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A comprehensive species-level molecular phylogeny of the New World blackbirds (Icteridae)

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ABSTRACT

The New World blackbirds (Icteridae) are among the best known songbirds, serving as a model clade in comparative studies of morphological, ecological, and behavioral trait evolution. Despite wide interest in the group, as yet no analysis of blackbird relationships has achieved comprehensive species-level sampling or found robust support for most intergeneric relationships. Using mitochondrial gene sequences from all ~108 currently recognized species and six additional distinct lineages, together with strategic sampling of four nuclear loci and whole mitochondrial genomes, we were able to resolve most relationships with high confidence. Our phylogeny is consistent with the strongly-supported results of past studies, but it also contains many novel inferences of relationship, including unexpected placement of some newly-sampled taxa, resolution of relationships among major clades within Icteridae, and resolution of genus-level relationships within the largest of those clades, the grackles and allies. We suggest taxonomic revisions based on our results, including restoration of *Cacicus melanicterus* to the monotypic *Cassiculus*, merging the monotypic *Ocyalus* and *Clypicterus* into *Cacicus*, restoration of *Dives atroviolaceus* to the monotypic *Ptiloxena*, and naming *Curaeus forbesi* to a new monotypic genus, *Anumara*. Our hypothesis of blackbird phylogeny provides a foundation for ongoing and future evolutionary analyses of the group.

1. Introduction

The New World blackbirds (Icteridae) are among the best known and studied songbirds, both through exemplar species such as the Red-winged Blackbird (*Agelaius phoeniceus*) and collectively as a model clade in numerous studies of morphological, ecological, and behavioral trait evolution. The size of the family (~108 species) and its variability along several dimensions of general theoretical interest makes Icteridae especially attractive for comparative studies. Topics that have been investigated comparatively in blackbirds include mating systems (Searcy et al., 1999), brood parasitism (Lanyon, 1992), sexual size dimorphism (Webster, 1992), sexual dichromatism (Irwin, 1994; Hofmann et al., 2008a, 2008b; Friedman et al., 2009), plumage pattern divergence (Omland and Lanyon, 2000; Price and Whalen, 2009), chemical bases of plumage color (Hofmann et al., 2006, 2007, 2008a, 2008b; Friedman et al., 2011), ultraviolet and structural color (Eaton, 2006; Shawkey et al., 2006), ecological correlates of plumage color (Johnson and Lanyon, 2000) and female song (Price, 2009; Price et al., 2009), song divergence (Price and Lanyon, 2002b, 2004a; Price et al., 2007), migration (Kondo and Omland, 2007), biogeographic history (Sturge et al., 2009), and ecological niche divergence (Eaton et al., 2008).

Knowledge of phylogeny is a prerequisite for comparative analysis and the basis for systematic classification, but past analyses of blackbird relationships lacked comprehensive species-level sampling and failed to find robust support for most intergeneric relationships. The first molecular phylogenies of Icteridae with broad taxonomic sampling provided revolutionary insights into relationships within the family (Lanyon, 1994; Freeman and Zink, 1995; Lanyon and Omland, 1999) and its subgroups (Johnson and Lanyon, 1999; Omland et al., 1999; Price and Lanyon, 2002a, 2004a; Barker et al., 2008). Those findings were a huge advance over the diffuse hypotheses of relationship presented in taxonomic reviews based on informal evaluation of the external anatomy of museum skins (e.g. Ridgway, 1902; Hellmayr, 1937; Blake, 1968) or very limited molecular sampling (e.g. Sibley and Monroe, 1990). Sequence-based molecular studies, for the first time, brought together large numbers of informative characters with objective analytical methods to resolve relationships among most species and clades, tasks for which morphological characteristics

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had proven to be weakly informative (e.g. Björklund, 1991) or even—in combination with informal and speculative methods of inference—misleading (e.g. Beecher, 1950, 1951).

In contrast to the other diverse families within the New World nine-primaried oscine clade—namely, the tanagers (Thraupidae), cardinal-grosbeaks (Cardinalidae), New World sparrows (Emberizidae), and wood-warblers (Parulidae)—among which many species and genera have recently been shuffled, the constitution of Icteridae has been unaffected by results from molecular phylogenetic studies (e.g. Burns, 1997; Klicka et al., 2000, 2007; Burns et al., 2002, 2003; Lovette and Bermingham, 2002; Yuri and Mindell, 2002; Klein et al., 2004; Alström et al., 2008; Lovette et al., 2010; Barker et al., 2013). Apparently, features that have traditionally been used to recognize blackbirds such as bill shape (e.g. casque of maxilla; see Webster, 2003), morphology related to gape-feeding by many species (Beecher, 1951; Orians, 1985), and general similarities in shape, plumage, voice, display, and ecology, have led to their accurate diagnosis. The only contrary assertions have been the following: (1) placement of *Spiza* in Icteridae (Beecher, 1951; Raikow, 1978), which was immediately disputed (see e.g. Tordoff, 1954) and is not currently supported (e.g. molecular evidence places *Spiza* deep within the Cardinalidae; Klicka et al., 2007); (2) unsubstantiated suggestions of affinity between *Compsothraupis loricata* and Icteridae (Jaramillo and Burke, 1999); and (3) lack thereof for *Amblycercus* (Fraga, 2011). Comprehensive genus-level multi-locus molecular sampling of the nine-primaried oscines strongly supports the monophyly of Icteridae (Barker et al., 2013) as traditionally defined.

Although molecular phylogenetic studies of Icteridae (e.g. Lanyon, 1992, 1994; Freeman and Zink, 1995; Lanyon and Omland, 1999) did not lead to its redefinition, they shed considerable light on relationships within the family, including recognition of constituent clades and discovery that several genera—*Molothrus*, *Agelaius*, *Cacicus*, and *Psarocolius*—as then defined, were not monophyletic. Lanyon and Omland (1999) found that Icteridae comprises five deeply-divergent lineages: the meadowlarks and allies (*Sturnella*, *Dolichonyx*, *Xanthocephalus*); cup-nesting caciques (*Amblycercus*); caciques and oropendolas (*Cacicus*, *Psarocolius*, *Clypicterus*, *Ocyalus*); orioles (*Icterus*); and a large set of genera collectively referred to as the grackles and allies (e.g. *Agelaius*, *Quiscalus*, *Molothrus*). However, they were unable to resolve basal divergences among those lineages. Similarly, Johnson and Lanyon (1999) found strong support for several groups within the grackles and allies clade, including cowbirds (*Molothrus*), marsh blackbirds (*Agelaius*), and grackles (*Quiscalus*), but poor support for the relationships among those lineages. Among the more surprising findings of these studies was a clade of South American endemics ("group 1" of Johnson and Lanyon, 1999) within the grackles and allies, composed largely of morphologically and ecologically enigmatic genera together with species that had been thought to be members of genera outside that clade (e.g., *Molothrus*, *Agelaius*). Subsequent studies have explored relationships *within* the basal icterid clades, especially the orioles (e.g. Omland et al., 1999; Jacobsen et al., 2010) and caciques and oropendolas (Price and Lanyon, 2002a, 2004a). Until recently (Barker et al., 2013; this study), none has aimed to resolve relationships *among* the basal icterid clades or major groups within the grackles and allies (but see Powell et al., 2013) with additional sequence or taxon sampling. Past phylogenies of Icteridae have not been comprehensive, and except within the orioles (Allen and Omland, 2003; Jacobsen et al., 2010; Jacobsen and Omland, 2011) and some meadowlarks (Barker et al., 2008), they have relied solely upon mitochondrial DNA. Therefore, a revision of the phylogeny of Icteridae, using new methods and additional data, is in order.

The overall goal of the present study was to infer phylogenetic relationships among all ~108 species of New World blackbirds (Icteridae) using both mitochondrial and nuclear DNA sequences. Key objectives were as follows: (1) sample all currently-recognized species not included in previous studies; (2) robustly resolve relationships among major clades within Icteridae; (3) robustly resolve relationships among the grackles and allies, especially within a phenotypically and ecologically diverse clade of South American endemics, which previous studies failed to resolve with confidence; (4) compare patterns of relationship found in previous mitochondrial studies to results from nuclear loci, and (5) suggest taxonomic revisions based on our results. Preliminary results from this project (i.e. phylogenies inferred from less comprehensive versions of our dataset) have already informed studies of female song (Price, 2009; Price et al., 2009) and plumage color evolution (Friedman et al., 2011).

2. Methods

2.1. Taxon and character sampling

Our analyses encompassed 114 ingroup and four outgroup taxa (Table 1). Sampling within Icteridae included all species currently recognized by taxonomic authorities (Dickinson, 2003; Remsen et al., 2012; Gill and Donsker, 2012) or in prominent references (Jaramillo and Burke, 1999; Fraga, 2011) except that we did not obtain samples of *Psarocolius b. bifaciatus*, *Agelaioides badius fringillarius* and *Molothrus aeneus armenti* (see also Dugand and Eisenmann, 1983) and we chose not to include samples of *Psarocolius angustifrons alfredi* (see Section 4.4) and *Agelaius phoeniceus gubernator* (see Dufort and Barker, 2013). About 10% of the sampled taxa had not been included in previous molecular phylogenies of Icteridae, including three meadowlarks (*Sturnella militaris*, *S. loyca*, *S. defilippii*), three caciques and oropendolas (*Cacicus koepckeae*, *Psarocolius cassini*, *P. guatimozinus*), an oriole (*Icterus jamacaii*), and three members of the grackles and allies subfamily (*Dives atroviolaceus*, *Curaeus forbesi*, *Macroagelaius subalaris*). We included more than one sample of a species if, in past studies, some of its subspecies appeared to be deeply divergent and geographically distinct lineages. Outgroups were selected based on results of recent molecular analyses of New World nine-primaried oscines with comprehensive genus-level sampling (Barker et al., 2013) and consisted of *Icteria virens, Teretistris fernandinae*, *Seiurus aurocapillus*, and *Oreothlypis gutturalis*.

Our molecular sampling design was informed by simulations and empirical phylogenetic studies (especially Wiens, 2005, 2006; Wiens et al., 2005; Wiens and Morrill, 2011) that found that incomplete data matrices, when properly assembled, can yield robust results. Our dataset included many more characters than previous studies, but practical limitations on obtaining all loci of interest from all taxa necessitated that most taxa be represented by a subset of characters. We aimed to sample strategically the types of loci most likely to be useful for resolving relationships in greatest need of additional study. To that end, our dataset comprised three overlapping "scaffolds" (Wiens, 2006)—two mitochondrial genes from >100 taxa, four nuclear loci from 46 of those taxa, and whole mitogenomes from 23 taxa—to which we opportunistically added other sequences as available (Table 1). This structure resulted in a substantial number of characters being shared among taxa, even though, overall, most characters were missing for most taxa. As a percentage of the complete data matrix, more characters were shared among more taxa than in less conservative, yet analytically successful, "sparse supermatrix" analyses (e.g. Thomson and Shaffer, 2010).

The set of 46 taxa (Table 1) from which we sequenced four nuclear loci (5266 bp total) included at least one representative from 26 of 28 ingroup genera (lacking only *Hypopyrrhus* and *Clypicterus*) and all four outgroup species. From each of those taxa, we

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Table 1
Taxa, specimens, and GenBank sequences used in phylogenetic analyses of New World blackbirds (Icteridae). Samples from multiple specimens of a given taxon were combined to form chimaeric sequences for analyses. Bolded text indicates the subset of taxa included in 46-taxon analyses. If tissue and skin specimens of the same individual are housed at different institutions, both are listed (tissue in parentheses). Loci or sets of loci not collected for a given specimen are indicated with a dash.

Taxon	English name[a]	Voucher specimen or tissue[b]	Collecting locality	mtDNA sample description	GenBank numbers of mtDNA samples	GenBank numbers of nucDNA loci (ACO1-I9, FGB-I5, MB-I2, RAG1)
Clypicterus oseryi	Casqued Oropendola	LSUMZ 120394	Peru: Loreto	ND2, Cyt b	AF472408, AF472383	KF810987, –, KF810968, –
Psarocolius decumanus	**Crested Oropendola**	FMNH 324065	Peru: Madre de Dios	ND2, Cyt b	AF472400, AF472375	KF810988, KF810953, KF810969, KF810938
		CUMV-Bird 52534 (MACN-Or-ct 1130)	Argentina: Jujuy	COX1	FJ028159	–
		none	Panama	16S	AY283889	–
Psarocolius viridis	Green Oropendola	USNM 609202	Guyana	ND2, Cyt b	AY117726, AY117698	–
		USNM 639199	Guyana: Cuyuni-Mazaruni	COX1	JQ175997	–
Psarocolius atrovirens	Dusky-green Oropendola	FMNH 324106	Peru: Cuzco	ND2, Cyt b	AF472391, AF472366	–
Psarocolius a. angustifrons	Russet-backed Oropendola	LSUMZ 120397	Peru: Loreto	ND2, Cyt b	AF472389, AF472364	–
Psarocolius wagleri	**Chestnut-headed Oropendola**	LSUMZ B27280	Costa Rica: Cartago	ND2, Cyt b	AF472394, AF472369	KC007919, KC007643, KC007727, KC007834
Psarocolius montezuma	**Montezuma Oropendola**	LSUMZ 164424	Panama: Colón	ND2, Cyt b	AF472403, AF472378	KC007921, KC007645, KC007729, KC007836
Psarocolius cassini	Baudo Oropendola	ANSP 147013	Colombia: Choco	Cyt b	KF810925	–
Psarocolius bifasciatus yuracares	Olive Oropendola	FMNH 324076	Peru: Madre de Dios	ND2, Cyt b	AF472404, AF472379	–
Psarocolius guatimozinus	Black Oropendola	LSUMZ B48620	Panama: Darién	Cyt b	KF810926	–
Ocyalus latirostris	**Band-tailed Oropendola**	ANSP 177928 (LSUMZ B3625)	Peru: Loreto	ND2, Cyt b	AF472407, AF472382	KC007920, KC007644, KC007728, KC007835
Cacicus cela cela	Yellow-rumped Cacique	KUMNH 88289 (USNM B04259)	Guyana: Berbice	ND2, COX1, Cyt b	AY117731, JQ174227, AY117703	–
Cacicus cela vitellinus	Yellow-rumped Cacique	LSUMZ 163850	Panama: Colón	ND2, Cyt b	AY117732, AY117704	–
Cacicus haemorrhous	Red-rumped Cacique	USNM 621068	Guyana	ND2, Cyt b	AY117733, AY117705	–
		USNM 586489	Guyana: Barima-Waini	COX1	JQ174230	–
Cacicus uropygialis uropygialis	Subtropical Cacique	LSUMZ B6093	Ecuador: Morona-Santiago	ND2, Cyt b	AY117736, AY117708	–
Cacicus uropygialis microrhynchus	Scarlet-rumped Cacique	STRI PACUR-PC99	Panama	ND2, Cyt b	AY117738, AY117710	–
		USNM 608010	Panama: Bocas del Toro	COX1	JQ174233	–
Cacicus uropygialis pacificus	Pacific Cacique	ANSP 182884	Ecuador: Esmeraldas	ND2, Cyt b	AY117735, AY117707	–
Cacicus chrysopterus	Golden-winged Cacique	USNM 620761	Argentina	ND2, Cyt b	AY117740, AY117712	–
		MACN-Or-ct 987	Argentina: Jujuy	COX1	FJ027255	–
Cacicus chrysonotus chrysonotus	Southern Mountain Cacique	LSUMZ 103278	Bolivia: La Paz	ND2, Cyt b	AY117745, AY117717	–
Cacicus chrysonotus leucoramphus	Northern Mountain Cacique	ANSP 182883	Ecuador: Imbabura	ND2, Cyt b	AY117743, AY117715	–
Cacicus sclateri	**Ecuadorian Cacique**	ANSP 177931 (LSUMZ B103568)	Peru: Loreto	ND2, ND2–COX3, Cyt b	AY117746, KF810923,AY117718	KC007922, KC007646, KC007730, KC007837
Cacicus koepckeae	Selva Cacique	LSUMZ B48621	Peru: Loreto	Cyt b	KF810927	–
Cacicus solitarius	Solitary Cacique	FMNH 324089	Peru: Cuzco	ND2, Cyt b	AY117747, AY117719	KF810989, –, KF810970, –
		MACN-Or-ct 1403	Argentina: Corrientes	COX1	FJ027264	–
Cacicus melanicterus	Mexican Cacique	UWBM 52185	Mexico: Oaxaca	ND2, Cyt b	AY117749, AY117721	KF810990, –, KF810971, –
Amblycercus h. holosericeus	Yellow-billed Cacique	KUMNH 1928	Mexico: Yucatán	ND2, Cyt b	AY117722, AY117750	–
		USNM 608009	Panama: Bocas del Toro	COX1	JQ174007	–

