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A MOLECULAR PHYLOGENY OF THE BLACKBIRDS (ICTERIDAE): FIVE LINEAGES REVEALED BY CYTOCHROME-*B* SEQUENCE DATA

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ABSTRACT.—New World blackbirds (Icteridae) have long served as model systems for studies of avian ecology, evolution, and behavior. However, this work has been conducted in the absence of a strong phylogenetic hypothesis for the group. We sequenced 890 base pairs (bp) of the mitochondrial cytochrome-*b* gene for 28 of the 29 icterid genera and subgenera recognized by Blake (1968). We found strong evidence of five lineages of blackbirds: grackles and allies; caciques and oropendolas; orioles; meadowlarks and allies; and a monotypic cup-nesting cacique lineage. However, we found little support for any further structure among these five lineages and no strong evidence supporting icterid monophyly. Our results set the stage for forthcoming work on relationships within lineages and for higher-level studies that address blackbird monophyly and relationships among lineages. *Received 9 February 1998, accepted 6 November 1998.*

FEW GROUPS OF BIRDS have been as well studied by evolutionary ecologists as the New World blackbirds (Icteridae). Icterids exhibit a wide range of behaviors (brood parasitism, coloniality, polygyny, monogamy, delayed breeding, vocal mimicry, long-distance migration), morphologies (sexual dichromatism, sexual size dimorphism, delayed plumage maturation) and ecologies (range of diets and habitats). Furthermore, icterids often have served as models for the study of evolutionary genetics and molecular evolution. These characteristics, and the ease with which blackbirds are observed, have made them popular study organisms.

Despite the impressive number of studies of blackbirds, knowledge of the phylogenetic relationships within the group is inadequate. This gap in knowledge limits the ability of evolutionary biologists to apply comparative methods in this assemblage (e.g. Brooks and McLennan 1991, Harvey and Pagel 1991). Here, we develop a phylogenetic framework to serve as the foundation for the study of behavioral, morphological, and ecological evolution in blackbirds. First, we briefly review past studies that have addressed generic affinities within blackbirds. Next, we use mitochondrial DNA sequence data from the cytochrome-*b* gene to derive a phylogeny for the described genera and subgenera of blackbirds.

Few studies have included enough taxa, characters, and methodological rigor to provide strong hypotheses of relationships among blackbird genera, and little agreement exists among these previous studies. The most comprehensive attempt to address generic relationships within the Icteridae was the morphological work of Beecher (1951). Based on extensive dissections of skull muscles, Beecher concluded that the cowbirds (*Molothrus*) were the most primitive blackbird genus and that three other lineages were derived from a cowbird-like ancestor. Lack of explicit tree-building methods, and the absence of a data matrix, make it difficult to interpret his results in a modern framework. Freeman and Zink (1995) published a study that included a data matrix and provided explicit statements of analytical methods. They analyzed restriction-enzyme cleavage sites in the mitochondrial genome of 47 blackbird species to derive a phylogeny for the group. However, their study did not provide strong resolution on the identity of the major lineages within blackbirds. They identified one major clade that consisted of *Icterus, Cacicus, Psarocolius,* and *Sturnella.* Most other studies have included only a few taxa and provided little resolution of blackbird lineages or their relationships (e.g. Smith and Zimmerman 1976, Raikow 1978, Sibley and Ahlquist 1990).

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Finally, many classifications of birds have implied generic affinities within blackbirds. For example, Blake (1968) placed the Bobolink (*Dolichonyx oryzivorus*) in its own subfamily, separate from the rest of the blackbirds. Although such classifications lack accompanying justification, we discuss them in light of our cytochrome-*b* phylogeny.

METHODS

Taxa.—We chose taxa from 28 of the 29 genera and subgenera recognized by Blake (1968) to adequately sample higher-level relationships within the blackbirds (*Hypopyrrhus* was not represented; Appendix 1). One individual from each taxon was sequenced. Our primary intent was to resolve generic affinities, so we concentrated our sequencing efforts on more species rather than more individuals. The sister taxon of the Icteridae is not known with certainty (Raikow 1978, Bledsoe 1988, Sibley and Ahlquist 1990). Therefore, we chose five outgroup taxa representing three other speciose families closely related to blackbirds (Thraupidae: *Thraupis episcopus*; Emberizidae: *Melospiza melodia*; Cardinalidae: *Passerina cyanea, Saltator coerulescens, Spiza americana*). Within the blackbirds, we use the nomenclature of Sibley and Monroe (1990), except in the case of *Icterus bullockii*, for which we follow AOU (1998). We used Sibley and Monroe (1990) because of its worldwide coverage and because it is a recent and widely available check-list. Appendix 1 lists voucher information for all the specimens used in this study. With 60 ingroup taxa and 5 outgroup taxa, our main objectives were to attempt to define major lineages within the blackbirds, define the relationships among these lineages, and begin to test blackbird monophyly.

