SHORT COMMUNICATIONS

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PHYLOGENETIC RELATIONSHIPS OF THE RED-BELLIED GRACKLE (ICTERIDAE: *HYPOPYRRHUS PYROHYPOGASTER*) INFERRED FROM MITOCHONDRIAL DNA SEQUENCE DATA

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Abstract. The phylogenetic affinities of the Red-bellied Grackle (*Hypopyrrhus pyrohypogaster*), a Colombian endemic and the only member of this genus, are enigmatic. Based on phylogenetic analyses of sequences from the cytochrome *b* and ND2 mitochondrial genes, we present a first hypothesis on the systematic position of *Hypopyrrhus*. In so doing, we complete the sampling at the genus level for a published phylogeny of New World blackbirds (Johnson and Lanyon 1999). *Hypopyrrhus* belongs in a clade composed of mostly South American species within the grackles and allies assemblage, one of the five main lineages in the Icteridae. Within this lineage, *Hypopyrrhus* is consistently placed in a clade with *Gymnomystax mexicanus* and *Lampropsar tanagrinus*, but parsimony and maximum-likelihood reconstructions do not agree on which of these species is its sister taxon. Vocal and morphological data suggest that *Hypopyrrhus* and *Gymnomystax* are likely sister taxa. The addition of *Hypopyrrhus* does not cause major topological changes to Johnson and Lanyon's (1999) phylogeny of the grackles and allies; thus, the conclusions of evolutionary studies that used this phylogeny as a baseline remain largely unaltered.

Key words: Andes, Colombia, Gymnomystax mexicanus, Hypopyrrhus pyrohypogaster*, Icteridae,* Lampropsar tanagrinus*, molecular phylogeny.*

Relaciones Filogenéticas de *Hypopyrrhus pyrohypogaster* (Icteridae) Inferidas a Partir de Secuencias de ADN Mitocondrial

Resumen. Las afinidades filogenéticas de *Hypopyrrhus pyrohypogaster*, el único miembro de este género endémico de Colombia, son enigmáticas. En este estudio establecemos la posición sistemática de *Hypopyrrhus* con base en análisis filogenéticos de secuencias de los genes mitocondriales citocromo *b* y ND2. Además, completamos el muestreo a nivel genérico para una filogenia del grupo publicada por Johnson y Lanyon (1999). *Hypopyrrhus* pertenece a un clado compuesto principalmente por especies suramericanas dentro del grupo de los changos y chamones, uno de los cinco clados principales de los Icteridae. Dentro de este grupo, *Hypopyrrhus* se ubica consistentemente en un clado junto con *Gymnomystax mexicanus* y *Lampropsar tanagrinus*, pero las reconstrucciones de parsimonia y máxima verosimilitud se contradicen en cuanto a cuál de estas especies es su taxón hermano. Datos de vocalizaciones y morfología sugieren que *Hypopyrrhus* y *Gymnomystax* son probablemente géneros hermanos. La incorporación de *Hypopyrrhus* a la filogenia de Johnson y Lanyon (1989) no causó cambios topológicos importantes, por lo que las conclusiones de los estudios evolutivos que usaron esta filogenia como base no fueron alteradas.

The Red-bellied Grackle (*Hypopyrrhus pyrohypogaster*) is one of the most poorly known New World blackbirds (Jaramillo and Burke 1999). The species is endemic to the Colombian Andes, where it occurs locally in the northern sector of the Central and Western Cordilleras, and in the Eastern Cordillera from Department Caquetá south to the Ecuadoran border

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(Cuervo 2002). Until very recently, basic information on the behavior, habitat, diet, and vocalizations of *Hypopyrrhus* was not available (Jaramillo and Burke 1999, Cuervo 2002).