(*continued on next page*)

Table 1 (*continued*)

Taxon	English name[a]	Voucher specimen or tissue[b]	Collecting locality	mtDNA sample description	GenBank numbers of mtDNA samples	GenBank numbers of nucDNA loci (ACO1-I9, FGB-I5, MB-I2, RAG1)
Amblycercus holosericeus australis	**Yellow-billed Cacique**	LSUMZ 98900	Peru: Puno	ND2, ND2–COX3, Cyt b	AF472411, KF810921, AF472386	KC007923, KC007647, KC007731, KC007838
Icterus icterus	Venezuelan Troupial	LSUMZ B11328	Puerto Rico	ND2, Cyt b	AF099335, AF099296	–
		LSUMZ B48559	Guyana	COX1	KF810934	–
Icterus croconotus	Orange-backed Troupial	FMNH 324092	Peru: Madre de Dios	ND2, Cyt b	AF099336, AF089031	–
		USNM 632494	Guyana: Upper Takutu-Upper Essequibo	COX1	JQ175139	–
Icterus jamacaii	Campo Troupial	LGEMA 2742	Brazil: Piaui	COX1	JN801752	–
Icterus pectoralis	Spot-breasted Oriole	MMNH 42544	USA: Florida	ND2, Cyt b	AF099348}, AF099304	–
		KUMNH 109733	El Salvador: La Paz	COX1	DQ432954	–
Icterus graceannae	White-edged Oriole	ANSP 181810	Ecuador: Loja	ND2, Cyt b	AF099329, AF089030	–
Icterus mesomelas	**Yellow-tailed Oriole**	LSUMZ 109279	Panama: Darién	almost whole	JX516068	KF810991, KF810954, KF810972, KF810939
Icterus cayanensis	Epaulet Oriole	MPEG 40.357	Brazil: Rondônia	ND2, Cyt b	AF099316, AF089027	–
		USNM 625332	Guyana	COX1	JQ175135	–
Icterus chrysocephalus	Moriche Oriole	FMNH 339734	Venezuela: Sucre	ND2, Cyt b	AF099317, AF099279	–
		USNM 625748	Guyana	COX1	JQ175138	–
Icterus pyrrhopterus	Variable Oriole	FMNH 334608	Bolivia: Santa Cruz	ND2, Cyt b	AF099319, AF099280	–
		USNM 614726	Argentina: Entre Ríos	COX1	JQ175136	–
Icterus bonana	Martinique Oriole	STRI MA-IBO2	Martinique	ND2, COX1, ATP8–ATP6, Cyt b	AF109445, AF109429, AF109413, AF099277	–
Icterus laudabilis	St. Lucia Oriole	STRI SL-ILA4	St. Lucia	ND2, COX1, ATP8–ATP6, Cyt b	AF109455, AF109439, AF109423, AF099298	–
Icterus oberi	Montserrat Oriole	STRI MO-IOB4	Montserrat	ND2, COX1, ATP8–ATP6, Cyt b	AF109447, AF109431, AF109415, AF099303	–
Icterus dominicensis	Hispaniolan Oriole	AMNH NKK1112	Dominican Republic	Cyt b, CR	AY216867, AY211217	–
Icterus portoricensis	Puerto Rican Oriole	STRI PR-IDO1	Puerto Rico	ND2, COX1, ATP8–ATP6, Cyt b	AF109451, AF109435, AF109419, AF099288	–
Icterus melanopsis	Cuban Oriole	MNHNCu 4/8/92	Cuba	ND2, Cyt b	AF099324, AF099286	–
Icterus northropi	Bahama Oriole	BNT REF024	Bahamas: Andros	ND2, Cyt b	AF099325, AF099287	–
Icterus prosthemelas	Black-cowled Oriole	KUMNH 89517	Mexico: Campeche	ND2, COX1, ATP8–ATP6	AF109448, AF109432, AF109416	–
		MMNH 42542	Mexico: Yucatán	Cyt b	AY211213	–
Icterus spurius	Orchard Oriole	NCSM	USA: Colorado	ND2	AF099352	–
		USNM 626504	USA: Florida	COX1	DQ432955	–
		FMNH 381975	USA: Illinois	Cyt b, CR	AY211198, AY211230	–
Icterus fuertesi	Ochre Oriole	MMNH 42538	Mexico: Veracruz	ND2, Cyt b, CR	AF099351, AY211215, AY211219	–
Icterus cucullatus	**Hooded Oriole**	BB-BEHB25	unknown	–	–	KF810992, KF810955, KF810973, KF810940
		FMNH 341931	USA: California	ND2, Cyt b	AF099323, AF099284	–
		UWBM 48323	USA: Arizona	COX1	DQ433692	–
Icterus wagleri	Black-vented Oriole	MZFC QRO-216	Mexico: Querétaro	ND2, Cyt b	AF099353, AF099308	–
Icterus maculialatus	Bar-winged Oriole	INIREB SRF-387	Mexico: Chiapas	ND2, Cyt b	AF099340, AF099299	–
Icterus parisorum	**Scott's Oriole**	FMNH 341943	USA: California	ND2, Cyt b	AF099347, AF089035	KC007924, KC007648, KC007732, KC007839
		FMNH 334367	USA: Arizona	COX1	DQ432953	–
Icterus auricapillus	Orange-crowned Oriole	FMNH 261843	Colombia: Boyacá	Cyt b	KF810928	–
Icterus chrysater	Yellow-backed Oriole	UWBM 69019	Nicaragua: Chinandega	ND2, Cyt b	AF099321, AF099281	–
Icterus graduacauda	Audubon's Oriole	LSUMZ B-4023	USA: Texas	ND2, Cyt b	AF099330, AF099291	–
Icterus galbula	Baltimore Oriole	UMMZ 226382	USA: Michigan	12S, ND2–COX1, COX2–ATP6	AF447237, AF447287, AF447337	–
		FMNH 350604	USA: Illinois	Cyt b, CR	AY607656, AY607621	–
		ROM 1B-131	Canada: Ontario	COX1	EU525431	–
Icterus abeillei	Black-backed Oriole	MZFC 9657	Mexico: Querétaro	ND2	AF099311	–
		MZFC keo-48	Mexico: Michoacán	Cyt b, CR	AY607617, AY607602	–

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Icterus bullockii	Bullock's Oriole	MBMC jk95–095	USA: Oregon	ND2, Cyt b	EF529839, EF529950	–
		UWBM 59056	USA: Washington	COX1	DQ433689	–
		UWBM 55975	USA: Washington	CR	AY611475	–
Icterus pustulatus	Streak-backed Oriole	UWBM 52129	Mexico: Chiapas	ND2, Cyt b	AF099349, AF099305	–
		MZFC keo38	Mexico: Jalisco	CR	AY611477	–
Icterus leucopteryx	Jamaican Oriole	FMNH 331145	Jamaica: Trelawny	ND2, COX1, ATP8–ATP6	AF109443, AF109427, AF109411	–
		FMNH 33144	Jamaica: Trelawny	Cyt b	AF089032	–
Icterus auratus	Orange Oriole	UAM 7222	Mexico: Yucatán	ND2, Cyt b	AF099312, AF099276	–
Icterus nigrogularis	Yellow Oriole	STRI TR-INI1	Trinidad	ND2, COX1, ATP8–ATP6, Cyt b	AF109456, AF109440, AF109424, AF099302	–
		USNM 627066	Guyana	COX1	JQ175145	–
Icterus gularis	Altamira Oriole	FMNH	Mexico: Oaxaca	ND2, Cyt b	AF099332, AF099293	–
		UWBM 52191	Mexico: Oaxaca	COX1	DQ433697	–
Nesopsar nigerrimus	**Jamaican Blackbird**	FMNH 331150	Jamaica: Portland	whole	JX516054	KC007925, KC007649, KC007733, KC007840
Gymnomystax mexicanus	**Oriole Blackbird**	FMNH 339743	Venezuela: Falcón	whole	JX516075	KC007926, KC007650, KC007734, KC007841
Macroagelaius subalaris	Colombian Mountain Grackle	LACM 40973	Colombia: Santander	Cyt b	KF810929	–
Macroagelaius imthurni	**Golden-tufted Mountain Grackle**	FMNH 339783	Venezuela: Bolívar	whole	JX516073	KC007938, KC007663, KC007747, KC007854
Hypopyrrhus pyrohypogaster	Red-bellied Grackle	ICN 33977 (IAvH 2078)	Colombia: Antioquia	ND2, Cyt b	AY572450, AY572451	–
Lampropsar tanagrinus	**Velvet-fronted Grackle**	ANSP 177921 (LSUMZ B103505)	Peru: Loreto	almost whole	JX516057	KC007937, KC007662, KC007746, KC007853
Gnorimopsar chopi	**Chopi Blackbird**	FMNH 334679	Bolivia: Santa Cruz	whole	JX516055	KC007935, KC007660, KC007744, KC007851
Curaeus curaeus	**Austral Blackbird**	AMNH 826156	Chile: Magallanes	whole	JX516070	KC007934, KC007659, KC007743, KC007850
Curaeus forbesi	**Forbes's Blackbird**	MPEG 72143 CPE-II 040	Brazil: Pernambuco	ND2–COX3, Cyt b	KF810920, KF823980	KF810993, KF810956, KF810974, KF810941
Amblyramphus holosericeus	**Scarlet-headed Blackbird**	FMNH 334662	Bolivia: El Beni	whole	JX516063	KC007933, KC007658, KC007742, KC007849
Agelasticus xanthophthalmus	Pale-eyed Blackbird	FMNH 324094	Peru: Madre de Dios	whole	JX516059	KF810994, –, KF810975, –
Agelasticus cyanopus	**Unicolored Blackbird**	FMNH 334636	Bolivia: El Beni	whole	JX516076	KC007929, KC007653, KC007737, KC007844
Agelasticus thilius	**Yellow-winged Blackbird**	FMNH 334615	Bolivia: Oruro	whole	JX516069	KF810995, KF810957, KF810976, KF810942
Chrysomus ruficapillus	Chestnut-capped Blackbird	FMNH 330775	Brazil: Rio Grande do Sul	whole	JX516056	–
Chrysomus icterocephalus	**Yellow-hooded Blackbird**	FMNH 339772	Venezuela: Sucre	whole	JX516060	KF810996, KF810958, KF810977, KF810943
Xanthopsar flavus	**Saffron-cowled Blackbird**	FMNH 330747	Brazil: Rio Grande do Sul	whole	JX516065	KC007928, KC007652, KC007736, KC007843
Pseudoleistes guirahuro	**Yellow-rumped Marshbird**	FMNH 330795	Brazil: Rio Grande do Sul	whole	JX516071	KF810997, KF810959, KF810978, KF810944
Pseudoleistes virescens	**Brown-and-yellow Marshbird**	FMNH 330796	Brazil: Rio Grande do Sul	whole	JX516066	KC007932, KC007657, KC007741, KC007848
Oreopsar bolivianus	**Bolivian Blackbird**	FMNH 334687	Bolivia: El Beni	whole	JX516058	KC007936, KC007661, KC007745, KC007852
Agelaioides badius	**Baywing**	FMNH 330801	Brazil: Rio Grande do Sul	whole	JX516074	KC007942, KC007667, KC007751, KC007858
Molothrus rufoaxillaris	**Screaming Cowbird**	FMNH 330805	Brazil: Rio Grande do Sul	ND2, ND2–COX3, Cyt b	AF109961, KF810924, AF089044	KF810999, KF810960, KF810979, KF810945
		none	Argentina: Formosa	CR	EU199785	–
Molothrus oryzivorus	**Giant Cowbird**	FMNH 324097	Peru: Madre de Dios	Cyt b	AF089060	KF810998, KF810961, KF810980, KF810946
		LSUMZ 134021	Bolivia: Pando	12S, ND2, ND6–CR	AF407089, AF407046, AF407132	–
		USNM 587829	Guyana	COX1	JQ175403	–
Molothrus aeneus	**Bronzed Cowbird**	BB-73 James	Mexico: Puebla	whole	JX516067	–
Molothrus bonariensis	Shiny Cowbird	LSUMZ 113963	Peru: Lambayeque	12S, ND2, ND6	AF407090, AF407047, AF407133	–
		MACN-Or-ct 3062	Argentina: Buenos Aires	COX1	FJ027842	–
		FMNH 334768	Puerto Rico	Cyt b	AF089043	–

(*continued on next page*)

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Table 1 (*continued*)