Laboratory methods.—DNA was extracted using standard phenolchloroform protocols (Maniatis et al. 1982). In the initial phase of the study, a 307-bp segment of the mitochondrial cytochrome-*b* gene was amplified with the so-called "universal" primers (B1 and B2; Kocher et al. 1989). Double-stranded amplifications (dsPCR) were performed using 30 to 35 cycles of denaturation at 93°C (1 min), annealing at 52°C (1 min), and extension at 72°C (2 min). Five microliters of the dsPCR product were run on a 3% NuSieve agarose gel. The amplified PCR product was excised from the gel and melted in 300 uL of water. A dilution of this solution was then used as template in a 100-uL asymmetric PCR to generate single-stranded DNA template for direct sequencing (Gyllensten and Erlich 1988). Excess primers, salts, and free nucleotides were removed by three cycles of centrifugal dialysis (Centricon-30, Amicon). The PCR product was then sequenced by the dideoxy method (Sanger et al. 1977) using a commercially available kit (Sequenase, United States Biochemical) with the primer that had been limiting in the second stage PCR. DNA sequence obtained from sequencing one strand was confirmed by sequencing the complementary strand.

An additional segment of the cytochrome-*b* gene was amplified with primers L15042 (5'-ATCTGCATCTACCTACACATCGG-3'; B3) and H15767 (5'-GATGAATGGGTGTTCTACTGGTTG-3'; B4), which target a 726-bp fragment overlapping that of the fragment produced with B1 and B2. Then, single-stranded amplification products were produced and sequenced with primers B3, B4, and B5 (L15243; 5'-ACCCTAGTAGAATGAGCCTGAGG-3') as described above. Alternatively, the double-stranded amplification product was freed of remaining nucleotides and primers using a glass powder suspension (GeneClean, Bio101, Inc.) and sequenced directly by the protocol of Thein (1989), modified by the addition of 10% dimethyl sulfoxide to annealing, labeling, and termination reactions. See Lanyon (1994) for further details on laboratory methods.

In total, an 890-bp region from the cytochrome-*b* gene was successfully sequenced and visually aligned for 60 blackbird taxa and 5 outgroups. Owing to occasional ambiguous banding, compressions on sequencing gels, and difficulty reading sequences at the ends, 19 bases, on average, were not scored for each taxon. With few exceptions, these unscored bases were at sites that were otherwise uninformative within the ingroup. The sequences have been deposited in GenBank under accession numbers AF089004 to AF089068.

Analysis of sequence data.—Data were analyzed using PAUP* (versions 4d56 to 4d64 provided by D. L. Swofford). Because transversions and transitions accumulate at different rates and, therefore, are not expected to be equally phylogenetically informative, we chose to differentially weight these two classes of character transformations. The weighting scheme was obtained by reconstructing transformations from the cytochrome-*b* data set on three different random trees using MacClade 3.04 (Maddison and Maddison 1992). All three reconstructions produced very similar transition biases (2.40, 2.42, and 2.30), which we rounded off to the nearest integer. As a result, our primary analyses are based on a 2:1 transversion : transition weighting (hereafter, 2× weighting). We conducted five heuristic searches with random addition of sequences using the TBR algorithm, and trees were rooted using the five outgroup taxa. All equally parsimonious trees resulting from the 2× weighted analysis were combined to produce a majority-rule consensus tree. To evaluate the degree to which the cytochrome-*b* data were saturated, we plotted transitions versus transversions for third positions, and first and second positions combined using the SAVEDIST command in PAUP*.

To estimate the degree to which the topology resulting from these parsimony analyses depended on

character and taxon composition, we used two data manipulations. Bootstrapping (Felsenstein 1985) examines the degree to which topology is dependent on the character composition of the data set. Jackknifing taxa (Lanyon 1985) determines the degree to which topology is dependent on the taxonomic composition of the data set. We conducted 100 bootstrap replications with heuristic searches and random addition of taxa. We jackknifed taxa by deleting each taxa one at a time using command lines in PAUP*. The output from these 65 jackknife pseudoreplicates was then synthesized using two programs written by S. M. Lanyon for DOS (available upon request).

