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SEASONAL MIGRATION, SPECIATION, AND MORPHOLOGICAL CONVERGENCE IN THE GENUS *CATHARUS* (TURDIDAE)

Kevin Winker[1] and Christin L. Pruett

University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775, USA

Abstract.—The effects of seasonal migration on evolutionary change within lineages is poorly understood, in terms of both differentiation (cladogenesis) and specialization (anagenesis). Regarding differentiation, two contradictory hypotheses exist: Seasonal migration counters differentiation; or it can stimulate differentiation by exposing lineages to new environments. Regarding specialization, the morphological consequences of a migratory life history have not been well explored. We examined these issues by reconstructing morphological and molecular phylogenies of the genus *Catharus* (Turdidae), a group of forest-dwelling, New World thrushes traditionally considered to include a small "species flock" of Nearctic–Neotropic migrants. DNA sequence data (2,920–3,027 base pairs) do not support traditional taxonomy, and morphological characters conflicted with these data. Results suggest that long-distance seasonal migration arose independently four times in *Catharus sensu lato* (including *Hylocichla mustelina*). Correlated morphological evolution occurred among several characters in these lineages, and these shared traits may stem from ecological conditions in Nearctic forests. *Received 28 April 2005, accepted 13 November 2005.*

Key words: *Catharus*, convergent evolution, ecological adaptation, molecular systematics, Nearctic–Neotropic migration, parallel evolution, species flocks, thrushes.

Migración Estacional, Especiación y Convergencia Morfológica en el Género *Catharus* (Turdidae)

Resumen.—Los efectos de la migración estacional sobre el cambio evolutivo de los linajes son poco conocidos en términos tanto de la diferenciación (cladogénesis) como de la especialización (anagénesis). Con respecto a la diferenciación, existen dos hipótesis contradictorias: que la migración estacional imposibilita la diferenciación, o que ésta puede estimular la diferenciación al exponer a los linajes a ambientes nuevos. Con respecto a la especialización, las consecuencias morfólogicas de la historia de vida migratoria no han sido bien exploradas. Examinamos estos aspectos reconstruyendo filogenias morfológicas y moleculares del género *Catharus* (Turdidae), un grupo de zorzales del nuevo mundo que tradicionalmente se ha considerado que contiene una pequeña "bandada de especies" de migrantes neártico-neotropicales. Los datos de secuencias de ADN (2,920–3,027 pares de bases) no apoyan la taxonomía tradicional, y los caracteres morfológicos se encuentran en conflicto con estos datos. Los resultados sugieren que la migración estacional que involucra grandes distancias surgió independientemente cuatro veces en *Catharus sensu lato* (incluyendo a *Hylocichla mustelina*). En estos linajes, sucedió evolución correlacionada entre varios caracteres morfológicos. Estos rasgos compartidos podrían aparecer como consecuencia de las condiciones ecológicas de los bosques del Neártico.

[1]E-mail: ffksw@uaf.edu

More than half of North American bird species north of Mexico are Nearctic–Neotropic migrants, migrating seasonally between their breeding and wintering grounds (338 of 650 species; Rappole 1995). Similarly large proportions of Eurasian bird species are also long-distance seasonal migrants (Rappole 1995). Despite the commonness of this life-history strategy and the added ecological complexity it brings to migratory lineages, the effects of seasonal migration on subsequent evolutionary change within a lineage remain unclear, in terms of both differentiation (cladogenesis, or generation of new forms) and increased specialization (anagenesis, or morphological change occurring independently of the splitting of new lineages within a clade). Montgomery (1896) first observed that levels of subspecific differentiation among migrant species are, on average, lower than among nonmigrants; this leads to the conclusion (which we shall call "Montgomery's Rule") that seasonal migration counters differentiation (see also Rensch 1933, Mayr 1963). The increased levels of movement associated with seasonal migration could readily diminish propensities for differentiation, but it seems unlikely that this simple explanation fully reflects the relationship between migration and differentiation (Mayr 1963). For example, long-distance migration exposes lineages to new environments and to greater environmental heterogeneity, both of which could result in strong differentiating selection. Winker (2000) suggested that migration may be a key innovation enabling lineages to radiate in new environments, despite the increased propensity for gene flow inherent in increased movement (e.g., Paradis et al. 1998).