Taxon	English name[a]	Voucher specimen or tissue[b]	Collecting locality	mtDNA sample description	GenBank numbers of mtDNA samples	GenBank numbers of nucDNA loci (ACO1-I9, FGB-I5, MB-I2, RAG1)
		none	Argentina: Buenos Aires	CR	DQ683553	–
Molothrus ater	**Brown-headed Cowbird**	FMNH 350707	USA: Chicago	–	–	KC007943, KC007668, KC007752, KC007859
		UMMZ none	USA: Michigan	12S, ND2–COX1, COX2–ATP6	AF447241, AF447291, AF447341	–
		BIOUG:SPP1681–70648	Canada: Ontario	COX1	DQ434680	–
		MBMC jk 96–016	USA: Minnesota	Cyt b	EF529951	–
Dives atroviolaceus	Cuban Blackbird	FMNH 375251	Cuba: Pinar del Río	Cyt b	KF810930	–
Dives dives	**Melodious Blackbird**	MBMC 7100	Honduras: Copán	whole	JX516061	KC007939, KC007664, KC007748, KC007855
Dives warczewiczi	**Scrub Blackbird**	LSUMZ 113959	Peru: Lambayeque	ND2, Cyt b	AF109962, AF089021	KF811000, KF810962, KF810981, KF810947
Agelaius phoeniceus	**Red-winged Blackbird**	BB-96 Tordoff	USA: Minnesota	whole	JX516062	–
		FMNH 341893	USA: Louisiana	–	–	KC007930, KC007654, KC007738, KC007845
Agelaius assimilis	Red-shouldered Blackbird	MNHNCu	Cuba	Cyt b	AF089004	–
Agelaius tricolor	**Tricolored Blackbird**	LSUMZ 130833	USA: California	ND2, Cyt b	AF109949, AF08911	KF811001, KF810963, KF810982, KF810948
		USNM 632199	USA: California	COX1	JQ173923	–
Agelaius humeralis	Tawny-shouldered Blackbird	none	Cuba	ND2, Cyt b	AF109947, AF089006	–
Agelaius xanthomus	**Yellow-shouldered Blackbird**	BB-SML 86–1	Puerto Rico	ND2, Cyt b	AF109948, AF089012	KF811002, KF810964, KF810983, KF810949
Euphagus carolinus	**Rusty Blackbird**	FMNH 333317	USA: Illinois	ND2, Cyt b	AF109950, AF089023	KF811003, KF810965, KF810984, KF810950
		ROM 1B-3617	Canada: Ontario	COX1	AY666525	–
Euphagus cyanocephalus	**Brewer's Blackbird**	FMNH 342000	USA: California	whole	JX516072	–
		FMNH 341985	USA: California	–	–	KC007941, KC007666, KC007750, KC007857
Quiscalus quiscula	**Common Grackle**	FMNH 341733	USA: Illinois	whole	JX516064	KC007940, KC007665, KC007749, KC007856
Quiscalus lugubris lugubris	Carib Grackle	FMNH 339797	Venezuela: Falcón	ND2, Cyt b	AF109952, AF089054	–
		USNM 627469	Guyana: Mahaica-Berbice	COX1	JQ176090	–
Quiscalus lugubris contrusus	Carib Grackle	USNM 612608	St. Vincent	ND2, COX1, Cyt b	FJ389553, JQ176089, FJ389562	–
		STRI SV-QLU2125	St. Vincent	ATP8–ATP6	AF132427	–
Quiscalus mexicanus E[c]	Great-tailed Grackle	MBMC JMD1014	USA: Texas	ND2, Cyt b	FJ389555, FJ389564	–
		UWBM 52154	Mexico: Chiapas	COX1	DQ434032	–
Quiscalus mexicanus W[c]	**Great-tailed Grackle**	FMNH 341975	USA: California	ND2, Cyt b	AF109954, AF089056	KF811004, KF810966, KF810985, KF810951
Quiscalus major	Boat-tailed Grackle	FMNH 341918	USA: Louisiana	ND2, Cyt b	AF109953, AF089055	–
		USNM 626311	USA: Florida	COX1	DQ433156	–
Quiscalus palustris	Slender-billed Grackle	USNM 194170	Mexico: Estado de México	Cyt b	FJ389557	–
Quiscalus nicaraguensis	**Nicaraguan Grackle**	MBMC 4375	Nicaragua: Tipitapa	ND2, Cyt b	FJ389549, FJ389558	KF811005, KF810967, KF810986, KF810952
Quiscalus niger	Greater Antillean Grackle	FMNH 331153	Jamaica: Trelawny	ND2, Cyt b	AF109955, AF089057	–
Sturnella militaris	Red-breasted Blackbird	FMNH 339777	Venezuela: Falcón	ND2, Cyt b	KF810937, KF810931	–
		USNM 625917	Guyana	COX1	JQ176296	–
Sturnella superciliaris	**White-browed Blackbird**	FMNH 334657	Bolivia: Santa Cruz	Cyt b	AF089038	KC007846, FJ154707, KC007655, KC007739
		LSUMZ B9630	Bolivia: Pando	12S, ND2–COX1, COX2–ATP6	AF447239, AF447289, AF447339	–
		USNM 635873	Uruguay: Atigas	COX1	JQ176299	–
		NRM 947221	Paraguay	ND3	JN715497	–
Sturnella bellicosa	Peruvian Meadowlark	ANSP 178118	Ecuador: Bolívar	ND2, Cyt b	FJ154660, AF089062	FJ154708, –, –, –
Sturnella defilippii	Pampas Meadowlark	AMNH 816591	Argentina: Buenos Aires	Cyt b	KF810932	–
Sturnella loyca	Long-tailed Meadowlark	MACN-Or 68357	Argentina: Buenos Aires	ND2, Cyt b	KF810936, KF810933	–
		AMNH DOT-13514	Argentina: Río Negro	COX1, CR	FJ028336, JN417869	–, JN417982, –, –
Sturnella magna	Eastern Meadowlark	FMNH 339780	Venezuela: Falcón	Cyt b	AF089063	FJ154709, –, –, –

		UMMZ 227823	USA: Louisiana	12S, ND2–COX1, COX2–ATP6	AF447257, AF447307, AF447357	–
		ROM SMM 88–1	Canada: Ontario	COX1	AY666282	–
Sturnella lilianae	Lilian's Meadowlark	FMNH 393903	Mexico: Sonora	ND2, Cyt b	FJ154691, FJ154636	FJ154725, –, –, –
		ROM JCB5473	USA: Texas	COX1	AY666267	–
Sturnella neglecta	**Western Meadowlark**	FMNH 341967	USA: California	ND2, Cyt b	FJ154698, FJ154651	–
		ROM 1B-1038	Canada: Ontario	COX1	EU525529	–
		FMNH 330040	USA: California	–	–	KC007931, KC007656, KC007740, KC007847
Xanthocephalus xanthocephalus	**Yellow-headed Blackbird**	LSUMZ 126564	USA: California	ND2, COX1, COX1–COX3, Cyt b	KC007584, KF810935, KF810922, AF089067	KC007927, KC007651, KC007735, KC007842
Dolichonyx oryzivorus	**Bobolink**	FMNH 334721	Bolivia: Santa Cruz	–	–	FJ154706, KC007669, KC007753, KC007860
		UMMZ 234583	USA: Michigan	12S, ND2–COX1, COX2–ATP6, Cyt b	AF447226, AF447276, AF447326, AF447367	–
		BIOUG: LMA 8101–91770	Canada: Ontario	COX1	DQ434587	–
Outgroups:						
Icteria virens	**Yellow-breasted Chat**	UWBM CDS4131 (STRI USIVI 4131)	USA: Washington	ND2–ATP6, Cyt b	GU932138, AF383028	GU931924, GU932031, GU932352, KC007812
		LSUMZ B3892	USA: Louisiana	12S	AF447236	–
Seiurus aurocapilla	**Ovenbird**	STRI-PRSAU1	Puerto Rico: Patillas	ND2–ATP6, Cyt b	GU932043, GU932365	GU931829, GU931936, GU932257, KC007800
		UMMZ 224992	USA: Michigan	12S	AF447254	–
Oreothlypis gutturalis	**Flame-throated Warbler**	LSUMZ B26458	Panama: Chiriquí	ND2–ATP6, Cyt b	GU932041, GU932363	GU931827, GU931934, GU932255, KC007792
Teretistris fernandinae	**Yellow-headed Warbler**	ANSP-B5548 (STRI CUTFE 5548)	Cuba: Guantánamo	ND2–ATP6, Cyt b	GU932143, AF382999	GU931929, GU932036, GU932357, KC007804

[a] Following Gill and Donsker (2012) or Jaramillo and Burke (1999).

[b] Specimens with "BB" codes are unvouchered; all other codes are museum catalog numbers. Abbreviations: ANSP = Academy of Natural Sciences of Drexel University; AMNH = American Museum of Natural History; BIOUG = Biodiversity Institute of Ontario; BNT = Bahamas National Trust; CUMV = Cornell University Museum of Vertebrates; FMNH = Field Museum of Natural History; IAvH = Instituto Alexander von Humbolt; ICN = Instituto de Ciencias Naturales, Universidad Nacional de Colombia; INIREB = Instituto de Historia Natural, San Cristóbal de las Casas, Chiapas, Mexico; KUMNH = University of Kansas Natural History Museum; LACM = Natural History Museum of Los Angeles County; LGEMA = Universidade de Sao Paulo, Departamento de Botanica; LSUMZ = Louisiana State University Museum of Natural Science; MACN = Museo Argentino de Ciencias Naturales, Bernardino Rivadavia; MBMC = Marjorie Barrick Museum of Natural History; MNHNCu = Museo Nacional de Historia Natural Cuba; MMNH = James Ford Bell Museum of Natural History; MPEG = Museu Paraense Emílio Goeldi; MZFC = Museo de Zoología de la Facultad de Ciencias, Universidad Nacional Autónoma de México; NCSM = North Carolina State Museum of Natural Sciences; NRM = Swedish Museum of Natural History; ROM = Royal Ontario Museum; STRI = Smithsonian Tropical Research Institute; UAM = University of Alaska Museum; UMMZ = University of Michigan Museum of Zoology; USNM = Smithsonian Institution, National Museum of Natural History; UWBM = University of Washington, Burke Museum of Natural History and Culture.

[c] Eastern and western lineages of *Quiscalus mexicanus* are treated as separate taxa.

sequenced one protein-coding autosomal gene, two autosomal introns, and one sex-linked (Z chromosome) intron. Those loci were, respectively, recombination activating gene 1 (RAG1), myoglobin intron 2 (MB-I2), β-fibrinogen intron 5 (FGB-I5), and aconitase 1 intron 9 (ACO1-I9). We also sequenced MB-I2 and ACO1-I9 from four additional taxa (including *Clypicterus*) and added ACO1-I9 or FGB-I5 sequences of another four taxa that were available in GenBank (Table 1).

How comprehensively the mitochondrial genome was represented in our dataset varied considerably among taxa (Table 1). We obtained sequences of the cytochrome *b* gene (1143 bp) for all 118 taxa in our study except *Icterus jamacaii*, for which we only had COX1 sequence from GenBank. Cytochrome *b* was the only gene that we sequenced from nine rarely-collected or extinct species that were sampled using DNA from toe-pads of museum skins. For all other taxa, we also obtained ND2 gene sequences (1041 bp). Preliminary phylogenetic analyses indicated that within the South American endemic clade our initial mitochondrial and nuclear dataset was unable to resolve any but a few trivial relationships, so we turned to more extensive mitochondrial sampling as a source of additional signal. We utilized whole mitochondrial genome sequences (~16,775 bp) of 23 species (20 of them within our 46-taxon set; Table 1). For five other ingroup taxa in the 46-taxon set and for the four outgroups, we obtained sequences of a ~5000 bp fragment encompassing ND2, COX1, COX2, ATP8, ATP6, and several tRNA genes. Further, we filled in remaining missing sequence for each taxon to the extent possible using GenBank records, provided we could be confident of their taxonomic identities. Most additional mitochondrial sequences were from the COX1, ATP6, and 12S rRNA genes. Whenever possible, all nuclear and mitochondrial gene sequences were obtained from the same specimen; for 45 taxa, we assembled chimaeric sequences from two or more individuals (Table 1).

2.2. Laboratory procedures and sequence preparation

Genomic DNA was extracted from frozen tissue and toe-pad samples as described in Powell et al. (2008) or with conventional phenol/chloroform methods (e.g. as in Lanyon, 1994). To avoid contamination, we processed toe-pad specimens in a lab not otherwise used for extraction or amplification of avian DNA. Target DNA fragments were amplified via the polymerase chain reaction (PCR). See the following references for details of primers and cycling parameters: cytochrome *b* and ND2 (Barker et al., 2008; Powell et al., 2008); whole mitogenomes and large fragments (Powell et al., 2013); RAG1 (Barker et al., 2002); and MB-I2, FGB-I5, and ACO1-I9 (Barker et al., 2008, 2013). Purification of PCR products, sequencing, sequence editing, and alignment were as described in Powell et al. (2013) except that some products were sent to Beckman Coulter Genomics (Danvers, MA) for sequencing.

2.3. Data partitioning and phylogeny inference

To probe for misleading effects of character and taxon sampling on phylogeny inference, we assembled the following datasets for analysis and comparison: (1) concatenated (to analyze with standard phylogenetic inference) and (2) unconcatenated (to analyze with species tree methods) nuclear sequences of the 46 taxa for which all four loci were sampled; (3) concatenated nuclear sequences of the 54 taxa with any nuclear data; (4) cytochrome *b*, (5) combined ND2 and cytochrome *b*, and (6) full mitochondrial alignments of the 46-taxon and (7–9) 117 or 118-taxon sets. Based on results from those datasets, we assembled the following datasets for our final analyses: (10) concatenated and (11) unconcatenated combined nuclear and full mitochondrial alignments of the 46-taxon sample; and (12) concatenated combined nuclear and full mitochondrial alignments of all 118 taxa. To maximize sequence coverage for *Molothrus* in the 46-taxon analyses of combined nuclear and mitochondrial loci, we utilized a chimaeric sequence composed of the mitogenome of *M. aeneus* with the nuclear sequences of *M. ater*.

All datasets were partitioned for analysis. Partitioning was accomplished by finely dividing each dataset according to *a priori* categories (such as gene and codon position), then using PartitionFinder 1.0.1 (Lanfear et al., 2012)—set to assess all models with the greedy algorithm under the Bayesian information criterion (BIC; Schwarz, 1978)—to find an optimal scheme for grouping subsets according to similarities in evolutionary tendencies. The most complicated datasets were the full-length mitochondrial alignments. As described in Powell et al. (2013), alignment positions of those datasets were sorted into 48 initial subsets according to all possible combinations of the following categories: noncoding/coding, heavy/light template strand, protein/RNA-coding, gene identity (done for rRNA and protein-coding genes only), codon position, and paired/unpaired bases in RNA secondary structure. Initial subdivision of nuclear markers was limited to separation by locus and, for RAG1, codon position. On occasion, PartitionFinder returned an inappropriately complicated model that led to spurious parameter estimates for a data subset. To reassess those cases, or when we needed to identify best models for individual data blocks, we used the BIC in jModelTest 2 (Darriba et al., 2012). We used the χ^2 test of homogeneity of base frequencies across taxa, as implemented in PAUP* 4.0b10 (Swofford, 2002), and χ^2 goodness-of-fit tests of individual taxa compared to the among-taxon average (Gruber et al., 2007), to check for overall stationarity of base composition at variable alignment positions within data subsets.