Although the understanding of the natural history of *H. pyrohypogaster* has increased substantially over recent years (Cuervo 2002), its phylogenetic affinities remain enigmatic. The species was originally described in the genus *Cassicus* (De Tarragon 1847), in which a wide variety of icterids including some oropendolas and caciques were initially grouped. Soon after, Bonaparte (1850) placed it in the monotypic genus *Hypopyrrhus* and although a few early authors listed it under *Quiscalus* (Sclater 1862, Cassin 1866), *Hypopyrrhus* was later generally accepted (e.g., Sclater and Salvin 1879). None of the studies of blackbird systematics or general revisions of the group (e.g., Beecher 1951, Jaramillo and Burke 1999) commented on the affinities of *Hypopyrrhus*, and aside from an unsupported statement of close relationship to the genus *Macroagelaius* (Ridgely and Tudor 1989), no hypotheses about its closest relative have been proposed. Likewise, the position of *Hypopyrrhus* in linear classifications (Sibley and Monroe 1990, Jaramillo and Burke 1999, Dickinson 2003) is variable, an indication of the uncertainty about its affinities. This uncertainty is likely the result of the morphological dissimilarity of *Hypopyrrhus* to other icterids and of the general lack of information about this taxon. There are very few museum specimens in existence and most of these are of limited scientific value; for example, the single skeletal specimen for the genus available in museum collections is unsexed and incomplete (Webster 2003). Moreover, the present whereabouts of the type specimen are unknown (Hellmayr 1937).

Hypopyrrhus is presumed to be a member of the grackles and allies assemblage, one of five main clades in the family Icteridae (Lanyon and Omland 1999). This monophyletic group comprises 42 species in 18 genera (Dickinson 2003) distributed through much of the New World. More than half of these genera are monotypic, which indicates a traditional lack of understanding of relationships within the group and the distinctiveness of many taxa. Based on mitochondrial DNA sequence data, Johnson and Lanyon (1999) developed a phylogeny for the grackles and allies that helped clarify relationships among genera and species and has served as a baseline for studies on the evolution of breeding behavior, nesting habitat, plumage characters, and traits presumed to be adaptations for brood parasitism (Searcy et al. 1999, Johnson and Lanyon 2000, Mermoz and Ornelas 2004). In their taxonomic sampling, Johnson and Lanyon (1999) included representatives of all the grackle genera except *Hypopyrrhus* because tissue samples of this taxon were lacking at the time of their study. Thus, the phylogeny of the grackles and allies is currently incomplete at the generic level, and the affinities of *Hypopyrrhus* to other genera remain uncertain.

Recently, we collected three Red-bellied Grackle specimens in the Central Cordillera of the Andes in the Department of Antioquia, Colombia. Based on mtDNA sequences obtained from tissue samples of this new material, here we present the first phylogenetic hypothesis on the affinities of *Hypopyrrhus*, completing the sampling at the generic level for the grackles and allies phylogeny.

METHODS

Specimens were collected at two localities in the Municipality of Amalfi (Dept. Antioquia) and deposited in the collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN). An unsexed juvenile (ICN 33976) and an adult female (ICN 33977) were taken at Finca Bodega Vieja, Río Riachón watershed, Vereda Salazar (6°58′N, 75°03′W; 1505 m), and an adult male (ICN 34534) at Bosque de Guayabito, Finca Hugo Roldán, Quebrada Caracolí watershed (6°51′N, 75°06′W; 1780 m). Tissue samples taken from the specimens were deposited in the collection of Instituto Alexander von Humboldt (catalog numbers IAvH-BT 2077, 2078, and 2261, respectively), together with blood samples drawn from each of 12 additional birds that were captured and released at the same study sites and at other locations in northern Antioquia.