The morphological consequences of increased specialization when a lineage gains a migratory life-history strategy are also not fully understood. There is evidence of convergence and parallel evolution (see Futuyma 1998, Wiens et al. 2003) in several phenotypic traits, leading to the expectation that with careful examination more homoplasy (structural resemblance not attributable to common ancestry) may be discovered. Evidence of convergence comes from physiological and behavioral traits such as *zugunruhe* (seasonal nocturnal restlessness among nocturnal migrants), hyperphagia (seasonal fattening behavior), and appropriately directed seasonal movement (Farner 1955; Berthold 1975, 1993). All of these are important characteristics for migratory lineages to possess when fitness is tied to ecological conditions showing substantial variation in space and time. The lack of expression of such complex traits in nonmigratory relatives can be considered strong evidence for convergence and parallel evolution. A tendency to gain more pointed wings (a continuous variable) has also long been recognized to be correlated with seasonal migration at both population and species levels (Kipp 1942, Rensch 1959, Winkler and Leisler 1992). However, aside from this commonly observed morphological change, readily explained by increased flight efficiency (Dorst 1956, Rensch 1959, Winkler and Leisler 1992), morphological consequences of migration have generally not been recognized (or studied using phylogenetically independent contrasts).

Here, we examine the New World thrush genus *Catharus* (Turdidae) to determine how long-distance seasonal migration is related to evolutionary differentiation and morphological specialization in the group. The genus *Catharus* is a New World assemblage of Neotropical origin comprising 12 or 13 species of forest-dwelling thrushes (American Ornithologists' Union [AOU] 1998). Until recently (AOU 1998), this assemblage has been considered to include two major subgeneric groups. The first group, the Neotropical "nightingale-thrushes" (seven species), is largely sedentary and constitutes the core of the genus (Salvin and Godman 1879). Some limited movements (such as elevational) occur among some individuals in this group during the nonbreeding season (Phillips 1991). The second group comprises the Nearctic–Neotropic "long-distance" migrants (five or six species), presently considered taxonomically a subgeneric group of closely related species that at times either includes or excludes the Wood Thrush (*Hylocichla mustelina*; AOU 1957, 1998; Winker and Rappole 1988; Sibley and Monroe 1990). Many species in this group, such as the Veery (*Catharus fuscescens*), Swainson's Thrush (*C. ustulatus*), and Hermit Thrush (*C. guttatus*), are well known to biologists and birdwatchers across North America.

Our first question focuses on cladogenesis—the history of speciation in this group—in relation to long-distance seasonal migration. An obvious issue left over from its taxonomic history is whether the group of long-distance

migrant Nearctic–Neotropic thrushes (*Catharus* spp. and *H. mustelina*) represents a small, postmigratory species flock—a small radiation into new environments at higher latitudes made available through an ancestor's acquisition of the key innovation of long-distance migration. This was proposed by Winker (2000) as an expectation following the traditional understanding of relationships in the genus. Although this traditional, morphologically based hypothesis has been contradicted by a recent phylogeny based on a single locus (Outlaw et al. 2003), phylogenetic resolution of this group remains inadequate for a detailed resolution of our questions (see below), and a rigorous examination for potential postmigratory species flocks in this group is still needed. We focus our question regarding the relationship between long-distance seasonal migration and lineage differentiation at this intrageneric level, recognizing that, although a conclusive test of the competing hypotheses will require a taxonomically broad meta-analysis, a reliable base of well-resolved phylogenies in exemplar groups such as *Catharus* (with obligate, long-distance, seasonal-migrant species and species lacking this trait) is an essential first step toward this goal. We do not believe that this essential base exists yet, so we have begun asking these questions within an exemplar group, in which hypothesized effects should be evident.