To explore the degree to which our results are dependent on our *a priori* assumptions concerning the best way to analyze these cytochrome-*b* data, we also conducted equally weighted searches and analyses with six-parameter weighting (Williams and Fitch 1989). We determined the six-parameter weights by mapping changes onto the shortest equally weighted tree and then used the negative natural log of these change frequencies following Cunningham (1997). We used the same analytical approach outlined above for both of these additional weighting schemes.

To determine whether alternative phylogenetic hypotheses differed significantly from each other, we used the Kishino-Hasegawa test (1989) in PAUP*. We evaluated the likelihood scores of the trees resulting from our three weighting schemes. We also (1) tested Blake's (1968) hypothesis that *Dolichonyx* is sister to all other blackbirds assuming the other relationships as determined by our 2× weighted tree and (2) evaluated Freeman and Zink's (1995: figure 1a) tree using the 36 taxa common to both studies. For all tests, we used a nested set of models of sequence evolution, beginning with a simple model assuming the same 2:1 transition : transversion ratio used by the parsimony analysis with empirical nucleotide frequencies. We then tested the topologies using more complex models (transition:transversion ratio estimated, general-time reversible, and general-time reversible with rate heterogeneity; Swofford et al. 1996).

Results

We found strong evidence of five lineages of blackbirds: (1) grackles and allies, (2) caciques and oropendolas, (3) orioles, (4) meadowlarks and allies, and (5) cup-nesting caciques (Fig. 1). Monophyly of each of these lineages was robust in all manipulations and weighting schemes employed. With 2× weighting, all five lineages received 100% jackknife support, and all of the lineages except the meadowlarks and allies received at least 94% bootstrap support. (Because *Amblycercus* is a monotypic lineage, this support is de facto because it was excluded from the other lineages at those jackknife and bootstrap levels.) In general, genetic distances within lineages were lower than those between lineages (Table 1).

Despite the strong support for the existence of the five lineages, our analyses did not resolve further structure among the five lineages. The parsimony analysis with 2× weighting of transversions identified 72 equally most parsimonious trees (two islands of 12 and 60 trees, respectively). The majority-rule consensus of these trees includes structure among the five lineages (grackles, (caciques/oropendolas, meadowlarks), (*Amblycercus*, orioles)). This additional structure did not receive any statistical support in the 2× weighted analysis. However, *Amblycercus* grouped with the orioles in 78% of the jackknife replications in the equally weighted analyses. The six-parameter weighting resulted in 78% jackknife support for a cacique, oriole, meadowlark group, and 82% jackknife support for a cacique, oriole, meadowlark, *Amblycercus* group. None of these groupings, nor any other structure among the other lineages, was supported in more than 50% of the bootstrap replications in any of the weighting schemes.

The 2× weighted and six-parameter weighted jackknife analyses revealed 94 and 95% support, respectively, for blackbird monophyly. However, monophyly of the Icteridae was not strongly supported, with bootstrap analyses revealing less than 50% support for blackbird monophyly in all weighting schemes. This is perhaps best reflected by the fact that in the 2× weighted analysis, the small island of most-parsimonious trees showed the blackbirds as non-monophyletic, whereas the larger island shows them as monophyletic. In the equally weighted analysis, the majority-rule consensus showed the blackbirds as non-monophyletic in a different way. However, the statistical support was not strong for either of these arrangements. Genetic distances mirror the branching patterns in these respects (Table 1). Although distances to the outgroups were not on average greater than distances among ingroup lineages, no one ingroup lineage had lower genetic distances to the outgroups.

We found no significant differences among the shortest trees created by any of the three