For single-locus and concatenated-loci datasets, we inferred phylogenetic relationships under maximum likelihood (ML) using GARLI 2.0 (Zwickl, 2006) and with Bayesian methods using MrBayes-3.2.1 (Ronquist et al., 2012). We also used Bayesian methods as implemented in *BEAST 1.7.4 (Drummond et al., 2012) to infer species trees from our unconcatenated multilocus 46-taxon datasets. Most GARLI analyses were run on the CIPRES Science Gateway (Miller et al., 2010), where we conducted heuristic searches for ML trees using 50 random starting points (i.e. searchreps) and evaluated nodal support with 500 bootstrap replicates, each with a single random starting point. Analyses with MrBayes used Metropolis coupling (four chains with default heating) and generally ran for 6–12 million generations, sampling every 100 generations, with a burn-in of 10–25%. We found that default settings in MrBayes yielded unrealistically long tree-length estimates in partitioned analyses, so following Marshall (2010), we set a shorter prior on mean branch length (brlenspr = unconstrained:exp (100.0)). Analyses using *BEAST ran for 200 million generations, sampling every 10,000 generations, with a burn-in of 10%. For all partitions or loci in those analyses, we used a lognormal relaxed clock model of evolutionary rate, with an exponential prior (mean = 0.1). All mitochondrial partitions in *BEAST analyses were linked under the same tree model. We used Tracer 1.5 (Rambaut and Drummond, 2009) and the AWTY server (Wilgenbusch et al., 2004) to check that effective sample sizes for parameter estimation in Bayesian analyses were adequate (i.e. >200) and that estimates of nodal posterior probability had converged.

Because sampling completeness varied substantially among taxa, we examined the results of the various datasets to assess their sensitivity to completeness of marker and taxon sampling, as well as congruence between inferences from nuclear loci and the mitochondrial genome. We looked for significant differences between analyses in their support for hypotheses of relationship, especially instances of strong conflict in pairwise comparisons (i.e. cases in which each of two incongruent hypotheses of relationship were supported by ⩾70% of bootstrap replicates or ⩾95% of

posterior samples at incompatible nodes). To further investigate conflict and congruence among the five independent loci used in this study, we inferred the phylogeny of the 46-taxon set separately for each locus under ML with 500 bootstrap replicates, then compared the bipartitions inferred from each locus to those inferred from each of the other loci at 70% and 90% thresholds of bootstrap support. For each pairwise comparison of loci, we tallied instances of strongly supported nodal conflict and congruence, and examined the extent to which the bipartitions inferred from each locus matched the nodes of the single best 46-taxon topology inferred from all loci combined.

3. Results

3.1. Partitions, substitution models, and base composition

Optimal partitioning was achieved using relatively few data groups. As in Powell et al. (2013), we found that the most salient categories for mitogenomic partitioning were codon position, RNA secondary structure pairing, and the coding/noncoding distinction (Table 2). The best scheme for cytochrome *b*, for both 46 and 117-taxon analyses, was by codon position. The ND2 plus cytochrome *b* datasets were partitioned by codon position and by gene for 3rd positions. Nuclear markers sorted separately from mitochondrial data groups. Even though codon position was a significant variable within RAG1, the best schemes for the concatenated datasets utilized only four nuclear data groups (Table 2) because some loci were so similar that they grouped together.

Base composition of variable sites in the nuclear data subsets did not differ significantly among taxa. The mitochondrial genome varies regionally (Powell et al., 2013), so testing that locus for stationarity was complicated by differences in the extent of sampling across species. No significant deviations were apparent within portions of the alignment with good taxonomic representation and nearly complete coverage for all sampled taxa (e.g. cytochrome b, ND2, COX1). As discussed in Powell et al. (2013), the composition of the mitochondrial genome of *Dives dives* differed significantly from the average of the 23 taxa for which we sequenced whole mitogenomes, but that difference appeared inconsequential for phylogeny inference because compositional similarity was not correlated with tree topology.

3.2. Phylogenies

Analyses of the datasets that we assembled using GARLI, MrBayes, and *BEAST, yielded a set of >20 summary phylogenetic trees. The primary purpose of most analyses was to investigate sensitivity of results to sampling and inference methods; consequently, most trees are not shown, but comparisons among them are described below and in Appendix S1. For a given dataset, different optimality criteria yielded trees without strongly-supported topological differences and with few differences in assignments of strong nodal support (see Section 3.7). For simplicity, we refer mainly to results from ML analyses in Sections 3.3-3.6. A representative set of trees, including those we consider to be our best estimates of phylogeny, are as follows: 118-taxon analyses of the full mitochondrial dataset (Fig. 1); 46-taxon analyses of the nuclear dataset (Fig. 2); 46-taxon analyses of the combined mitochondrial and nuclear datasets (Fig. 3); and the 118-taxon analyses of the combined mitochondrial and nuclear datasets (Fig. 4).

3.3. Effects of taxon sampling on phylogeny inference

Taxon addition can sometimes bolster phylogeny inference (Wiens, 2005; Wiens and Tiu, 2012), but in this study, after prun-

Table 2
Characteristics of data subsets used in molecular phylogenetic analyses of New World blackbirds (Icteridae). Parameter values are those estimated for the partitioned maximum likelihood analysis of the 118-taxon dataset using the full mitochondrial alignment and four nuclear loci.

Data subset	Positions	Number of positions			Model[a]	Parameter values
		Total	Variable	Parsimony informative		(r_{AG}, r_{AT}, r_{CG}, r_{CT}, r_{GT}), (π_A, π_C, π_G, π_T), α, p_{Inv}
mtDNA 1	Codon 1st positions of ATP6, COX2, Cyt *b*, ND1–6	2958	716	507	TVM + I + G[b]	(0.54, 10.67, 0.70, 0.15, 10.67, 1), (0.30, 0.33, 0.18, 0.18), 0.671, 0.620
mtDNA 2	Codon 2nd positions (all mitochondrial)	3620	251	138	TrN + I + G[b]	(4.11, 73.33, 1, 4.11, 17.64, 1), (0.19, 0.29, 0.12, 0.40), 0.535, 0.870
mtDNA 3	Codon 3rd positions of all except ND1–2	3121	2601	2034	GTR + I + G	(0.22, 14.47, 0.58, 0.22, 9.89, 1), (0.43, 0.42, 0.04, 0.10), 1.991, 0.030
mtDNA 4	Codon 3rd positions of ND1–2	672	624	554	TrN + G[c]	(1, 43.93, 1, 1, 27.45, 1), (0.41, 0.37, 0.07, 0.15), 3.408, NA
mtDNA 5	RNA paired positions; codon 1st positions of COX1 and COX3	2880	270	160	K81 + I + G[b]	(1, 22.91, 0.23, 0.23, 22.91, 1), (0.25, 0.25, 0.25, 0.25), 0.627, 0.830
mtDNA 6	RNA unpaired positions; codon 2nd positions of ND6	2160	384	241	TIM + I + G[b]	(1, 8.35, 0.58, 0.58, 12.13, 1), (0.44, 0.23, 0.12, 0.21), 0.557, 0.667
mtDNA 7	Noncoding positions; codon 1st positions of ATP8	1290	390	267	HKY + I + G	(1, 6.11, 1, 1, 6.11, 1), (0.31, 0.30, 0.11, 0.28), 0.607, 0.533
nucDNA 1	ACO1-I9, FGB-I5	1673	425	147	HKY + G	(1, 3.76, 1, 1, 3.76, 1), (0.29, 0.17, 0.21, 0.33), 1.043, NA
nucDNA 2	MB-I2, codon 3rd positions of RAG1	1671	295	112	TrNef + I + G[d]	(1, 5.79, 1, 1, 9.20, 1), (0.25, 0.25, 0.25, 0.25), 0.977, 0.522
nucDNA 3	Codon 1st positions of RAG1	961	57	17	HKY + I	(1, 3.61, 1, 1, 3.61, 1), (0.32, 0.20, 0.30, 0.17), NA, 0.892
nucDNA 4	Codon 2nd positions of RAG1	961	35	14	HKY + I	(1, 8.20, 1, 1, 8.20, 1), (0.36, 0.19, 0.18, 0.27), NA, 0.925

[a] Abbreviations as used in PartitionFinder 1.0.1 (Lanfear et al., 2012).
[b] GTR + I + G model implemented in MrBayes.
[c] GTR + G model implemented in MrBayes.
[d] HKY + I + G model implemented in MrBayes.

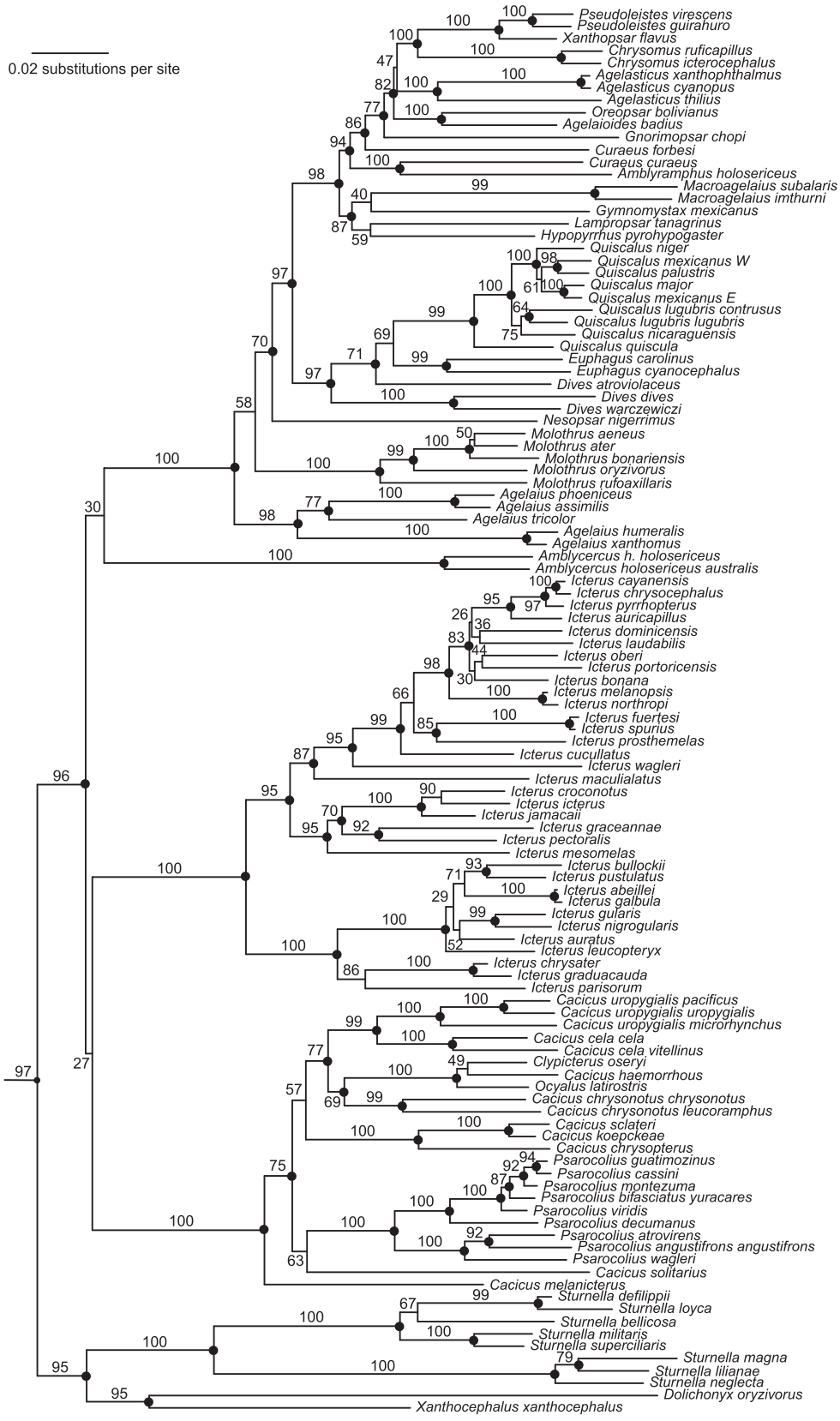

Fig. 1. Phylogeny of the New World blackbirds (Icteridae) inferred from mitochondrial DNA sequences of 118 taxa (outgroups not shown). The topology shown here is the single best tree ($-\ln L = 112464.25$) found under maximum likelihood (ML). Nonparametric bootstrap percentages from ML analysis appear immediately above or below branches. Filled circles indicate nodes with estimated posterior probabilities of $\geqslant 0.95$ in Bayesian analyses of the same concatenated dataset.

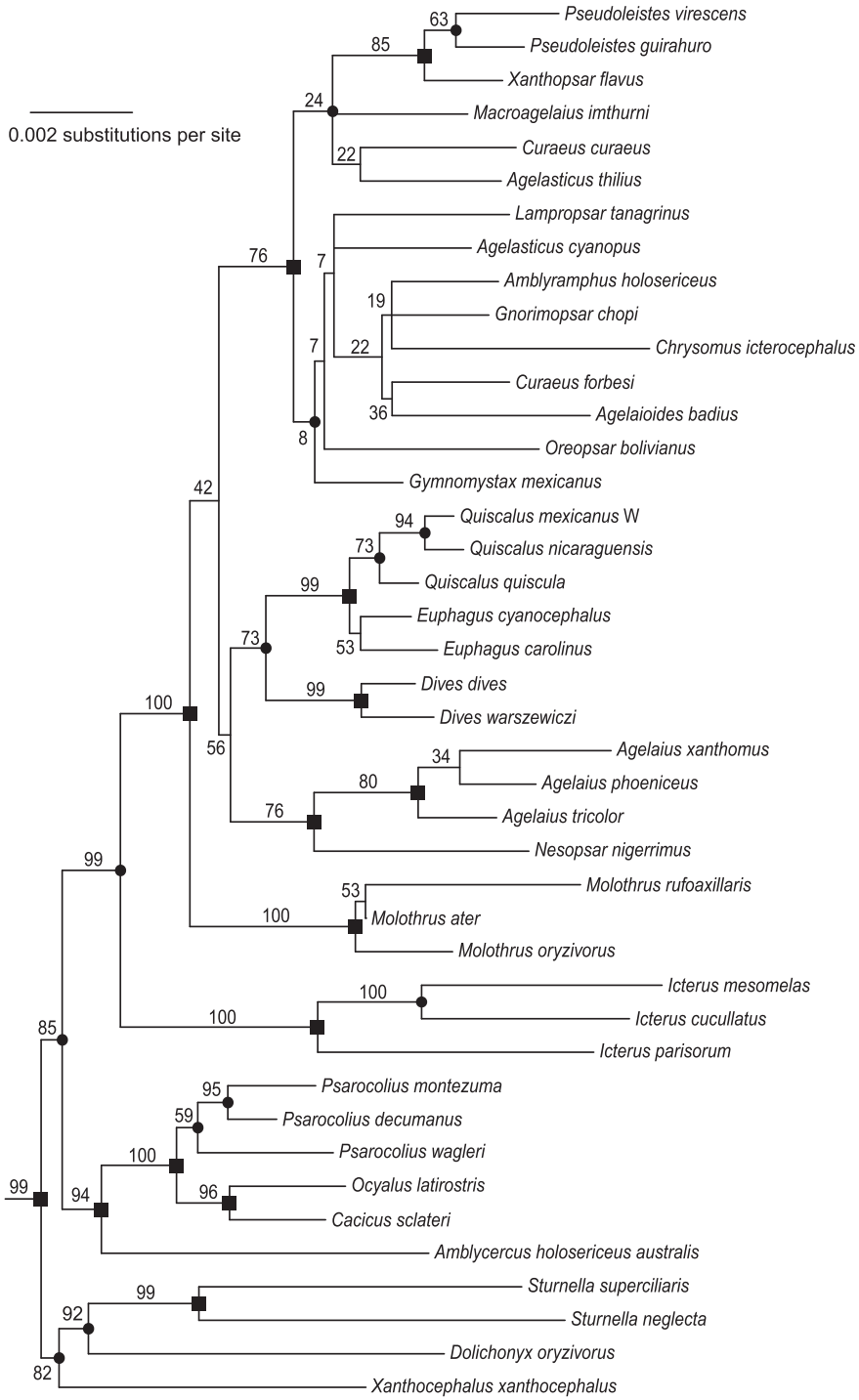

Fig. 2. Phylogeny of the New World blackbirds (Icteridae) inferred from nuclear DNA sequences of 46 taxa (outgroups not shown). The topology shown here is the single best tree ($-\ln L = 14620.36$) found under maximum likelihood (ML). Nonparametric bootstrap percentages from ML analysis appear immediately above or below branches. Filled circles indicate nodes with estimated posterior probabilities of $\geqslant 0.95$ in Bayesian analyses of the concatenated dataset, and filled squares indicate nodes that also received posterior probability estimates of $\geqslant 0.95$ in species-tree analyses.

