean islands to mainland South America best explains the patterns of distribution observed for orioles within clade A. Future, more detailed, analysis using additional clock calibrations and relaxed molecular-clock approaches (Thorne and Kishino 2002) can further investigate causes of speciation among the Caribbean orioles, as well as the timing of the dispersal to mainland South America that we document here.

Note that our reconstructions and most published reconstructions of ancestral areas assume an equal probability of dispersal from islands to continents and vice versa (see Cook and Crisp 2005). This caveat is important for all biogeographic analyses, but in the case of reasonably large and abundant islands, such as those in the Caribbean, with close continental mainlands, such as North and South America, equal transition rates seem reasonable as a starting assumption. This assumption is much more problematic for distant and/or small oceanic islands (e.g., Hawaii, Kerguelen Island; Omland 1997).

CONCLUSIONS

There is strong agreement between the equally-weighted parsimony search with PAUP* (the method used in 1999) and the maximum-likelihood search with GARLI (a more complex model-based method). *Icterus auricapillus* is placed within clade A as sister to the *I. cayanensis* complex. Complete sequences of cytochrome *b* and ND2 for *I. d. dominicensis* also place it within clade A and show that the Greater Antillean Oriole (*I. dominicensis*) is not monophyletic with respect to mitochondrial DNA. The placement of both orioles within a mostly Caribbean section of clade A has important implications for biogeography, as most models of biogeography assume that mainland species colonize islands. Our results provide a counter example, with evidence indicating that clade A orioles colonized mainland South America from Caribbean islands.

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