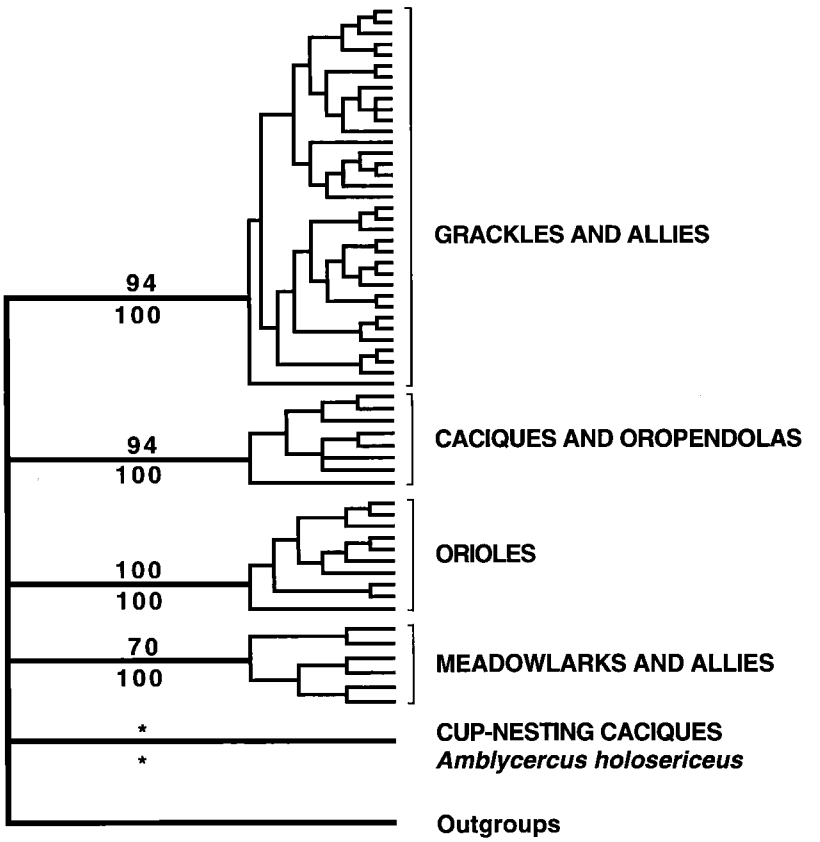

FIG. 1. Five lineages of Icterids as revealed by parsimony analysis of cytochrome-*b* sequences. Statistical support for lineages indicated by bootstrap values (above branches) and jackknifed taxon values (below branches). Values shown are based on the analysis with 2× weighting of transversions.

weighting methods (Kishino-Hasegawa test, $P > 0.05$). Furthermore, using this approach revealed no significant support or rejection of blackbird monophyly. The small island of 2× weighted trees that showed the blackbirds as non-monophyletic was not significantly different than the large island supporting monophyly. There were no significant differences among any of the alternative shortest trees that we found regardless of the model of sequence evolution used for the test. In contrast, the alternative trees based on the previous work of Blake (1968) and Freeman and Zink (1995) were significantly worse fits to the sequence data ($P \leq 0.001$), again regardless of the model used.

TABLE 1. Mean percent divergence within (on diagonal) and between (above diagonal) the five lineages of Icteridae and outgroups. Standard deviations in distances are in parentheses.

	Grackles and allies	Caciques and oropendolas	Orioles	Meadowlarks and allies	Cup-nesting caciques	Outgroups
Grackles and allies	7.8 (1.3)	10.8 (0.7)	10.3 (0.6)	10.6 (0.8)	9.5 (0.5)	10.5 (0.9)
Caciques and oropendolas		7.8 (1.2)	9.9 (0.7)	10.8 (1.1)	9.4 (0.6)	10.6 (0.8)
Orioles			7.1 (1.3)	11.0 (1.0)	9.3 (0.7)	10.4 (0.8)
Meadowlarks and allies				9.1 (1.9)	9.7 (1.2)	10.9 (1.1)
Cup-nesting caciques					—	11.5 (1.3)
Outgroups						9.5 (0.9)