ing trees to include only the taxa in the less comprehensive analyses, we found little effect on the pattern or number of strongly-supported nodes. By those measures, ML reconstructions from the 46 (Fig. 2) and 54-taxon concatenated nuclear-only datasets were identical, as were results from the 46 and 118-taxon datasets of combined nuclear and mitochondrial sequences (Figs. 3 and 4). Only the trees generated exclusively from mitochondrial data exhibited any differences in topology or assignments of strong support (see Appendix S1), but no discrepancy was an instance of strongly-supported conflict.

The phylogenetic position inferred for *Nesopsar*, and confidence for its placement, depended on data sampling and analytical method. We were concerned that its unstable placement (e.g. sister to *Agelaius* versus sister to all grackles and allies exclusive of *Molothrus* and *Agelaius*) might disproportionately shape reconstruction of basal divergences in the grackles and allies clade. To test for such

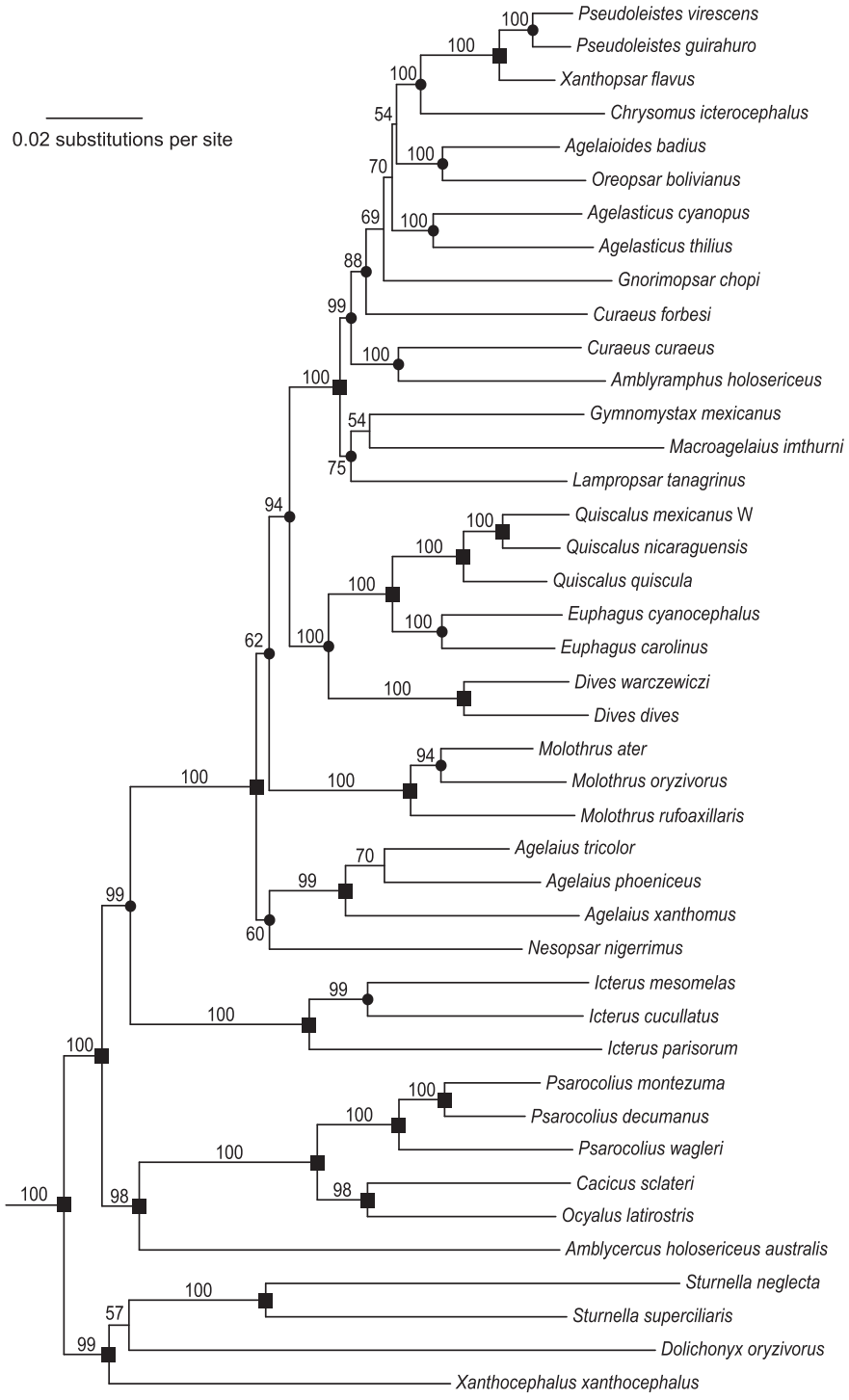

Fig. 3. Phylogeny of the New World blackbirds (Icteridae) inferred from mitochondrial and nuclear DNA sequences of 46 taxa (outgroups not shown). The topology shown here is the single best tree ($-\ln L = 105577.92$) found under maximum likelihood (ML). Nonparametric bootstrap percentages from ML analysis appear immediately above or below branches. Filled circles indicate nodes with estimated posterior probabilities of $\geqslant 0.95$ in Bayesian analyses of the concatenated dataset, and filled squares indicate nodes that also received posterior probability estimates of $\geqslant 0.95$ in species-tree analyses.

effects, we analyzed the 118-taxon combined full mitochondrial and nuclear dataset after excluding *Nesopsar* and found the resulting tree topology unchanged apart from its absence. However, ML bootstrap support for the monophyly of all grackles and allies exclusive of *Agelaius* increased to 73% from 52%, and support for monophyly of the remaining grackles and allies exclusive of *Agelaius* and *Molothrus* increased to 99% from 95%.

3.4. Effects of mitochondrial locus sampling on phylogeny inference

We found that adding sequence, even when unevenly sampled across taxa, led to addition of strongly-supported nodes, and not to switches in patterns of strongly-supported relationships. For example, in the 117 or 118-taxon analyses, the full mitochondrial dataset yielded a ML tree (Fig. 1) with strong support for 93 of

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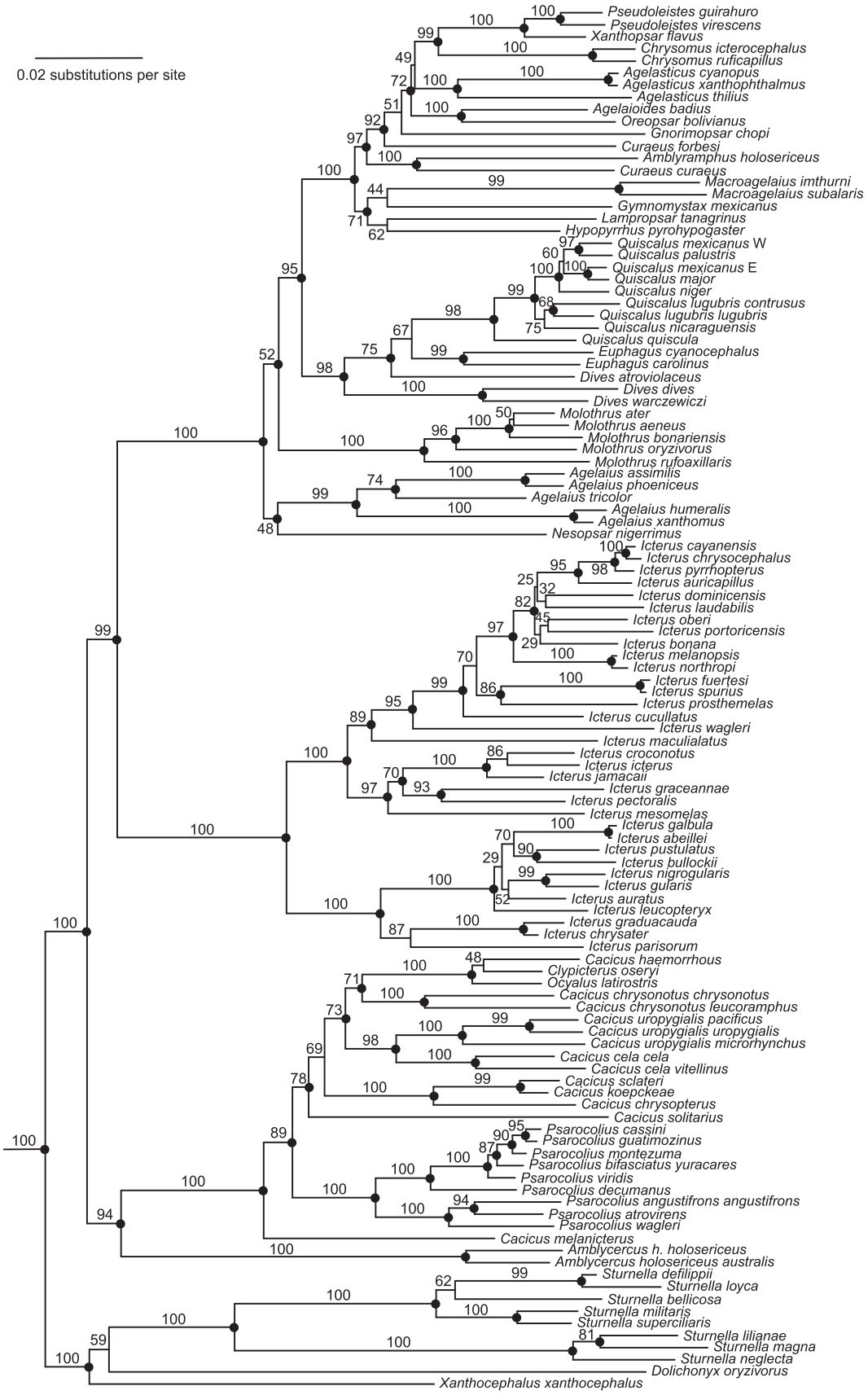

Fig. 4. Phylogeny of the New World blackbirds (Icteridae) inferred from mitochondrial and nuclear DNA sequences of 118 taxa (outgroups not shown). The topology shown here is the single best tree ($-\ln L = 127652.47$) found under maximum likelihood (ML). Nonparametric bootstrap percentages from ML analysis appear immediately above or below branches. Filled circles indicate nodes with estimated posterior probabilities of $\geqslant 0.95$ in Bayesian analyses of the same concatenated dataset.

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115 nodes, including all 53 and all but one of 78 strongly-supported nodes recovered with cytochrome *b* and the ND2 plus cytochrome *b* datasets, respectively. Support for the position of *Nesopsar* differed by dataset. The ND2 plus cytochrome *b* dataset found strong (76% bootstrap) support for the monophyly of all grackles and allies exclusive of *Nesopsar*, whereas the full dataset supported (70% bootstrap) grouping *Nesopsar* with *Dives*, *Euphagus*, *Quiscalus*, and the South American endemics. For further details of effects of mitochondrial locus sampling, see Appendix S1.

3.5. Congruence of inferences from nuclear loci and mtDNA

Our analyses of congruence among individual loci (Table 3) revealed no conflict of the mitochondrial locus with nuclear markers except FGB-I5, which conflicted with other loci at several bipartitions despite its modest resolving power. The nuclear markers with the highest resolving power, ACO1-I9 and RAG1, were incongruent at only 1 bipartition. Combined support for nodes of the tree inferred from the 46-taxon full mitochondrial and nuclear dataset was sometimes higher than might be expected given low or contradictory support from individual loci (Fig. S1). No node with strong combined support lacked support from at least one locus, and none exhibited strong conflict with mtDNA, but four nodes received strong combined support without strong support from mtDNA and despite, in two cases, strong conflict between nuclear markers. Five clades with strong combined nuclear support did not receive strong support from any single nuclear locus (see Appendix S1 for more details).

Phylogenies generated from separate 46-taxon mitochondrial (not shown) and concatenated nuclear datasets (Fig. 2) showed strong support for a majority of relationships but yielded somewhat different topologies. However, with one exception, differences occurred at nodes that were poorly supported by at least one of those two datasets. According to mitochondrial data, *Xanthocephalus* and *Dolichonyx* are sister taxa (97% bootstrap support) that compose a clade sister to *Sturnella*. By contrast, phylogenies inferred from nuclear data placed *Xanthocephalus* sister to a strongly supported (92% bootstrap) *Dolichonyx-Sturnella* clade.

Placements of the eight taxa with partial data in our 54-taxon nuclear phylogenies (not shown) were congruent with the tree from the 118-taxon full mitochondrial alignment (Fig. 1). The nuclear data recovered the following relationships: *Sturnella bellicosa* and *S. loyca* with *S. superciliaris*, thus supporting monophyly of the red-breasted meadowlarks (83% bootstrap, 100% posterior probability); *Sturnella lilianae* and *S. magna* together (73, 98), and that pair sister to *S. neglecta* (99, 100), thus supporting monophyly of the yellow-breasted meadowlarks; *Cacicus solitarius* and *Clypicterus* into a poorly-resolved grouping with *Ocyalus* and *Cacicus sclateri* (90, 100); *Cacicus melanicterus* outside a well-supported (76, 99) clade containing *Psarocolius, Ocyalus, Clypicterus,* and all other *Cacicus;* and *Agelasticus xanthopthalmus* with *A. cyanopus* (99, 100).