In recent years, the mitochondrial genes cytochrome *b* (cyt *b*) and ND2 have been sequenced for the majority of blackbird species (Lanyon 1992, 1994, Johnson and Lanyon 1999, Lanyon and Omland 1999, Omland et al. 1999, Price and Lanyon 2002, 2004). By sequencing these same two genes for *Hypopyrrhus* we were able to capitalize on the preexisting database to establish its evolutionary affinities. We followed the laboratory protocols outlined in Johnson and Lanyon (1999) to sequence a total of 1941 base pairs of mtDNA (900 of cyt *b* and 1041 of ND2) for two of the new *Hypopyrrhus* specimens (ICN 33977 and ICN 34534). These sequences (GenBank accession numbers AY572450–AY572453) were aligned to blackbird sequences obtained from GenBank using Sequencher 3.1. First, to determine whether *Hypopyrrhus* fell clearly within one of the five major blackbird lineages identified by Lanyon and Omland (1999), we did a preliminary unweighted parsimony analysis using a dataset containing ND2 and cyt *b* sequence data for 80 blackbird taxa (see Appendix for species list and GenBank accession numbers). The results indicated that *Hypopyrrhus* in fact belongs within the grackles and allies clade, and specifically within group 1 of that assemblage as defined by Johnson and Lanyon (1999). This result was supported by 90% of bootstrap pseudoreplicate data sets. An additional parsimony analysis in which transversions were weighted 2 to 1 over transitions produced the same result with 93% bootstrap support.

Having confirmed that *Hypopyrrhus* belongs within group 1 of the grackles and allies clade, we restricted intensive phylogenetic analyses to this assemblage, considering the 16 species for which DNA sequence data were available (data are lacking only for *Curaeus forbesi* and *Macroagelaius subalaris*). The Rusty Blackbird (*Euphagus carolinus*), a member of group 2 of the grackles and allies clade (Johnson and Lanyon 1999), was used as an outgroup. We employed both parsimony and maximum-likelihood analyses in PAUP* (Swofford 2002) to ensure that our conclusions regarding the phylogenetic affinities of *Hypopyrrhus*

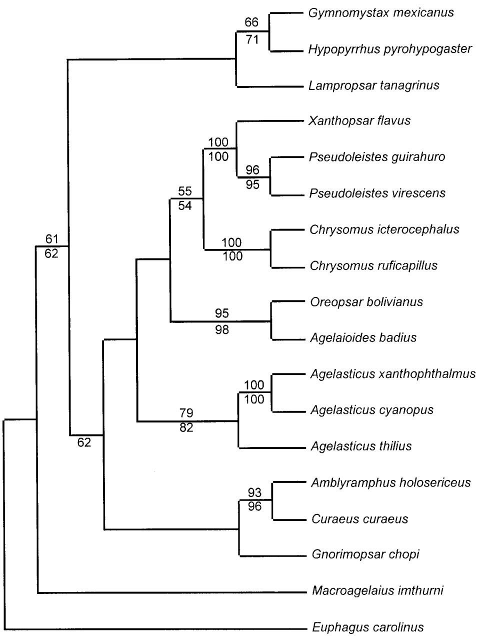

FIGURE 1. Phylogenetic relationships in group 1 of the grackles and allies. The single most parsimonious tree (length = 1316, rescaled consistency index = 0.224) obtained from analysis of 1981 equally weighted nucleotide sites of the cytochrome *b* and ND2 genes, indicates a sister taxon relationship between *Hypopyrrhus pyrohypogaster* and *Gymnomystax mexicanus*. Numbers above branches are bootstrap values for the equally weighted analysis; numbers below are bootstrap values for the analysis in which transversions were weighted 2:1 over transitions. Nomenclature follows Dickinson (2003) except as modified by Remsen et al. (2004) and Lowther et al. (in press).

were robust to the choice of analytical method. The cyt *b* and ND2 data were combined for all the analyses because the two genes did not differ significantly in phylogenetic signal as suggested by the incongruence length difference test (Farris et al. 1995). We conducted a parsimony analysis in which all nucleotide sites were weighted equally, and a weighted parsimony analysis in which transversions were twice as costly as transitions (Johnson and Lanyon 1999). For each analysis we used 100 random stepwise addition replicates to increase the probability of exploring multiple topological islands should they exist. Bootstrap analyses with 1000 replicates were performed to estimate level of nodal support (Felsenstein 1985). We used ModelTest 3.06 (Posada and Crandall 1998) to identify the most appropriate maximum-likelihood model for the data; of the 56 models tested, TVM + I + G (relative transformation rates A–C = 1.3315, A–G = 15.6905, A–T = 0.8854, C–G = 0.2967, C–T = 15.6905, G–T = 1.0; gamma distribution shape parameter = 1.8527) could not be rejected in favor of a more complex model and was used for the maximum-likelihood analysis.