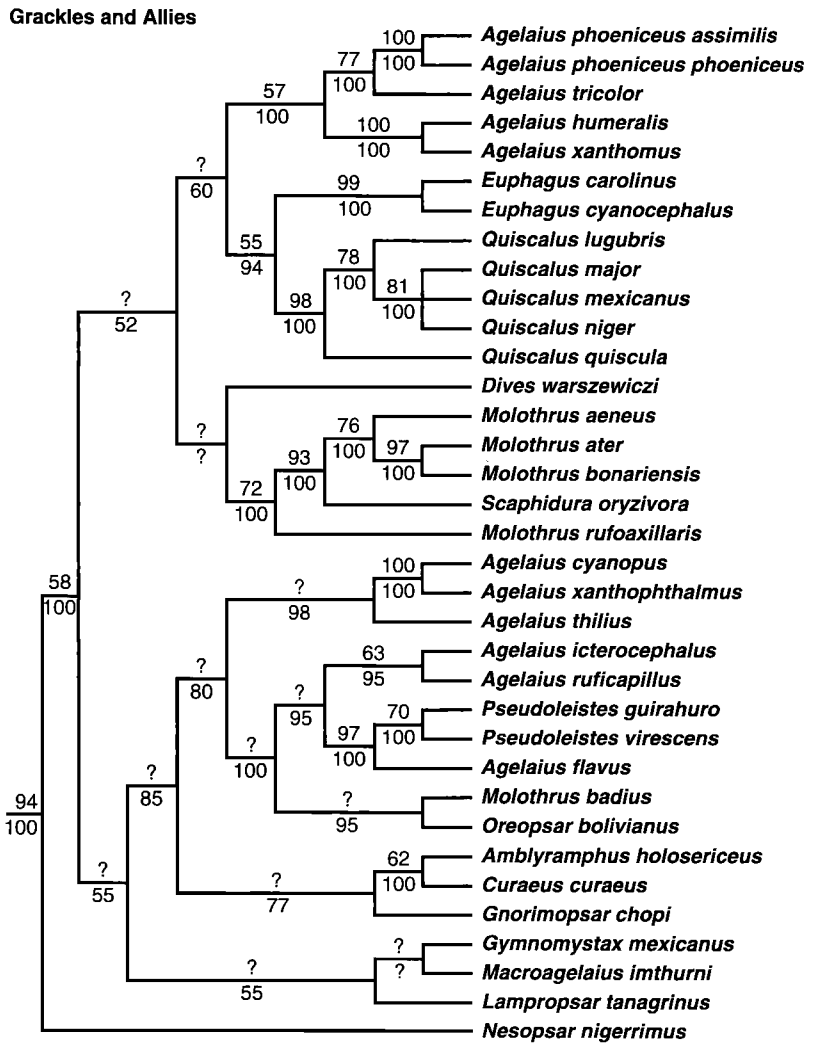

FIG. 2. Detail of relationships within the grackle and allies lineage based on a majority rule consensus of the 2× weighed trees. Statistical support for lineages based in 2× weighting indicated by bootstrap values (above branches) and jackknifed taxon values (below branches). Nodes supported by fewer than 50% of the pseudoreplicates are indicated with a question mark.

The relationships within the four polytypic blackbird lineages are shown in Figures 2 to 5. These trees are our best estimate of the relationships among these taxa. However, the completeness of taxon sampling varies among lineages. We counted the number of species that should probably be included in these lineages based on the placement of their congeners. Our study included 34 of 41 grackles and allies, 8 of 20 caciques and oropendolas, 10 of 25 orioles, 6 of 9 meadowlarks and allies, and the single species of cup-nesting cacique.

Base composition (26.7% adenine, 35.0% cytosine, 13.3% guanine and 24.9% thymine) was similar to that reported for other bird groups (e.g. Burns 1998). Third-position transitions showed strong evidence of saturation (Fig. 6). However, plots of first- and second-position transitions showed no evidence of saturation.

DISCUSSION

We found strong evidence of five lineages within the Icteridae. However, as with several

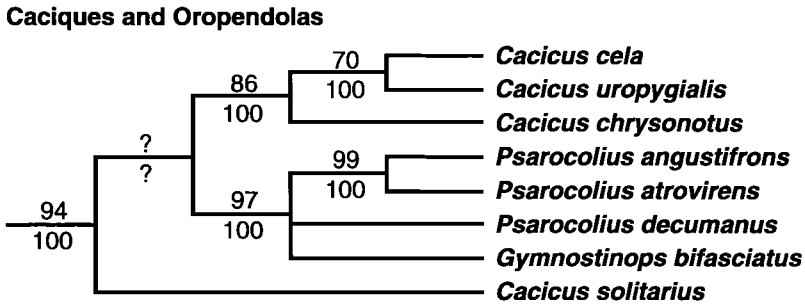

Fig. 3. Detail of relationships within the cacique and oropendola lineage (see Fig. 2 legend).

previous molecular and nonmolecular studies, we were unable to resolve the branching order among lineages. Moreover, we did not find strong support for monophyly of the Icteridae. Future higher-level studies will be aimed at addressing these latter two issues (J. Klicka et al. unpubl. data). Furthermore, more detailed studies within lineages are being completed for the orioles (Omland et al. 1999) and the grackles and allies (Johnson and Lanyon 1999; also see Lanyon 1994), and detailed analysis of the other two lineages are planned.

Our findings mostly disagree with the few previous studies of blackbird systematics. Beecher's (1951) major finding was that cowbirds were primitive blackbirds from which three major radiations were derived: orioles, meadowlarks, and ageline blackbirds; grackles; and oropendolas and caciques. Beecher's conclusion could be interpreted in two ways in modern terms. Either he believed that cowbirds were the actual ancestors of all other blackbirds, in which case cowbirds would be paraphyletic with respect to all other icterids, or that cowbirds were remnants of an early lineage, in which case cowbirds would be the sister taxon to all other icterids. The cytochrome-*b* data provide no support for either of these possibilities. Of Beecher's three blackbird lineages, the cytochrome-*b* data contradict all but the lineage consisting of the oropendolas and caciques.