3.6. Inferences from separate and combined nuclear and mtDNA datasets

In our study, mitochondrial data proved superior for resolving short internodes and relationships among closely-related species, whereas nuclear data were somewhat better at resolving basal relationships. A striking feature of the 46-taxon ML analysis of combined nuclear loci (Fig. 2) was its nearly complete failure to resolve robustly relationships within the South American endemic clade—only one node out of 13 received strong support. By contrast, ML analysis of the mitochondrial dataset, which included full mitogenomic sequences of most species in that clade, recovered 11 well-supported nodes. With respect to the rest of the tree, built from less comprehensive sampling of the locus, the mitochondrial dataset performed no better than the nuclear dataset—both datasets resolved 24 of 30 nodes with confidence.

To the extent that their strengths were complementary, the nuclear and mitochondrial datasets had potential for fusion of their best qualities (Wiens, 2005, 2006). However, the datasets had some limitations in common and they did exhibit some conflict (see Section 3.5). Consequently, the 46-taxon ML phylogeny built from the combined data (Fig. 3) had 37 strongly-supported nodes out of 43, a net gain of only two more than the tree from the mitochondrial dataset. Similarly, the ML analysis of the combined datasets for all 118 taxa (Fig. 4) contained 96 well-supported nodes—three more than the mitochondrial tree (Fig. 1). The combined dataset trees were very similar to the mitochondrial trees. They had strong support at some nodes robustly recovered by nuclear loci, including the sister relationship of *Amblycercus* to all other caciques and oropendolas, the sister relationship of *Icterus* to the grackles and allies, and in the case of the 118-taxon tree, robust placement of *Cacicus solitarius* as sister to the other caciques (excepting *C. melanicterus* and *Amblycercus*). On the other hand, the combined dataset trees exhibited lower confidence for some nodes within the South American blackbirds, and placements of *Xanthocephalus* and *Nesopsar* were as robustly recovered with nuclear loci but with poor support due to conflict with the mitochondrial signal.

We compared the 46-taxon species-tree from nuclear loci to the species-tree from the combined dataset and found no significant

Table 3
Congruence among DNA sequences with respect to inferring the phylogeny of New World blackbirds (Icteridae) using a 46-taxon dataset. For each pairwise comparison of loci, the number of conflicting (bold text, above diagonal) and concordant (below diagonal) bipartitions in the trees inferred from them under maximum-likelihood (ML) are shown at two levels of bootstrap support (90% and 70%). Each of those quantities is also shown (in parentheses) scaled as a percentage of the bipartitions retained in a semistrict (combinable component) consensus of the trees being compared. In addition, for each locus, the total number of bipartition conflicts with other loci, the number of bipartitions resolved at a given support level, and the ratio of those values, are given. Note that the total number of conflicts for a given locus can exceed the number of nodes it resolves because a given bipartition can conflict with multiple loci and multiple bipartitions inferred from each locus.

Support level	Locus	Locus					No. conflicting bipartitions	No. resolved bipartitions	Ratio conflict/resolution
		mtDNA	ACO1-I9	FGB-I5	MB-I2	RAG1			
90% ML	mtDNA	–	**0** (**0**)	**1** (**3.2**)	**0** (**0**)	**0** (**0**)	1	30	0.03
	ACO1-I9	5 (16.1)	–	**0** (**0**)	**0** (**0**)	**0** (**0**)	0	6	0
	FGB-I5	3 (9.7)	2 (25.0)	–	**0** (**0**)	**1** (**8.3**)	2	4	0.50
	MB-I2	2 (6.5)	3 (50.0)	2 (40.0)	–	**0** (**0**)	0	3	0
	RAG1	8 (25.0)	2 (14.3)	2 (16.7)	2 (18.2)	–	1	10	0.10
70% ML	mtDNA	–	**0** (**0**)	**4** (**10.0**)	**0** (**0**)	**0** (**0**)	4	35	0.11
	ACO1-I9	14 (35.9)	–	**5** (**20.0**)	**1** (**4.5**)	**1** (**4.5**)	7	18	0.39
	FGB-I5	6 (15.0)	4 (16.0)	–	**0** (**0**)	**2** (**10.0**)	11	11	1.00
	MB-I2	6 (16.2)	4 (18.2)	4 (26.7)	–	**1** (**6.3**)	2	8	0.25
	RAG1	10 (27.0)	8 (36.4)	3 (15.0)	4 (25.0)	–	4	12	0.33

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incongruence. Placement of *Nesopsar* as sister to *Agelaius* got strong (98% posterior) support using nuclear sequences, but not with the combined dataset (87% posterior); the other 14 strongly-supported nodes in the former analyses were recovered in the latter, which found robust support for 21 of 43 nodes.

3.7. Concordance of results from analyses based on different optimality criteria

We found no strongly-supported topological differences between trees inferred from a given dataset using different optimality criteria. Furthermore, analyses using GARLI and MrBayes almost always agreed in assigning support to nodes according to the thresholds that we selected for comparing bootstrap values to posterior probability ($\geqslant$70% and $\geqslant$95%, respectively). However, in a very few cases, assessments were sharply discordant. For example,apart from uniting *Xanthopsar* with *Pseudoleistes*, relationships within the South American clade received extremely poor support in ML analyses of the 46-taxon nuclear locus dataset, but the same topology was recovered by MrBayes with strong support at four additional nodes (Fig. 2).

Using the 118-taxon combined dataset, we found that the topologies of the single best tree from GARLI and the consensus tree from MrBayes were identical, even at poorly supported nodes, with one exception—the Bayesian tree found *Curaeus forbesi* sister to *Gnorimopsar* with poor (58% posterior) support, whereas in ML, those lineages were sequentially nested branches in relationship to other taxa (Fig. 4). Assessments of strong support agreed at all but 6 of 115 nodes (Fig. 4). To test whether strong Bayesian support for the monophyly of all other grackles and allies exclusive of a well-supported *Nesopsar-Agelaius* clade was peculiar to MrBayes, we used BEAST to analyze the same concatenated dataset and got the same result. For further details of effects of optimality criteria, see Appendix S1.

4. Discussion

We present the first comprehensive species-level phylogeny of Icteridae. By using mitochondrial gene sequences from all currently recognized taxa, together with strategic sampling of four nuclear loci and whole mitochondrial genomes, we were able to resolve most relationships with high confidence. Our best estimate of phylogeny (Fig. 4) exhibits a topology that is consistent with the strongly supported results of past studies, but that also contains many new and robustly resolved inferences of relationship. These novel hypotheses of relationship include some unexpected placements of taxa that had not been included in previous molecular phylogenies, resolution of the relationships among major clades within Icteridae, and resolution of genus-level relationships within the grackles and allies.

4.1. Congruence of results from different analyses

Although it is possible that inferences made with our most inclusive dataset were biased by uneven coverage of sequence sampling across taxa, previous studies have found phylogenetic analyses robust to missing data when they include an adequate number of shared informative characters (Wiens, 2005; Wiens and Moen, 2008; Wiens and Morrill, 2011). We can state with confidence that heterogeneous addition of data did not undermine recovery of relationships that received robust support with smaller datasets having uniform coverage. The congruent results of our analyses demonstrate that most findings were robust to variation in mitochondrial sampling, taxon sampling, and use of signal derived from either the mitochondrial or nuclear genomes. In general, nuclear loci were less successful than mitochondrial loci for inferring relationships at the tips of the tree, but they provided stability to relationships throughout the tree and corroborated many results of previous studies based on mitochondrial data alone.

4.2. Icteridae and its major subclades

Although the composition of Icteridae has rarely been questioned, until recently, robust support for its monophyly (Barker et al., 2013) and basal relationships within it has been lacking. Lanyon and Omland (1999), using mitochondrial cytochrome *b* sequences, found support for five major clades within Icteridae, but not for their interrelationships or for icterid monophyly. Klicka et al. (2007), using ND2 plus cytochrome *b*, found strong support for Icteridae excluding meadowlarks and allies, but not for the family as a whole, for monophyly of the meadowlarks and allies, or for basal relationships. Using our expanded mitochondrial dataset, we recovered Icteridae and the meadowlarks and allies with strong support, but we were unable to resolve robustly relationships among the other four major clades.

Nuclear loci allowed us to reconstruct basal relationships within Icteridae with high confidence, and they resolved homoplasy in the mitochondrial signal such that support values were even higher using the combined dataset. We found a graded pattern of relationship among major clades, with the meadowlarks and allies sister to the rest of Icteridae (as in previous studies). Within the latter, the caciques and oropendolas (including *Amblycercus*) were sister to a pairing of the orioles with the grackles and allies. This pattern does not match mitochondrial topologies, which grouped (with poor support) the orioles with the caciques and oropendolas, a position that concurred with traditional views (e.g. American Ornithologists' Union, 1983).

4.3. Meadowlarks and allies

Meadowlarks (*Sturnella*) generally inhabit open grasslands and are notable for their stocky build, long bill, relatively short tail, and red or yellow breast versus cryptically-streaked dorsal coloration. Prior to the present study, a thorough molecular treatment was lacking. Lanyon and Omland (1999) included six of 10 species in their study of Icteridae, and Barker et al. (2008) included six species in their treatment of the yellow-breasted meadowlarks, but the three red-breasted species served only as outgroups. We found that placements of the red-breasted species not included in previous studies fit traditional expectations: each is sister to the species with which it has sometimes been considered conspecific—*S. militaris* with *superciliaris*, and *loyca* with *defilippii*. Both our mitochondrial and nuclear datasets supported monophyly of red and yellow-breasted groups, which are genetically more divergent (~15%) than any other congeners within Icteridae. The meadowlarks were once divided between *Sturnella*, *Leistes*, and *Pezites*, until Short (1968) merged them for lack of substantial morphological and ecological divergence. Sibley and Monroe (1990) gave new life to *Leistes*, citing Parker and Remsen (1987), who argued for its continued recognition based on behaviors shared with *Agelaius phoeniceus* and not with *Sturnella*. When molecular studies later found *S. bellicosa* more closely related to *L. superciliaris* than to the yellow-breasted *Sturnella* species, *Leistes* was abandoned since it made *Sturnella* as then defined (i.e. inclusive of *Pezites*), paraphyletic. We found that all meadowlark genera are monophyletic as originally defined, though support for placement of *S. bellicosa* with *S. loyca* and *S. defilippii*, to constitute *Pezites*, was weak in most analyses.

One of the most surprising findings of the first molecular phylogenies of Icteridae (Lanyon, 1994; Lanyon and Omland, 1999) was that *Xanthocephalus* is not allied with *Agelaius*, as had been supposed from behavioral and ecological similarities, but rather

is most closely related to *Dolichonyx* and *Sturnella*. Our nuclear and mitochondrial datasets both supported that unexpected grouping, but in the pattern of divergences among those genera we encountered the only instance of conflict between strongly-supported nodes inferred from nuclear versus mitochondrial sequences. Nuclear data placed *Xanthocephalus* sister to a *Dolichonyx-Sturnella* clade, whereas mitochondrial data supported a sister relationship between *Xanthocephalus* and *Dolichonyx*. We obtained all four nuclear loci and a substantial amount of mitochondrial sequence from each of these taxa, so it seems that many more loci will be necessary to resolve these relationships with confidence. Although *Xanthocephalus* and *Dolichonyx* are more closely related to *Sturnella* than to other icterids, they are genetically and phenotypically divergent. *Dolichonyx* is unique among blackbirds for undergoing two complete molts per year and is unusual among New World passerines for being an interhemispheric migrant. *Xanthocephalus* and *Dolichonyx* are so different from one another that their morphologies and behaviors are not particularly suggestive of one resolution of relationships over another.

4.4. Caciques and oropendolas, including Amblycercus

The caciques and oropendolas (~23 spp.) are inhabitants of tropical forests, where their pendant nests and displays can make them conspicuous, especially in the case of colonial species. They span a wide range of sizes, from *Cacicus sclateri* (23 cm, 57 g) to *Psarocolius montezuma* (up to 53 cm, 560 g; Fraga, 2011). Perhaps because of small effective population sizes in polygynous species, phylogenetic studies of the group have yielded well-resolved and strongly-supported hypotheses of relationship, even when internodes are short (e.g. this study, Price and Lanyon, 2002a, 2002b). Our main concerns were to achieve complete taxon sampling and to use nuclear loci to test some of the surprising findings of previous studies. We also propose a number of taxonomic revisions, many of them long overdue given results of previous studies (i.e. Price and Lanyon, 2004a, 2004b).

Mitochondrial DNA, even with increased sample size, was not able to recover the cup-nesting cacique, *Amblycercus*, as sister to the typical caciques and oropendolas, but nuclear loci did so with very strong support, as did the combined dataset. Like mitochondrial data, the nuclear loci indicate that the genetic divergence of *Amblycercus* from the other caciques and oropendolas is substantial. Nuclear markers also supported the position of *Cacicus melanicterus* outside the rest of the typical caciques and oropendolas, and the combined dataset placed it sister to them with strong support; consequently, that taxon should be restored to *Cassiculus* (e.g. Fraga, 2011). The remaining caciques and oropendolas sort into two clades, one containing all species currently placed in *Psarocolius*, and the other comprising mostly *Cacicus* species.

Mitochondrial data placed *Cacicus solitarius* sister to *Psarocolius*, but with only weak support. By contrast, nuclear loci strongly supported a sister relationship of *Cacicus solitarius* to the other *Cacicus* spp., as did analysis of the combined dataset under ML (Bayesian analysis recovers the same topology with weak support). Consequently, our study found that *Cacicus solitarius* need not be reassigned to *Procacicus*, as proposed by Fraga (2005). A very surprising finding of previous studies was the close relationship between *Ocyalus* and *Clypicterus* (Freeman and Zink, 1995; Price and Lanyon, 2002a, 2004a) and the position of those taxa well outside of *Psarocolius*. Subsequent work (Price and Lanyon, 2004a), that even more surprisingly found those genera imbedded within *Cacicus*, has thus far been ignored in taxonomic revisions. We found strong nuclear (and combined) support for placement of *Ocyalus* and *Clypicterus* in the *Cacicus* clade; consequently, those species should be reassigned to that genus. Elsewhere within *Cacicus*, we recovered the same pattern of relationships found by Price and Lanyon (2004a), except that we included *C. koepckeae*, which we recovered as sister to *C. sclateri* as anticipated (Cardiff and Remsen, 1994). Following Price and Lanyon (2004a), we included deeply divergent subspecies of *Amblycercus* and several *Cacicus* spp., which should probably be recognized as species. Some authorities (e.g. Jaramillo and Burke, 1999; Fraga, 2011; Gill and Donsker, 2012) recognize *Cacicus* (*uropygialis*) *microrhynchus* as a species and treat *C. u. pacificus* as a subspecies of *C. microrhynchus*, when in fact, mitochondrial DNA indicates that *pacificus* is more closely related to *C. u. uropygialis*.