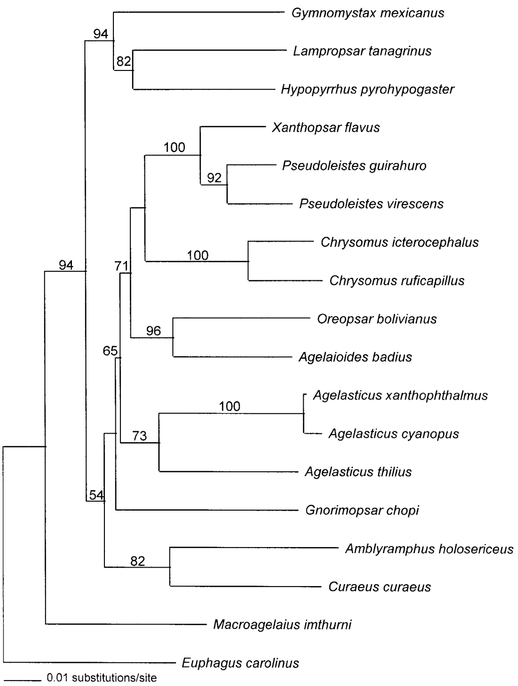

FIGURE 2. Phylogram showing relationships among species in group 1 of the grackles and allies assemblage, based on maximum-likelihood analysis of cytochrome *b* and ND2 sequences (-ln likelihood = 9335.029), indicating a sister taxon relationship between *Hypopyrrhus pyrohypogaster* and *Lampropsar tanagrinus*. Bootstrap values are shown on branches.

RESULTS

All the phylogenetic analyses resulted in majority-rule consensus trees containing a monophyletic group consisting of *Hypopyrrhus pyrohypogaster*, the Oriole Blackbird (*Gymnomystax mexicanus*), and the Velvet-fronted Grackle (*Lampropsar tanagrinus*). However, the various analytical approaches did not agree on relationships within this clade. The equal-weight parsimony analysis and the weighted parsimony analysis both identified *Gymnomystax* as the sister taxon to *Hypopyrrhus*; bootstrap support for this node in these two analyses was 66% and 71%, respectively (Fig. 1). In contrast, the maximum-likelihood analysis identified *Lampropsar* as the sister taxon to *Hypopyrrhus* with 82% bootstrap support (Fig. 2). Aside from this incongruence, a comparison of the trees resulting from the three analyses demonstrates no conflict among them in nodes with greater than 50% bootstrap support.

The two *Hypopyrrhus* individuals assayed had identical mtDNA haplotypes in both cyt *b* and ND2. In cyt *b*, they differed by 0.064 (uncorrected *p* distance) from *Gymnomystax* and by 0.062 from *Lampropsar*. In ND2, they differed by 0.081 and 0.080 from *Gymnomystax* and *Lampropsar*, respectively.

The addition of *Hypopyrrhus* to the grackles and allies dataset did not cause any changes to the nodes receiving greater than 50% bootstrap support in the phylogeny of Johnson and Lanyon (1999). Our trees are completely compatible with their results with the exception of the placement of the genus *Macroagelaius*. The Golden-tufted Grackle (*M. imthurni*) was identified as the sister taxon to *Gymnomystax* by Johnson and Lanyon (1999), but this hypothesis of relationship was not well supported by their data. In contrast, our analyses consistently showed *M. imthurni* in a basal position, sister to all other species in the grackles and allies assemblage (Fig. 1, 2).