Our findings also disagree with several aspects of published classifications. In particular, Blake (1968) recognized two major lineages within the Icteridae: Dolichonychinae (containing only *Dolichonyx*) and Icterinae (containing all other blackbirds; also see AOU 1983:722, in which *Dolichonyx* is placed in its own tribe). The current study does not support this arrangement, and Blake's hypothesis was a significantly worse fit to the sequence data. Although our data show that *Dolichonyx* is very distant from all other blackbirds in cytochrome-*b* sequence (mean sequence divergence = 11%), *Dolichonyx*, *Xanthocephalus*, *Sturnella*, and *Leistes* nevertheless seem to be more closely related to each other than they are to the remaining blackbirds. These taxa form the meadowlark and allies lineage with at least 70% bootstrap support. Within this lineage, the meadowlarks themselves (*Leistes* and *Sturnella*) form a strongly supported monophyletic

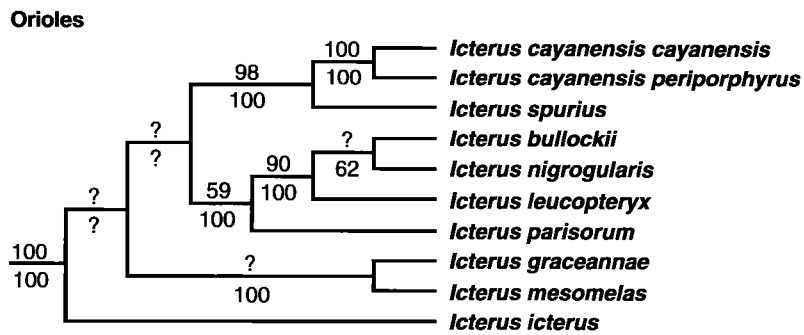

Fig. 4. Detail of relationships within the oriole lineage (see Fig. 2 legend).

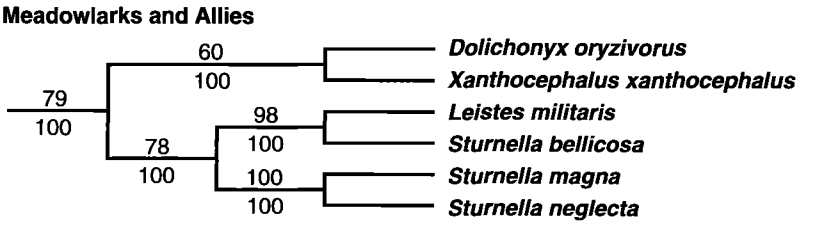

Fig. 5. Detail of relationships within the meadowlark and allies lineage (see Fig. 2 legend).

group. Conversely, bootstrap support for placing the Bobolink and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) with the meadowlarks, or with each other, is not that strong in any weighting scheme (≤70%). These two taxa are distant from each other (8.1% uncorrected cytochrome-*b* sequence divergence) and from meadowlarks (≥9.0%) and other icterids (≥8.2).

The DNA-DNA hybridization study of Sibley and Ahlquist (1991: figure 384) included only seven genera of blackbirds (all of which we examined) and resolved six nodes. The cytochrome-*b* data support only one of these nodes: a cluster containing *Cacicus* and *Psarocolius*. We note, however, that only three of the seven taxa were radioactively labeled, making it unclear how the six nodes were derived (Lanyon 1992b).

Finally, our results differ from Freeman and Zink's mitochondrial restriction-site study in three important respects (Freeman and Zink 1995: figure 1b; their well-supported tree). First, their data indicate that the Troupial (*Icterus icterus*) does not group with the other orioles and may be basal to all other blackbirds (although they mention that this finding was "not common to all the equally likely trees analyzed"). In contrast, we found strong support for the monophyly of *Icterus*, with the genus being monophyletic in at least 97% of bootstrap replications under all three weighting schemes. The monophyly of the orioles is further supported by additional taxon sampling and a second mitochondrial gene (Omland et al. 1999). Second, the strongly supported tree of Freeman and Zink (1995) included an oriole, cacique, and oropendola plus meadowlark clade.