Within *Psarocolius*, we recovered the same pattern of relationships found by Price and Lanyon (2002a, 2002b, 2004a) but added two species missing from previous studies.[1] We found that the newly sampled taxa, *P. cassini* and *P. guatimozinus*, are sister to one another, that *P. montezuma* is sister to that pair, and that those three taxa are sister to *P.* (*bifasciatus*) *yuracares*, all of which were placed in the formerly-recognized *Gymnostinops*. The sister relationship between *Gymnostinops* and *P. viridis* was a surprise when first discovered (Price and Lanyon, 2004b), although song characteristics supported the alliance (Price and Lanyon, 2002b). Indeed, that result has yet to be embraced by taxonomic authorities (e.g. Gill and Donsker, 2012; Remsen et al., 2012), who still list *P. viridis* between the much more distantly related *P. atrovirens* and *P. decumanus*. Divergences among all these taxa are very shallow, but all nodes were strongly supported. For the sake of clarity, we chose not to include multiple representatives of *P. decumanus* and *P. angustifrons*, even though both species contain divergent lineages (Price and Lanyon, 2002a, 2002b, 2004a). Both complexes require further investigation and taxonomic revision. Some authorities have treated *P. angustifrons alfredi* as a species (e.g. Sibley and Monroe, 1990), yet mitochondrial DNA indicates that *P. angustifrons atrocastaneus* is even more divergent from *P. a. angustifrons* than is *P. angustifrons alfredi*.

4.5. Orioles

The orioles, a group of small arboreal or shrub-dwelling icterids, many with distinctive orange and black plumage patterns, represent the second-largest of the major clades within Icteridae, yet all ~33 species are classified in one genus, *Icterus*. The orioles have been the subject of intensive systematic study (Omland et al., 1999; Lovette et al., 2001; Allen and Omland, 2003; Sturge et al., 2009; Jacobsen et al., 2010; Jacobsen and Omland, 2011), including very thorough sampling at the subspecies level, and use of both mitochondrial DNA and nuclear introns. These studies have generally found high concordance between signals and resolved very short internodes (Jacobsen et al., 2010), but have also uncovered instances of conflict between nuclear and mitochondrial markers that are unlikely to be outcomes of incomplete lineage sorting (Jacobsen and Omland, 2011). It seems that introgression among the ancestors of a few species, some of which are presently involved in different hybridization interactions, has complicated the histories of their genomes.

Nuclear sampling in our study was limited to one representative from each of the three major clades within *Icterus*; consequently, we did not have much opportunity to, nor did we, encounter cases of conflict between nuclear and mitochondrial signals. Although our mitochondrial sampling was more extensive than in previous studies, the pattern of relationships we recovered was equivalent to, and no better resolved than, results of those studies from which the data was largely derived (e.g. Omland et al., 1999). We included *I. jamacaii*, the only oriole missing from previous phylogenies, as a COX1 sequence from GenBank (Table 1),

[1] Note that *P. b. bifasciatus* was ostensibly treated in Powell (2012) but is not included here because the tissue sample was later found, based on voucher examination, to be *P. viridis*.

in hope of resolving its position among troupials, a group of orioles unusual for their large size, white irides, and blue-colored bare skin around the eyes. A closer relationship of *I. icterus* to *I. croconotus* than to *I. jamacaii* received strong support under ML, but not using Bayesian methods. If accurate, this placement is contrary to treatment of *I. croconotus* as a subspecies of *I. jamacaii* in classifications that recognize only two species of troupial (e.g. Sibley and Monroe, 1990). Inclusion of samples of *I. cayanensis*, *I. chrysocephalus*, and *I. pyrrhopterus* in our study should not be interpreted as an endorsement of resolving species limits within that complex (D'Horta et al., 2008) to those taxa, but rather, was done to illustrate representative divergences within it using names that appear in current taxonomic lists and other references.

4.6. Grackles and allies

Grackles and allies compose the most taxonomically diverse of the major clades within Icteridae despite the superficial similarity of many species, especially those with all black plumage. Although ours was more successful than any previous study, a definitive resolution of genus-level relationships within the clade remains elusive, as neither whole mitochondrial genomes nor the nuclear loci we sampled provided consistently robust support for all nodes. Studies based on ND2 plus cytochrome *b* (e.g. Johnson and Lanyon, 1999; Eaton, 2006) found *Nesopsar* and *Dives* to be sequentially sister to all other grackles and allies, whereas in this study whole mitochondrial genomes placed *Nesopsar* in a poorly-resolved basal position relative to *Agelaius*, *Molothrus*, and a strongly-supported *Dives-Euphagus-Quiscalus* plus South American endemics clade. Although the finding of a sister relationship between the South American clade and *Dives-Euphagus-Quiscalus* also received strong support in combination with nuclear loci, it was dependent on the signal from whole mitogenomes, and thus was novel to this study. Nuclear loci (together) supported the *Dives-Euphagus-Quiscalus* clade and a sister relationship between *Nesopsar* and *Agelaius*, but the latter relationship conflicted with placement of *Nesopsar* sister to the *Dives-Euphagus-Quiscalus* plus South American endemics clade, as found with the 118-taxon full mitochondrial dataset. As a consequence of those antagonistic signals, the *Nesopsar-Agelaius* pairing received inconsistent (48% ML bootstrap, 99% Bayesian posterior probability) support in the combined dataset analysis, as did monophyly of the remaining grackles and allies (52%, 99%), thus yielding an imperfectly robust resolution of basal relationships in the grackles and allies, the topology of which (Fig. 4) is altogether unique to this study. Note that recovering that topology was not dependent on placement of *Nesopsar*; in fact, when it was excluded from the dataset, ML support for the monophyly of all grackles and allies exclusive of *Agelaius* increased to 73% (from 52%). We cannot explain the apparently differing signals contained in the nuclear and mitochondrial genomes of *Nesopsar*, but we have ruled out effects of overall base composition (Powell et al., 2013) or accelerated rates of replacement substitutions in the mitochondrial genome.

Another goal of our study was to resolve robustly relationships among the assemblage of species of the South American clade, which is exceptional for its variety of plumage patterning, morphology, habitat preferences, and reports of cooperative breeding in many species (Fraga, 2008). The diversity of the group is reflected in its taxonomy—with 13 genera, eight of them monotypic, its 19 species account for nearly half of all genera in Icteridae. We sequenced nuclear loci from most species, but analyses of those sequences resolved only four nodes with strong support. Two of those inferences were almost certainly erroneous because of the following: they received strong support only with Bayesian analysis of the concatenated dataset; they were not found, even with weak support, in trees recovered with mitochondrial data, combined nuclear and mitochondrial data, or any species-tree analyses; and they strongly contradicted a number of strongly-supported relationships found in other analyses. The noise and misleading signal from nuclear loci was substantial enough to nullify the signal from ND2 plus cytochrome *b* sequences, yielding a tree with a unique topology and only two strongly supported nodes within the clade (Barker et al., 2013). By contrast, trees inferred from ND2 plus cytochrome *b* alone (Johnson and Lanyon, 1999; Cadena et al., 2004; Eaton, 2006) had better support and were topologically similar to our best inferences. We found that whole mitochondrial genomes were able to resolve robustly most nodes in the group, even in combination with the nuclear dataset (though its inclusion weakened support values). The only case of strongly supported agreement between those markers was the sister relationship between *Xanthopsar* and *Pseudoleistes*.

Apart from stronger support for many nodes (especially with mitochondrial data; Fig. 1), the novel findings of this study with respect to the South American clade include recovery of a *Macroagelaius-Gymnomystax-Lampropsar-Hypopyrrhus* clade and inclusion of two species that were absent from previous molecular studies. As expected, *Macroagelaius subalaris* was recovered as sister to *M. imthurni*. By contrast, *Curaeus forbesi* did not group with *C. curaeus* in any analyses, but rather defined its own long branch in a grade between a strongly supported *C. curaeus-Amblyramphus* clade and *Gnorimopsar*. Morphologically, *C. curaeus*, *C. forbesi*, and *Gnorimopsar* are similar—for example, they all have distinctively lanceolate feathers, with robust and very shiny rachides, on and near the head (but note that distantly-related *Hypopyrrhus* also has these traits)—and *forbesi* has been mistaken for *Gnorimopsar*, both in the field (Mazzoni et al., 2012) and in collections (Short and Parkes, 1979). In a few analyses, we recovered *C. forbesi* as sister to *Gnorimopsar* with very weak support, but mitochondrial data provided strong support for the graded set of relationships described above. The taxon clearly does not belong in *Curaeus*, so unless a wholesale taxonomic revision of the South American clade is undertaken to lump most of the group into a single genus, it seems that naming *C. forbesi* to a new monotypic genus is in order; we propose renaming it as *Anumara forbesi* (see Appendix A).

Elsewhere within the South American endemic clade, our results concur with past studies and so taxonomic revisions made in the past decade remain appropriate, including assigning several former *Agelaius* species to *Agelasticus* and *Chrysomus* (Lowther et al., 2004). Taxonomies currently differ in the naming of *Oreopsar*, either as *Oreopsar badius* or, following Lowther (2001), as *Agelaioides oreopsar*, a usage that recognizes the sister relationship between that taxon and *A. badius*. That case, and the South American clade in general, presents a challenge for taxonomists who dislike placing species with distinctly different characteristics (judged according to a subjective threshold) within the same genus, but who also wish to avoid naming monotypic genera. Results of molecular phylogenetic studies have not led to reappraisals of phenotypic similarity among the South American endemic species, so unless a different standard is adopted to measure the utility of generic naming, the taxonomy of the clade does seem an appropriate reflection of its diversity.

Another case in which taxonomic revision is in order is *Dives atroviolaceus*, which we found sister to *Quiscalus-Euphagus*, not to other *Dives*. Although exact placement of *D. atroviolaceus* relative to *Euphagus* and *Quiscalus* was somewhat unstable, its closer relationship to one or both of those taxa than to *Dives* received strong support. Consequently, *D. atroviolaceus* should be restored to its former monotypic genus, *Ptiloxena*. Fraga (2011) adopted this scheme based on behavioral characteristics and following the suggestion of Webster (2003), who measured skeletal divergences among species. Ironically (because it is in some ways opposite to our finding despite leading to the same nomenclatural change),

Webster (2003) argued for the distinctiveness of *D. atroviolaceus*, and thus its renaming, based on its morphological divergence from *Quiscalus*, and he suggested that the revised *Dives* and *Quiscalus* were morphologically similar enough that they might be merged. *Quiscalus* warrants additional phylogeographic study and revision of species limits because several species contain deeply divergent lineages (see Powell et al., 2008).

5. Uncited reference

Q4 Yang (2007).

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Appendix A

Anumara (new genus); Type species: *Agelaeus forbesi* P.L. Sclater; Included taxa: monotypic; Etymology: this masculine name is a formalization of the local Brazilian name, anumará, for the type species (van Perlo, 2009; reported as arumará, per W.A. Forbes, by Short and Parkes (1979)); Diagnosis: The genus is diagnosed by characters of the type species, *forbesi* (see Sclater, 1886; Short and Parkes, 1979). An icterid (Family Icteridae) with all-blackish plumage, smaller than similar *Curaeus curaeus* and somewhat smaller than *Gnorimopsar chopi* but like them in appearance with respect to having lanceolate feathers, with robust and very shiny rachides, on and around the head and neck region. Bill about as long as head, with straight culmen, flattened on top (especially above the nostrils). Mouth lining red (Jaramillo and Burke, 1999). Wing short and rounded; primary projection 5–8 mm (Short and Parkes, 1979). Tail graduated; outer retrices shorter than central retrices by 12–18 mm (Short and Parkes, 1979). Song consists of two unmusical buzzes (Jaramillo and Burke, 1999).

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2013.11.009.