DISCUSSION

SYSTEMATICS

Parsimony and maximum-likelihood analyses of cytochrome *b* and ND2 sequences suggest that the closest relatives of *Hypopyrrhus pyrohypogaster* are *Lampropsar tanagrinus* and *Gymnomystax mexicanus*, two South American species in monotypic genera restricted to the lowlands east of the Andes (Ridgely and Tudor 1989). In contrast, *Macroagelaius*, a genus that shares with *Hypopyrrhus* a montane distribution in northern South America and some behavioral traits such as gregariousness and cooperative breeding (Cadena et al. 2002, Cuervo 2002, Hilty 2003) appears not to be one of its closest relatives as Ridgely and Tudor (1989) had suggested. The close relationship of *Hypopyrrhus* to lowland taxa supports the idea of an upper Amazonian or East Andean origin for this taxon proposed by Chapman (1917) on the basis of its occurrence on the eastern slope of the Colombian Andes.

Based on an approximate evolutionary rate of 1.6–2.0% sequence divergence per million years for passerine cytochrome *b* (Fleischer et al. 1998, Lovette 2004), our data suggest that *Hypopyrrhus* last shared an ancestor with its closest relatives some 3–4 million years ago. While this estimate represents a wide range, we can certainly conclude that *Hypopyrrhus* is a relatively old taxon that has been isolated from its relatives for a substantial time span. Such a long period of independent evolution has allowed considerable morphological differentiation to proceed among *Hypopyrrhus*, *Gymnomystax*, and *Lampropsar*, which in addition to the lack of knowledge about *Hypopyrrhus* may explain why they had not been previously hypothesized to be close relatives.

The close relationship between *Hypopyrrhus*, *Gymnomystax*, and *Lampropsar* shown by the mtDNA data suggests that linear classifications should now place these three genera consecutively. In contrast, Webster (2003) recently proposed an alternative linear sequence based on skeletal characters that places *Hypopyrrhus* near the Giant Cowbird (*Molothrus oryzivorus*), and caciques (*Cacicus*) and oropendolas (*Psarocolius*). If linear classifications are to convey evolutionary relationships and not simply phenetic similarity, we argue that *Hypopyrrhus* should be placed near *Gymnomystax* and *Lampropsar*. The clade formed by these three genera is supported by several molecular synapomorphies, while we believe that most of the superficial morphological similarity between *Hypopyrrhus*, *Molothrus oryzivorus*, *Cacicus*, and *Psarocolius* noted by Webster (2003) is very likely the result of homoplasy.

Due to the conflicting results of the parsimony and maximum-likelihood analyses, the answer to the question of which genus is sister to *Hypopyrrhus* is unclear. However, the sequence data did reduce the possibilities to two taxa (*Lampropsar* or *Gymnomystax*), facilitating inferences of relationships based on other types of information such as morphology and vocalizations. *Hypopyrrhus* and *Gymnomystax* share several traits including their large body size (unrivaled by any other member of this icterid clade), their strong and long bills, the presence of carotenoid coloration in the underparts and of a bare patch of skin around the eye, and their loud and complex voices with whistled screech calls (Jaramillo and Burke 1999, A. Jaramillo, pers. comm.). In contrast, *Lamproposar* is a slim blackbird with a short and thin bill and completely black plumage without bare skin in the face, and its song is a relatively simple series of chucks ending in an ‘‘explosive and liquid *kuk-weeetew*’’ (Jaramillo and Burke 1999:322). Taken together, the similarities between *Hypopyrrhus* and *Gymnomystax*, which seem unlikely to be the result of convergence due to their very different ecologies, suggest that they may be more closely related to each other than they are to *Lampropsar*.