Our second question focuses on anagenesis—lineage specialization—and asks how potentially phylogenetically informative morphological traits have been associated with the evolutionary history of long-distance migration and the associated exposure to ecological conditions at higher latitudes. Our expectation is that migration affects morphology in as-yet-undetermined ways. We use morphological and molecular (DNA sequence) data to address these questions.

METHODS

Phylogeny reconstruction was undertaken first with morphological characters, then with molecular data. Our goals were to obtain these two data sets independently and to map morphological characters and long-distance seasonal migration onto the molecular phylogeny, recognizing that migration can cause at least some phenotypic convergence, wing pointedness and *zugunruhe* being well known examples (see above). Our morphological examination was not intended as an ecomorphological study, but instead one to examine the relationship between morphology (specifically, potentially phylogenetically informative characters) and the evolutionary history of the group (with its concomitant distribution of obligate, long-distance, seasonal migration). Outgroup taxa were selected at the generic level on the basis of Sibley and Ahlquist (1990) and at the species level on the basis of specimen availability.

Morphology.—Before initiating molecular genetic studies, we examined museum specimens of *Catharus* spp., *H. mustelina*, and five outgroup taxa. We scored 39 phenotypic characters from adult external morphology, juvenal (i.e., fledgling) plumage, and skeletons (Appendix). We also scored six characters based on the song of adult males (Hardy and Parker 1985), for a total of 45 phenotypic characters (Appendix). *Catharus minimus* and *C. bicknelli*, considered cryptic species (Ouellet 1993, AOU 1998), were lumped because they exhibited no morphological differences among the characters scored here.

DNA sequencing.—We extracted whole genomic DNA from tissues of *Catharus* spp., *H. mustelina*, and six close relatives in the family Turdidae (Sibley and Ahlquist 1990) using a DNeasy tissue kit (Qiagen, Valencia, California; Table 1). We next amplified 1,060 base pairs (bp) of the mitochondrial cytochrome-*b* gene, the entire mitochondrial NADH dehydrogenase subunit 2 gene (ND2; 1,041 bp), and part of the nuclear β-fibrinogen intron 7 (FIB7; 819–926 bp) using standard polymerase chain reaction (PCR) protocols (Palumbi 1996). Sequencing reactions were performed using ABI PRISM (Applied Biosystems, Foster City, California) dye terminators and four primers (Table 1) for each DNA template, so that sequence data overlapped in both directions. The cytochrome-*b* gene was amplified and sequenced using the reverse primer H16064 (Harshman 1996), internal primers L15350 (Klicka and Zink 1997) and H15299 (Hackett 1996), and the forward primers L14703 (C. Huddleston pers. comm.), L14841 (Kocher et al. 1989), L14851 (Kornegay et al. 1993), or L1650ND5 (5′-ATTGCCTCCCACCTAATCGACC-3′), depending on species (Table 1). We used primers L5216, H6313, L5758, and H5766 (Sorenson et al. 1999) to amplify and sequence

TABLE 1. Taxa, specimens, GenBank accession numbers, and primers used in molecular phylogenetic analyses.