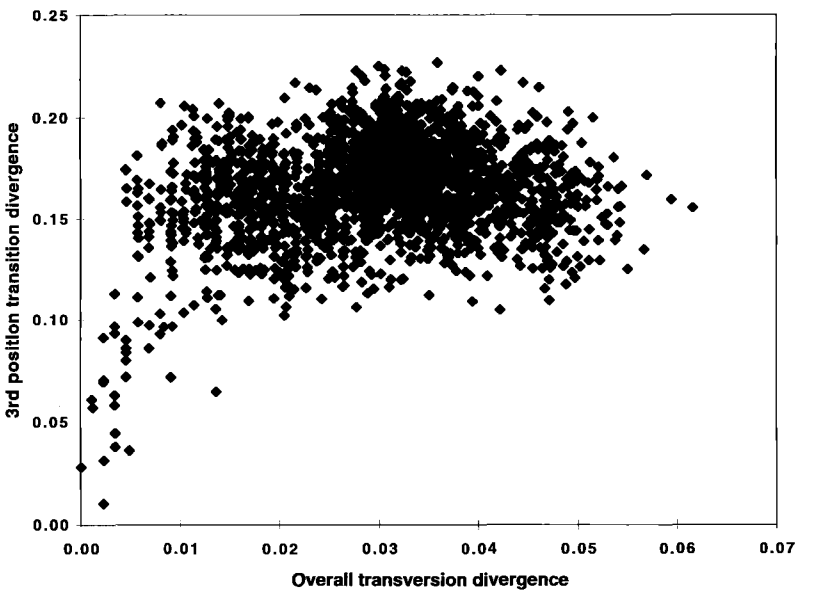

FIG. 6. Saturation plot showing third position transitions plotted as a function of overall transversion divergence.

This arrangement, especially the inclusion of meadowlarks, is not supported by our data. Third, Freeman and Zink (1995) found that the *Dolichonyx/Xanthocephalus* clade grouped with the Red-winged Blackbird (*Agelaius phoeniceus*). Our data contradict this grouping in that the latter was in the grackle and allies lineage and the former in the meadowlark and allies lineage, both with bootstrap support. However, these are not strong disagreements because bootstrap analysis of Freeman and Zink's (1995) matrix resulted in only a few nodes with bootstrap support that exceeded 50%, none of which conflicted with our lineages. Furthermore, when we combined our data set with the restriction-site data, the total-evidence tree supported the same five lineages defined by cytochrome-*b* alone. However, the Kishino-Hasegawa test showed that Freeman and Zink's (1995) best estimate of blackbird relationships was a significantly worse fit to the sequence data.

Felsenstein (1978) and others have shown that long branches can be attracted to each other in parsimony analysis. We found that both *Dolichonyx* and *Xanthocephalus* are distant from each other (8.1% uncorrected cytochrome-*b* sequence divergence) and from meadowlarks (≥9.0%) and other icterids (≥8.2). Thus, the placement of these two taxa could be affected by long-branch attraction in either the Freeman and Zink (1995) study, our study, or both. Regardless, our data show that *Xanthocephalus xanthocephalus* did not share a recent ancestor with *Agelaius phoeniceus* because these species show 10.3% sequence divergence in cytochrome-*b*.

The distant relationship between *Agelaius phoeniceus* and *Xanthocephalus xanthocephalus* is one of our most surprising findings. These taxa have long been considered to be closely related for the purposes of behavioral and ecological studies (e.g. Willson 1966, Miller 1968, Orians and Christman 1968). Most classifications place the two genera adjacent to each other (Blake 1968, Morony et al. 1975, Sibley and Monroe 1990), and Lack (1968) assumed a close relationship when discussing the ecological similarities of these taxa with the ploceid *Euplectes*. Our results indicate that the ecological similarities between *Agelaius* and *Xanthocephalus* are convergent.

Our data set corroborates the polyphyly of *Agelaius* demonstrated by Lanyon (1994). Similarly, our study confirms the paraphyly of *Molothrus* (Lanyon 1992a). In both cases, the earlier work based on a more limited number of taxa is supported by the more complete taxon sampling in our study. The non-monophyly of *Agelaius* and *Molothrus* underscores the need to establish phylogenetic relationships before conducting comparative studies.