IMPLICATIONS FOR EVOLUTIONARY STUDIES

The molecular phylogeny of grackles and allies developed by Johnson and Lanyon (1999) has been used as a framework for evolutionary studies on breeding behavior, nesting habitat, plumage characters, and life-history traits in the group (Searcy et al. 1999, Johnson and Lanyon 2000, Mermoz and Ornelas 2004). What are the implications of our results for these studies on character evolution? As described above, the only change in the phylogeny caused by the addition of *Hypopyrrhus* to the dataset is the breakup of the clade formed by *Macroagelaius*, *Lampropsar*, and *Gymnomystax*, and the appearance of *Macroagelaius* as sister to the rest of the taxa in the grackles and allies assemblage. This reorganization would not lead to changes in the inferred evolutionary gains and losses of traits like marsh nesting, polygynous mating system, carotenoid pigmentation, presence of carotenoid epaulets, or various life-history characters possibly representing adaptations for brood parasitism; thus, the conclusions of the studies by Searcy et al. (1999), Johnson and Lanyon (2000), and Mermoz and Ornelas (2004) would remain largely unchanged. However, resolving the position of *Macroagelaius* in the grackles and allies tree would be important for future studies on the evolution of other behavioral characters such as cooperative breeding (Cadena et al. 2002).

Some minor comments apply to Johnson and Lanyon’s (2000) study, which documented an association between evolutionary changes in plumage color patches and marsh nesting. These authors suggested that five evolutionary changes had occurred, all corresponding to independent gains of carotenoid pigmentation. The number of changes would remain unaltered if *Hypopyrrhus* (which is yet another taxon with carotenoid coloration) were sister to *Gymnomystax* as suggested by our parsimony analyses and by the morphological and vocal traits described above. Alternatively, if it were sister to *Lampropsar* as suggested by maximum likelihood, it would be necessary to assume two independent origins of carotenoid coloration in *Hypopyrrhus* and *Gymnomystax*, or a single origin and a secondary loss in *Lampropsar*. In any case, *Hypopyrrhus* is not a marsh nester and shows carotenoid plumage, a pattern that weakens the evolutionary correlation between these two traits documented by Johnson and Lanyon (2000).

DIRECTIONS FOR FUTURE RESEARCH AND CONSERVATION

Although the Red-bellied Grackle is very poorly studied, it is clearly an interesting model species for studies addressing questions on evolutionary and behavioral ecology. For instance, *Hypopyrrhus* is a highly gregarious bird that forms groups of up to 30 individuals in the nonbreeding season, and breeds cooperatively, with three to seven individuals carrying out nesting activities and caring for offspring (Cuervo 2002, AMC, unpubl. data). Evaluating the degree of relatedness of individuals within the social and breeding groups and the occurrence of extragroup and extrapair mating in this species would further our understanding of behavioral patterns in the blackbirds within an evolutionary framework. In addition, *Hypopyrrhus* possesses an extraordinary but little known vocal repertoire that deserves further study, especially considering that vocalizations seem to show geographic variation (AMC, pers. obs.).

Finally, intensive human colonization and forest clearance and fragmentation have drastically reduced the habitat of the Red-bellied Grackle, and the species is currently listed as Endangered under IUCN criteria (Cuervo 2002). The evolutionary uniqueness of *Hypopyrrhus* confirmed by our study represents yet an additional solid reason to conserve this threatened taxon.

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APPENDIX. Taxa used for molecular analyses, with GenBank accession numbers of their cytochrome *b* and ND2 sequences. Nomenclature follows Dickinson (2003) except as modified by Remsen et al. (2004) and Lowther et al. (in press).