Species	Voucher [a]	Locality	Genbank accession numbers [b]	Primers [c]
Catharus gracilirostris	LSUMNS JMB1065	Costa Rica	AY049497, 049521, 049476	L14703, BFIB-CathU1, BFIB-B17L
C. aurantiirostris	FMNH343,295	Mexico	AY049489, 049515, 049470	L14703, BFIB-CathU2, BFIB-B17L
C. fuscater	LSUMNS MJB593	Peru	AY049494, 049518, 049473	L14703, BFIB-B17U, BFIB-B17L
C. occidentalis	FMNH343,304	Mexico	AY049505, 049523, 049478	L14841, BFIB-CathU1, BFIB-B17L
	FMNH343,305	Mexico	AY049506	
C. frantzii	FMNH346,799	Mexico	AY049493, 049517, 049472	L14841, BFIB-B17U, BFIB-B17L
	FMNH346,797	Mexico	AY049492	
C. mexicanus	FacCiMEX66	Mexico	AY049501, 049522, 049477	L14841, BFIB-B17U, BFIB-B17L
	FacCiMEX106	Mexico	AY049500	
C. dryas	LSUMNS TJD3015	Peru	AY049491, 049516, 049471	L14841, BFIB-B17U, BFIB-B17L
C. fuscescens	UAM13414	Nova Scotia	AY049496, 049519, 49474	L14841, BFIB-B17U, BFIB-B17L
	UAM13416	Nova Scotia	AY049495	
C. minimus	UAM13406	Newfoundland	AY049502, 049526, 049481	L14703, BFIB-CathU1, BFIB-CathL1
	UAM13410	Alaska	AY049503	
C. bicknelli	UAM13408	Vermont	AY049490, 049520, 049475	L14703, BFIB-B17U, BFIB-CathL1
C. ustulatus	UAM13411	British Colombia	AY049508, 049527, 049482	L14703, BFIB-B17U, BFIB-CathL1
	UAM13409	Newfoundland	AY049507	
C. guttatus	UAM13412	Alaska	AY049499, 049524, 049479	L14703, BFIB-B17U, BFIB-B17L
	UAM13415	Newfoundland	AY049498	
Sialia sialis	UAM11769	Minnesota	AY049488, 049510, 049465	L14703, BFIB-B17U, BFIB-CathL1
Myadestes unicolor	CNAV25200	Mexico	AY049487, 049513, 049468	L1650, BFIB-B17U, BFIB-B17L
Entomodestes leucotis	LSUMNS TJD3558	Peru	AY049483, 049509, 049464	L14703, BFIB-B17U, BFIB-B17L
Ixoreus naevius	UAM8579	Alaska	AY049485, 049512, 049467	L14703, BFIB-B17U, BFIB-B17L
Hylocichla mustelina	UAM13413	Virginia	AY049504, 049525, 049480	L14851, BFIB-B17U, BFIB-CathL1
Platycichla leucops	LSUMNS TAP2293	Peru	AY049486, 049514, 049469	L14703, BFIB-CathU1, BFIB-CathL1
Turdus obscurus	UAM9090	Alaska	AY049484, 049511, 049466	L14703, BFIB-B17U, BFIB-B17L

[a] Collections: LSUMNS = Louisiana State Museum of Natural Science; FMNH = Field Museum of Natural History; FacCiMEX = Museo de Alfonso Herrera, Facultad de Ciencias, Universidad Nacional Autonoma de Mexico (UNAM); UAM = University of Alaska Museum; and CNAV = Coleccion Nacional de Aves, Instituto de Biologia, UNAM.

[b] Accession numbers for cytochrome *b*, ND2, and the β-fibrinogen intron.

[c] Primer list includes species-specific primers for cytochrome *b* and β-fibrinogen amplification and sequencing. All other cytochrome *b*, ND2, and β-fibrinogen primers used are listed in text.

ND2. Different forward and reverse primers were used to amplify and sequence β-fibrinogen, depending on species (Table 1). The β-fibrinogen primers included FIB-B17U (Prychitko and Moore 1997), FIB-CathU1 (5′-GCATGTACTTCAGTACTTATG-3′), FIB-CathU2 (5′-CTTATGACAGAGACAATGATGG-3′), FIB-B17L (Prychitko and Moore 1997), FIBCathL1 (5′-CCCAGTAGTATCTGCCATTAGG-3′), FIBCathUint(5′-CTCTAATCTATGCTTAATACC-3′), and FIBCathLint (5′-GCAATGAGAAATG-TATGTCTTC-3′).