Surprisingly, we did not find strong evidence for blackbird monophyly. Monophyly was not supported by a majority of bootstrap or jackknife replications, outgroup taxa branched with the ingroup in shortest trees, genetic distances were no greater to outgroup taxa than among ingroup lineages, and monophyletic trees did not have significantly better fits to the sequence data. However, although no strong support existed for blackbird monophyly, neither did strong support exist for any of the outgroups branching consistently within the Icteridae. Furthermore, Raikow's (1978) morphological work provided at least one morphological synapomorphy for the blackbirds. Specifically, he stated that "In the forelimb the Icteridae show a modification of the flexor digitorum profundus in which the caudal border of the muscle is narrowed." Although this is not a profound modification, it occurs in all forms examined, and this consistency suggests that it is a useful character for reliably defining the family. The lack of resolution among blackbird lineages, and the lack of support for blackbird monophyly, suggest two possible explanations that are not mutually exclusive. The first is that cytochrome-*b* is too saturated in third positions to reliably recover these relationships (Fig. 6). Second, it is possible that the blackbirds were formed and diversified during a rapid radiation among all nine-primaried oscines. Future work using sequencing and other lines of inquiry are needed to address these hypotheses and further resolve higher-level relationships within the Icteridae. However, our current findings provide a strong foundation for such work at higher levels, as well as detailed studies within the five lineages of blackbirds.

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APPENDIX. Voucher information for the specimens sequenced in this study. Museum abbreviations: AMNH = American Museum of Natural History; ANK = Museo de Historia Natural "Noel Kempff Mercado," Santa Cruz, Bolivia; ANSP = Academy of Natural Sciences, Philadelphia; Cuba = Museo de Historie Natural, Havana, Cuba; FMNH = Field Museum of Natural History; MPEG = Muesu Paraense Em'lio Goeldi, Belem, Brazil.

Species	Museum number
Agelaius cyanopus	FMNH 334636
Agelaius flavus	FMNH 330747
Agelaius humeralis	No voucher specimen
Agelaius icterocephalus	FMNH 339772
Agelaius phoeniceus assimilis	Cuba
Agelaius phoeniceus phoeniceus	FMNH 341893
Agelaius ruficapillus	FMNH 330775
Agelaius thilius	FMNH 334615
Agelaius tricolor	LSUMZ 130833
Agelaius xanthomus	No voucher specimen
Agelaius xanthophthalmus	FMNH 324095
Amblycercus holosericeus	LSUMZ 98900
Amblyramphus holosericeus	FMNH 334662
Cacicus cela	FMNH 324080
Cacicus chrysonotus	LSUMZ 103278
Cacicus solitarius	FMNH 324091
Cacicus uropygialis	ANSP 182884
Curaeus curaeus	AMNH 826156
Dives warszewiczi	LSUMZ 113959
Dolichonyx oryzivorus	FMNH 334721
Euphagus carolinus	FMNH 333317
Euphagus cyanocephalus	FMNH 341985
Gnorimopsar chopi	FMNH 334679

APPENDIX. Continued.

Species	Museum number
Gymnomystax mexicanus	FMNH 339743
Gymnostinops bifasciatus	FMNH 324076
Icterus cayanensis cayanensis	MPEG 40.357
Icterus cayanensis periporphyrus	FMNH 334609
Icterus bullockii	FMNH 341938
Icterus graceannae	ANSP 181810
Icterus icterus	FMNH 324092
Icterus leucopteryx	FMNH 331149
Icterus mesomelas	ANSP 181806
Icterus nigrogularis	FMNH 339736
Icterus parisorum	FMNH 341943
Icterus spurius	FMNH MEX 8495
Lampropsar tanagrinus	LSUMZ 125586
Leistes militaris	FMNH 334657
Macroagelaius imthurni	FMNH 339783
Molothrus aeneus	LSUMZ 130743
Molothrus ater	FMNH 350707
Molothrus badius	FMNH 330801
Molothrus bonariensis	FMNH 334768
Molothrus rufoaxillaris	FMNH 330805
Nesopsar nigerrimus	FMNH 331150
Oreopsar bolivianus	FMNH 334687
Passerina cyanea	FMNH 341743
Psarocolius angustifrons	FMNH 324068
Psarocolius atrovirens	FMNH 324106
Psarocolius decumanus	FMNH 324065
Pseudoleistes guirahuro	FMNH 330795
Pseudoleistes virescens	FMNH 330796
Quiscalus lugubris	FMNH 339797
Quiscalus major	FMNH 341918
Quiscalus mexicanus	FMNH 341975
Quiscalus niger	FMNH 331153
Quiscalus quiscula	FMNH 341733
Saltator coerulescens	ANK 170
Scaphidura oryzivora	FMNH 324097
Spiza americana	FMNH MEX 2733
Sturnella bellicosa	ANSP 178.118
Sturnella magna	FMNH 339780
Sturnella neglecta	FMNH 330039
Thraupis episcopus	FMNH 339708
Xanthocephalus xanthocephalus	LSUMZ 126564
Zonotrichia melodia	FMNH 341624