References

Allen, E.S., Omland, K.E., 2003. Novel intron phylogeny supports plumage convergence in orioles (Icterus). Auk 120, 961–969.
Alström, P., Olsson, U., Lei, F., Wang, H., Gao, W., Sundberg, P., 2008. Phylogeny and classification of the Old World Emberizinae (Aves, Passeriformes). Mol. Phylogenet. Evol. 47, 960–973.
American Ornithologists' Union, 1983. Check-list of North American Birds, sixth ed. American Ornithologists' Union, Washington, DC.
Barker, F.K., Barrowclough, G.F., Groth, J.G., 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. Proc. R. Soc. Lond. B. Biol. Sci. 269, 295–308.
Barker, F.K., Burns, K.J., Klicka, J., Lanyon, S.M., Lovette, I.J., 2013. Going to extremes: contrasting rates of diversification in a recent radiation of New World passerine birds. Syst. Biol. 62, 298–320.
Barker, F.K., Vandergon, A.J., Lanyon, S.M., 2008. Assessment of species limits among yellow-breasted meadowlarks (*Sturnella* spp.) using mitochondrial and sex-linked markers. Auk 125, 869–879.
Beecher, W.J., 1950. Convergent evolution in the American orioles. Wilson Bull. 62, 51–86.
Beecher, W.J., 1951. Adaptations for food-getting in the American blackbirds. Auk 68, 411–440.
Blake, E.R., 1968. Family Icteridae: American Orioles and Blackbirds. In: Paynter, R.A., Jr. (Ed.), Check-list of Birds of the World: a Continuation of the Work of James L. Peters. Museum of Comparative Zoology, Cambridge, Massachusetts, pp. 138–202.
Björklund, M., 1991. Evolution, phylogeny, sexual dimorphism and mating system in the grackles (*Quiscalus* spp.: Icterinae). Evolution 45, 608–621.
Burns, K.J., 1997. Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of Neotropical birds. Mol. Phylogenet. Evol. 8, 334–348.
Burns, K.J., Hackett, S.J., Klein, N.K., 2002. Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. Evolution 56, 1240–1252.
Burns, K.J., Hackett, S.J., Klein, N.K., 2003. Phylogenetic relationships of Neotropical honeycreepers and the evolution of feeding morphology. J. Avian Biol. 34, 360–370.
Cadena, C.D., Cuervo, A.M., Lanyon, S.M., 2004. Phylogenetic relationships of the Red-bellied Grackle (Icteridae: *Hypopyrrhus pyrohypogaster*) inferred from mitochondrial DNA sequence data. Condor 106, 664–670.
Cardiff, S.W., Remsen Jr., J.V., 1994. Type specimens of birds in the Museum of Natural Sciences, Louisiana State University. Occas. Pap. Mus. Nat. Sci. 68, 1–33.
Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. JModelTest 2: more models, new heuristics and parallel computing. Nat. Methods 9, 772.
Dugand, A., Eisenmann, E., 1983. Rediscovery of, and new data on, *Molothrus armenti* Cabanis. Auk 100, 991–992.
D'Horta, F.M., Cardosa da Silva, J.M., Ribas, C.C., 2008. Species limits and hybridization zones in *Icterus cayanensis–chrysocephalus* group (Aves: Icteridae). Biol. J. Linnean Soc. 95, 583–597.
Dickinson, E.C. (Ed.), 2003. The Howard and Moore Complete Checklist of the Birds of the World. Princeton University Press, Princeton, New Jersey.
Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973.
Dufort, M.J., Barker, F.K., 2013. Range dynamics, rather than convergent selection, explain the mosaic distribution of red-winged blackbird phenotypes. Ecol. Evol. doi. http://dx.doi.org/10.1002/ece3.859.
Eaton, M.D., 2006. A phylogenetic perspective on the evolution of chromatic ultraviolet plumage coloration in grackles and allies (Icteridae). Auk 123, 211–234.
Eaton, M.D., Soberón, J., Peterson, A.T., 2008. Phylogenetic perspective on ecological niche evolution in American blackbirds (Family Icteridae). Biol. J. Linnean Soc. 94, 869–878.
Fraga, R.M., 2008. Phylogeny and behavioral evolution in the family Icteridae. Ornitol. Neotrop. 19, 61–71.
Fraga, R.M., 2011. Family Icteridae (New World blackbirds). In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World, Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, pp. 684–807.
Freeman, S., Zink, R.M., 1995. A phylogenetic study of the blackbirds based on variation in mitochondrial DNA restriction sites. Syst. Biol. 44, 409–420.
Friedman, N.R., Hofmann, C.M., Kondo, B., Omland, K.E., 2009. Correlated evolution of migration and sexual dichromatism in the New World Orioles (Icterus). Evolution 63, 3269–3274.
Friedman, N.R., Kiere, L.M., Omland, K.E., 2011. Convergent gains of red carotenoid-based coloration in the New World blackbirds. Auk 128, 678–687.
Gill, F., Donsker, D. (Eds.), 2012. IOC World Bird Names (version 3.2). <http://www.worldbirdnames.org> (accessed 08.12.12).
Gruber, K.F., Voss, R.S., Jansa, S.A., 2007. Base-compositional heterogeneity in the RAG1 locus among Didelphid marsupials: implications for phylogenetic inference and the evolution of GC content. Syst. Biol. 56, 83–96.
Hellmayr, C.E., 1937. Catalogue of Birds of the Americas and the Adjacent Islands. Part X. Icteridae. Field Museum of Natural History, Zoological Series 13.
Hofmann, C.M., Cronin, T.W., Omland, K.E., 2006. Using spectral data to reconstruct evolutionary changes in coloration: carotenoid color evolution in New World orioles. Evolution 60, 1680–1691.
Hofmann, C.M., Cronin, T.W., Omland, K.E., 2007. Melanin coloration in New World orioles II: ancestral state reconstruction reveals lability in the use of carotenoids and phaeomelanins. J. Avian Biol. 38, 172–181.
Hofmann, C.M., Cronin, T.W., Omland, K.E., 2008a. Evolution of sexual dichromatism. 1. Convergent losses of elaborate female coloration in New World orioles (Icterus spp). Auk 125, 778–789.

Hofmann, C.M., Cronin, T.W., Omland, K.E., 2008b. Evolution of sexual dichromatism. 2. Carotenoids and melanins contribute to sexual dichromatism in New World orioles (*Icterus* spp.). Auk 125, 790–795.
Irwin, R.E., 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness? Am. Nat. 144, 890–907.
Jacobsen, F., Friedman, N.R., Omland, K.E., 2010. Congruence between nuclear and mitochondrial DNA: Combination of multiple nuclear introns resolves a well-supported phylogeny of New World orioles (*Icterus*). Mol. Phylogenet. Evol. 56, 419–427.
Jacobsen, F., Omland, K.E., 2011. Species tree inference in a recent radiation of orioles (Genus *Icterus*): Multiple markers and methods reveal cytonuclear discordance in the northern oriole group. Mol. Phylogenet. Evol. 61, 460–469.
Jaramillo, A., Burke, P., 1999. New World Blackbirds: the Icterids. Princeton University Press, Princeton, NJ.
Johnson, K.P., Lanyon, S.M., 1999. Molecular systematics of the grackles and allies, and the effect of additional sequence (cytochrome *b* and ND2). Auk 116, 759–768.
Johnson, K.P., Lanyon, S.M., 2000. Evolutionary changes in color patches of blackbirds are associated with marsh nesting. Behav. Ecol. 11, 515–519.
Klein, N.K., Burns, K.J., Hackett, S.J., Griffiths, C.S., 2004. Molecular phylogenetic relationships among the wood warblers (Parulidae) and historical biogeography in the Caribbean Basin. J. Caribbean Ornithol. 17, 3–17.
Klicka, J., Johnson, K.P., Lanyon, S.M., 2000. New World nine-primaried oscine relationships: constructing a mitochondrial DNA framework. Auk 117, 321–336.
Klicka, J., Burns, K., Spellman, G.M., 2007. Defining a monophyletic Cardinalini: a molecular perspective. Mol. Phylogenet. Evol. 45, 1014–1032.
Kondo, B., Omland, K.E., 2007. Ancestral state reconstruction of migration: multistate analysis reveals rapid changes in New World orioles (*Icterus* spp.). Auk 124, 410–419.
Lanfear, R., Calcott, B., Ho, S.Y.W., Guindon, S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29, 1695–1701.
Lanyon, S.M., 1992. Interspecific brood parasitism in blackbirds (Icterinae): a phylogenetic perspective. Science 255, 77–79.
Lanyon, S.M., 1994. Polyphyly of the blackbird genus *Agelaius* and the importance of assumptions of monophyly in comparative studies. Evolution 48, 679–693.
Lanyon, S.M., Omland, K.E., 1999. A molecular phylogeny of the blackbirds (Icteridae): five lineages revealed by cytochrome-*b* sequence data. Auk 116, 629–639.
Lovette, I.J., Bermingham, E., 2002. What is a wood-warbler? Molecular characterization of a monophyletic parulidae. Auk 119, 695–714.
Lovette, I.J., Bermingham, E., Ricklefs, R.E., 2001. Mitochondrial DNA phylogeography and the conservation of endangered Lesser Antillean Icterus orioles. Conserv. Biol. 13, 1088–1096.
Lovette, I.J., Pérez-Emán, J.L., Sullivan, J.P., Banks, R.C., Fiorentino, I., Córdoba-Córdoba, S., Echeverry-Galvis, M., Barker, F.K., Burns, K.J., Klicka, J., Lanyon, S.M., Bermingham, E., 2010. A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). Mol. Phylogenet. Evol. 57, 753–770.
Lowther, P.E., 2001. New name for the Bolivian Blackbird. Bull. Brit. Ornithol. Club 121, 280–281.
Lowther, P.E., Fraga, R., Schulenberg, T.S., Lanyon, S.M., 2004. Nomenclatural solution for a polyphyletic *Agelaius*. Bull. Brit. Ornithol. Club 124, 171–175.
Marshall, D.C., 2010. Cryptic failure of partitioned Bayesian phylogenetic analyses: lost in the land of long trees. Syst. Biol. 59, 108–117.
Mazzoni, L.G., Esser, D., de Carvalho Dutra, E., Perillo, A., Morais, R., 2012. New records of the Forbes's Blackbird *Curaeus forbesi* (Sclater, 1886) in the state of Minas Gerais, with comments on its conservation. Rev. Brasil. Ornitol. 20, 44–47.
Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proc. Gateway Computing Environments Workshop (GCE 2010), 14 November 2010, New Orleans, Louisiana. Institute of Electrical and Electronics Engineers, pp. 1–8.
Omland, K.E., Lanyon, S.M., 2000. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal in patterns. Evolution 54, 2119–2133.
Omland, K.E., Lanyon, S.M., Fritz, S.J., 1999. A molecular phylogeny of the New World orioles (*Icterus*): the importance of dense taxon sampling. Mol. Phylogenet. Evol. 12, 224–239.
Orians, G.H., 1985. Blackbirds of the Americas. University of Washington Press, Seattle.
Parker III, T.A., Remsen Jr., J.V., 1987. Fifty-two Amazonian bird species new to Bolivia. Bull. Brit. Ornithol. Club 107, 94–107.
Powell, A.F.L.A., 2012. Molecular Phylogenetics of the New World Blackbirds (Icteridae). Ph.D. dissertation, University of Minnesota, Minneapolis and St. Paul.
Powell, A.F.L.A., Barker, F.K., Lanyon, S.M., 2008. A complete species-level phylogeny of the grackles (*Quiscalus* spp.), including the extinct Slender-billed Grackle, inferred from mitochondrial DNA. Condor 110, 718–728.
Powell, A.F.L.A., Barker, F.K., Lanyon, S.M., 2013. Empirical evaluation of partitioning schemes for phylogenetic analyses of mitogenomic data: an avian case study. Mol. Phylogenet. Evol. 66, 69–79.
Price, J.J., 2009. Evolution and life-history correlates of female song in the New World blackbirds. Behav. Ecol. 20, 967–977.
Price, J.J., Friedman, N.R., Omland, K.E., 2007. Song and plumage evolution in the New World Orioles (Icterus) show similar lability and convergence in patterns. Evolution 61, 850–863.
Price, J.J., Lanyon, S.M., 2002a. A robust phylogeny of the oropendolas: polyphyly revealed by mitochondrial sequence data. Auk 119, 335–348.
Price, J.J., Lanyon, S.M., 2002b. Reconstructing the evolution of complex bird song in the oropendolas. Evolution 56, 1514–1529.
Price, J.J., Lanyon, S.M., 2004a. Patterns of song evolution and sexual selection in the oropendolas and caciques. Behav. Ecol. 15, 485–497.
Price, J.J., Lanyon, S.M., 2004b. Song and molecular data identify congruent but novel affinities of the Green Oropendola (*Psarocolius viridis*). Auk 121, 224–229.
Price, J.J., Lanyon, S.M., Omland, K.E., 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. Proc. R. Soc. Lond. B. Biol. Sci. 276, 1971–1980.
Price, J.J., Whalen, L.M., 2009. Plumage evolution in the oropendolas and caciques: different divergence rates in polygynous and monogamous taxa. Evolution 63, 2985–2998.
Raikow, R.J., 1978. Appendicular myology and relationships of the New World nine-primaried oscines (Aves: Passeriformes). Bull. Carnegie Mus. Nat. Hist. 7, 1–43.
Rambaut, A., Drummond, A.J., 2009. Tracer v1.5. <http://tree.bio.ed.ac.uk/software/tracer>.
Remsen Jr., J.V., Cadena, C.D., Jaramillo, A., Nores, M., Pacheco, J.F., Pérez-Emán, J.F., Robbins, M.B., Stiles, F.G., Stotz, D.F., Zimmer, K.J., Version 7 December 2012. A Classification of the Bird Species of South America. American Ornithologists' Union. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.html>.
Ridgway, R., 1902. The birds of North and Middle America. Part II. Bull. U.S. National Mus, No. 50.
Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61, 539–542.
Schwarz, G., 1978. Estimating the dimension of a model. Ann. Stat. 6, 461–464.
Sclater, P.L., 1886. Catalogue of the Birds in the British Museum. Coerebidae, Tanagridae, and Icteridae, vol. 11. British Museum, London.
Searcy, W.A., Yasukawa, K., Lanyon, S.M., 1999. Evolution of polygyny in the ancestors of Red-Winged Blackbirds. Auk 116, 5–19.
Shawkey, M.D., Hauber, M.E., Estep, L.K., Hill, G.E., 2006. Evolutionary transitions and mechanisms of matte and iridescent plumage coloration in grackles and allies (Icteridae). J. R. Soc. Interface 3, 777–786.
Short Jr., L.L., 1968. Sympatry of red-breasted meadowlarks in Argentina, and the taxonomy of meadowlarks (Aves: *Leistes*, *Pezites*, and *Sturnella*). Am. Mus. Novitates 2349, 30.
Short, L.L., Parkes, K.C., 1979. The status of *Agelaius forbesi* Sclater. Auk 96, 179–183.
Sibley, C.G., Monroe Jr., B.L., 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, CT.
Sturge, R.J., Jacobsen, F., Rosensteel, B.B., Neale, R.J., Omland, K.E., 2009. Colonization of South America from Caribbean islands confirmed by molecular phylogeny with increased taxon sampling. Condor 111, 575–579.
Swofford, D.L., 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer, Sunderland, Massachusetts.
Thomson, R.C., Shaffer, H.B., 2010. Sparse supermatrices for phylogenetic inference: taxonomy, alignment, rogue taxa, and the phylogeny of living turtles. Syst. Biol. 59, 42–58.
Tordoff, H.B., 1954. Relationships in the New World nine-primaried oscines. Auk 71, 273–284.
van Perlo, B., 2009. A Field Guide to the Birds of Brazil. Oxford University Press, New York.
Webster, M.S., 1992. Sexual dimorphism, mating system and body size in New World Blackbirds. Evolution 46, 1621–1641.
Webster, J.D., 2003. Skeletal characters and the genera of blackbirds (Icteridae). Condor 105, 239–257.
Wiens, J.J., 2005. Can incomplete taxa rescue phylogenetic analyses from long-branch attraction? Syst. Biol. 54, 731–742.
Wiens, J.J., 2006. Missing data and the design of phylogenetic analyses. J. Biomed. Inform. 39, 34–42.
Wiens, J.J., Fetzner, J.W., Parkinson, C.L., Reeder, T.W., 2005. Hylid frog phylogeny and sampling strategies for speciose clades. Syst. Biol. 54, 719–748.
Wiens, J.J., Moen, D.S., 2008. Missing data and the accuracy of Bayesian phylogenetics. J. Syst. Evol. 46, 307–314.
Wiens, J.J., Morrill, M.C., 2011. Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. Syst. Biol. 60, 719–731.
Wiens, J.J., Tiu, J., 2012. Highly incomplete taxa can rescue phylogenetic analyses from the negative impacts of limited taxon sampling. PLoS ONE 7 (8), e42925.
Wilgenbusch, J.C., Warren, D.L., Swofford, D.L., 2004. AWTY: A System for Graphical Exploration of MCMC Convergence in Bayesian Phylogenetic Inference. <http://ceb.csit.fsu.edu/awty>.
Yang, Z., 2007. PAML 4: Phylogenetic analysis by maximum likelihood. Mol. Biol. Evol. 24, 1586–1591.
Yuri, T., Mindell, D.P., 2002. Molecular phylogenetic analysis of Fringillidae, "New World nine-primaried oscines" (Aves: Passeriformes). Mol. Phylogenet. Evol. 23, 229–243.
Zwickl, D.J., 2006. Genetic Algorithm Approaches for the Phylogenetic Analysis of Large Biological Sequence Datasets Under the Maximum Likelihood Criterion. Ph.D. dissertation, University of Texas at Austin.