Cycle-sequenced products were electrophoresed on an automated sequencer (ABI 373A, Applied Biosystems). Sequences from opposite strands were reconciled, data were critically examined, and protein coding was verified for cytochrome *b* and ND2 using SEQUENCHER, version 3.0 (Gene Codes, Ann Arbor, Michigan). To avoid accidental amplification of nuclear copies of mitochondrial genes (Sorenson and Quinn 1998), we used only muscle tissue for extractions, because avian blood is nucleated. We also amplified fragments that were ≥1,000 bp in length, no co-amplified peaks were observed in any of the mtDNA sequences, and each of the protein-coding gene sequences yielded uninterrupted amino acid open-reading frames. All sequences were deposited in GenBank (Table 1).

Because an initial phylogeny based on cytochrome *b* was strikingly different from the traditional understanding of relationships in the group, we analyzed multiple individuals for several species to verify their monophyly (Table 1). These additional sequences supported the initial cytochrome-*b* results, so we continued with the original set of individuals, sequencing both ND2 and the nuclear β-fibrinogen intron to achieve better resolution of the implied relationships and to be more likely to recover the group's phylogeny rather than a single gene tree.

Phylogenetic analyses.—We used PAUP*, version 4.0b8 (Swofford 2001) and unweighted parsimony to analyze the morphological data, and PAUP* and MACCLADE, version 4.03 (Maddison and Maddison 2001), to estimate morphological character states on topologies (Swofford 2001). Morphological character states were unordered. Maximum-likelihood (ML) analyses were used to reconstruct relationships for each molecular data set using PAUP* (Swofford 2001). Minimum parameter substitution models were determined using MODELTEST, verison 3.06 (using Akaike's Information Criterion [AIC]; Posada and Crandall 1998). Bootstrap support was evaluated for each tree by resampling the data matrices 1,000 times (Felsenstein 1985). Because the gene trees had similar topologies, we did a partition homogeneity test to verify that the molecular data sets could be combined (Farris et al. 1995a, b; Swofford 2001). The combined data set was then examined as above using MODELTEST to determine ML parameters. The most appropriate model was the general time-reversible model with among-site rate variation approximated using the proportion of invariable sites and the gamma distribution (GTR+I+Γ). To evaluate whether MODELTEST parameters gave the best likelihood score, we used sequential approximations and ran to termination to re-estimate both the proportion of invariable sites and the gamma distribution. The values produced were not markedly different from MODELTEST scores. The combined data set was then bootstrapped heuristically using ML (GTR+I+ Γ) and 1,000 replicates.

We also conducted Bayesian analyses on the combined molecular data set because of the additional strengths and complementarity that such analysis can bring to phylogenetic reconstruction (Huelsenbeck et al. 2001, Holder and Lewis 2003). This method provides the most probable tree and the posterior probabilities for each clade under a Bayesian framework using a Markov chain Monte Carlo algorithm (Larget and Simon 1999). The same model of evolution as that used in the ML analyses was implemented using MRBAYES, version 2.01 (Huelsenbeck and Ronquist 2001). Two runs with random starting trees were used to ensure that the Markov chain converged on optimal log likelihood values, and that they converged to similar values that were themselves similar to those obtained in ML analyses. The initial 24,449 generations sampled (of a total of 60,000 generations) before the Markov chain reached a plateau were discarded (Huelsenbeck and Ronquist 2001), and a majority-rule consensus tree was constructed from 3,550 trees sampled following the burn-in using PAUP*. The posterior probabilities of clades were determined as the percentage of occurrence of each clade among the 3,550 sampled trees (Huelsenbeck and Ronquist 2001). This consensus tree had

a topology identical to that of the ML tree for nodes that were strongly supported under ML (e.g., >75% bootstrap support) but, in general, this Bayesian consensus tree provided better resolution, including for some nodes that were less well-supported under ML.