	GenBank accession no.	
Taxon	Cyt *b*	ND2
Psarocolius angustifrons	AF472362	AF472387
Psarocolius atrovirens	AF472366	AF472391
Psarocolius viridis	AY117698	AY117726
Psarocolius wagleri	AF472368	AF472393
Psarocolius montezuma	AF472377	AF472402
Psarocolius decumanus	AF472371	AF472396
Psarocolius bifasciatus	AF472379	AF472404
Clypicterus oseryi	AF472383	AF472408
Ocyalus latirostris	AF472382	AF472407
Cacicus chrysonotus	AY117715	AY117743
Cacicus sclateri	AY117718	AY117746
Cacicus solitarius	AY117719	AY117747
Cacicus cela	AY117700	AY117728
Cacicus haemorrhous	AY117705	AY117733
Cacicus uropygialis	AY117707	AY117735
Cacicus chrysopterus	AY117712	AY117740
Cacicus melanicterus	AY117721	AY117749
Amblycercus holosericeus	AY117722	AY117750
Icterus icterus	AF099296	AF099335
Icterus i. jamacaii	AF099297	AF099337
Icterus pectoralis	AF099304	AF099348
Icterus graceannae	AF089030	AF099329
Icterus mesomelas	AF099300	AF099341
Icterus cayanensis	AF089027	AF099316
Icterus bonana	AF099277	AF099313
Icterus laudabilis	AF099298	AF099338

APPENDIX. Continued.

Taxon	GenBank accession no.	
	Cyt *b*	ND2
Icterus oberi	AF099303	AF099346
Icterus dominicensis	AF099286	AF099324
Icterus spurius	AF099307	AF099351
Icterus cucullatus	AF099283	AF099322
Icterus wagleri	AF099308	AF099353
Icterus maculialatus	AF099299	AF099340
Icterus parisorum	AF089035	AF099347
Icterus chrysater	AF099281	AF099321
Icterus graduacauda	AF099291	AF099330
Icterus galbula	AF099290	AF099328
Icterus pustulatus	AF099305	AF099349
Icterus leucopteryx	AF089032	AF099339
Icterus auratus	AF099276	AF099312
Icterus nigrogularis	AF099302	AF099345
Icterus gularis	AF099293	AF099332
Nesopsar nigerrimus	AF089045	AF099359
Dives warszewiczi	AF089021	AF109962
Macroagelaius imthurni	AF089039	AF109945
Gymnomystax mexicanus	AF089026	AF109944
Hypopyrrhus pyrohypogaster ICN33977	AY572451	AY572450
Hypopyrrhus pyrohypogaster ICN34534	AY572452	AY572453
Lampropsar tanagrinus	AF089037	AF109946
Gnorimopsar chopi	AF089025	AF109941
Curaeus curaeus	AF089020	AF109943
Amblyramphus holosericeus	AF089014	AF109942
Agelasticus xanthophthalmus	AF089013	AF109932
Agelasticus cyanopus	AF290174	AF109931
Agelasticus thilius	AF089010	AF109933
Chrysomus ruficapillus	AF089009	AF109935
Chrysomus icterocephalus	AF089007	AF109934
Xanthopsar flavus	AF089066	AF109938
Pseudoleistes guirahuro	AF089051	AF109936
Pseudoleistes virescens	AF089052	AF109937
Oreopsar bolivianus	AF089046	AF109940
Agelaioides badius	AF089042	AF109939
Molothrus rufoaxillaris	AF089044	AF109961
Molothrus oryzivorus	AF089060	AF109960
Molothrus aeneus	AF089040	AF109957
Molothrus bonariensis	AF089043	AF109959
Molothrus ater	AF290172	AF109958
Agelaius phoeniceus	AF290173	AF290134
Agelaius tricolor	AF089011	AF109949
Agelaius humeralis	AF089006	AF109947
Agelaius xanthomus	AF089012	AF109948
Euphagus carolinus	AF089023	AF109950
Euphagus cyanocephalus	AF089024	AF109951
Quiscalus lugubris	AF089054	AF109952
Quiscalus mexicanus	AF089056	AF109954
Quiscalus quiscula	AF089058	AF109956
Quiscalus major	AF089055	AF109953
Quiscalus niger	AF089057	AF109955
Sturnella militaris	AF089038	AF447289
Sturnella magna	AF089063	AF447307
Sturnella neglecta	AF290164	AF290127
Dolichonyx oryzivorus	AF447367	AF447276