Our data set was computationally tractable for ML heuristic bootstrapping, and we therefore obtained two estimates of support for each node in our reconstructed trees. Although under some conditions Bayesian analysis may provide overconfident probability levels for phylogenetic reconstructions (Suzuki et al. 2002, Simmons et al. 2004), under appropriate models of molecular evolution these analyses appear to perform well compared with nonparametric bootstrapping methods (Alfaro et al. 2003, Erixon et al. 2003). Because uncertainties remain in just how to interpret Bayesian probability values, we chose to be conservative and accept only nodes with 1.0 Bayesian posterior probability.

Two molecular phylogenies of *Catharus* have appeared since we began our study (Outlaw et al. 2003, Klicka et al. 2005). *Catharus* data were shared between these two studies. Both studies used a single locus (mtDNA), and Outlaw et al. (2003) omitted *H. mustelina* (despite longstanding recognition of its close relationship), included unvouchered material in a notoriously difficult taxon (Phillips 1969), and did not state methods used to eliminate possible nuclear DNA contamination from blood samples (avian red blood cells are nucleated). Given these issues, we considered that replication, inclusion of nuclear sequence data, and inclusion of *H. mustelina* were all imperative to conclusively resolve the phylogeny of the genus in relation to the questions we pose. Our results corroborate some of the findings of these studies (e.g., multiple origins of migration) but provide important extensions and a conclusive resolution to the long problem of *Catharus–Hylocichla* relationships (see Winker and Rappole [1988] for a summary), including the evolutionary distribution of long-distance migration in this group.

We compared topologies reconstructed from the morphological and combined molecular data sets under our null, *a priori* hypothesis that they would be equivalent. Initially, we tested whether both phylogenies were equally supported by the morphological data using a parsimony-based form of the Kishino-Hasegawa (Kishino and Hasegawa 1989) test (K-H) as implemented in PAUP* with 1,000 bootstrap replicates. Because *Entomodestes leucotis* and *C. bicknelli* were not represented in the morphological data set, we eliminated them from the molecular tree without changing the overall topology. Outgroup species in three genera (*Turdus*, *Myadestes*, and *Platycichla*) differed between the morphological and molecular data sets; we considered them equivalent generic-level taxa for outgroup purposes. We then used the K-H, one-tailed, likelihood-based method with 1,000 bootstrap replicates to test whether both phylogenies were equally supported by the molecular data set. Because the K-H test can be inappropriate for *a posteriori* topology comparisons (Goldman et al. 2000), we also compared topologies using the Shimodaira-Hasegawa (Shimodaira and Hasegawa 1999) likelihood test (S-H) in PAUP* to determine whether the two phylogenies were equally good explanations of the molecular data set. We also used the S-H test to evaluate whether the combined molecular phylogeny was a significantly better representation of the molecular data than a topology in which the migratory species of *Catharus* (with and without *H. mustelina*) were constrained to be monophyletic (an *a posteriori* test).

Tests for correlated evolution between long-distance migration and morphological traits were made using DISCRETE (Pagel 1994, 1999). This test for correlated evolution between pairs of traits uses the Markov model in an ML context and does not require reconstruction of ancestral states; uncertainty of ancestral states is accounted for in the analyses. *P* values were obtained through estimates after 150 simulations. This test requires a fully resolved, bifurcating tree, and binary characters. Thus, we used the fully resolved Bayesian tree, which gave weak support (66% posterior probability from a consensus of 3,550 sampled trees) to a sister relationship between *C. gracilirostris* and the *C. fuscescens–minimus–frantzii* clade. An alternative, omission of *C. gracilirostris*, did not appreciably change the results. Multistate characters were collapsed to binary states for testing as required by DISCRETE (Pagel 1994, 1999). This binarization was in some cases very simple (e.g., character 9 became a solid-colored [0] vs. bicolored [1] lower mandible) and in others more complex (e.g., predominant character state among long-distance migrants [1] vs. all other states [0]; see DISCRETE documentation).

Although many other analyses could be made to examine morphological and molecular evolution in the group (and we have explored some of these), they do not bear directly on the questions posed and do not affect the outcome of the analyses presented here.

RESULTS

Phylogenetics.—Analysis of the morphological data set resulted in 27 equally parsimonious trees (length 185 steps), and a 50% majority-rule consensus tree had a topology identical to that of the bootstrapped consensus tree (1,000 replicates; Fig. 1). There was weak morphological support for a monophyletic group that included all presently recognized *Catharus* species and *H. mustelina* (Fig. 1; recognize that morphological data sets typically have fewer characters than molecular data sets and often have correspondingly lower bootstrap values). Within this clade, there was also weak support for the traditional hypothesis that the Nearctic–Neotropic migratory *Catharus* species (*fuscescens, minimus–bicknelli*, *guttatus*, and *ustulatus*) are members of a clade that includes *H. mustelina* (Fig. 1, clade B). This group (clade B) was, in fact, once treated as the genus *Hylocichla* (AOU 1957). The characters associated with this migratory clade will be considered in more detail below.

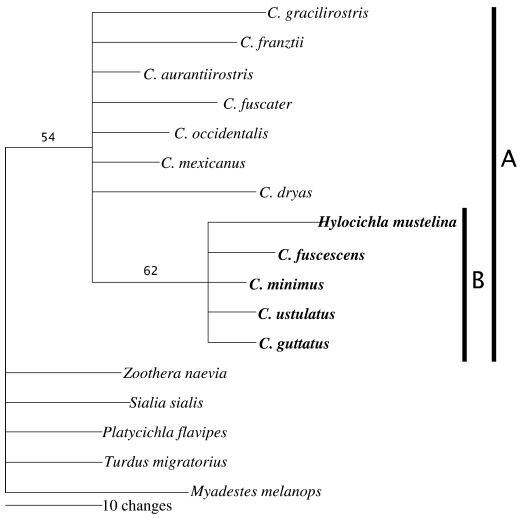

FIG. 1. Morphological phylogeny of the *Catharus* species and *H. mustelina* (clade A) based on 45 characters (Appendix), showing branch lengths, bootstrap support (consensus of 1,000 replicates), and the occurrence of long-distance seasonal migration in the traditional subgenus *Hylocichla* (clade B). Within the ingroup, taxa in bold are obligate, long-distance seasonal migrants.

Molecular analyses showed strikingly different results. Maximum-likelihood and Bayesian analyses for each of the three molecular data sets yielded trees with similar topologies (not shown), and the partition homogeneity test indicated that these sequences could be combined for analysis ($P = 0.09$). Here, we present results of the combined analyses.

There was strong molecular support for monophyly of the genus *Catharus* as presently recognized (without the monotypic genus *Hylocichla*; AOU 1998), and also strong support for *H. mustelina* being sister to this group (Fig. 2; presented as though unrooted; changing outgroups had no effect on relationships of the ingroup, including *Hylocichla*). This evidence supports the traditional recognition of the close relationship between these two genera and, henceforth, we will treat them as the genus *Catharus sensu lato* while continuing to use the present name of *H. mustelina* for clarity (see AOU 1957, Winker and Rappole 1988, Sibley and Monroe 1990, AOU 1998).

Relationships among the *Catharus* species were quite different from those suggested by morphology (Figs. 1 and 2). There was no support for the traditionally grouped "migratory clade," even without *H. mustelina* (S-H tests, $P < 0.0001$). Among the outgroup taxa, the rather distant relationship of *Entomodestes* to *Myadestes* was also a surprise, running counter to traditional and previous molecular arrangements (e.g., Sibley and Ahlquist 1990; but see also Klicka et al. 2005).

The two best-supported topologies (Figs. 1 and 2) provided alternative hypotheses determined *a priori* to be testable using each data set. Importantly, the two phylogenies were not significantly different reconstructions of the morphological data, which reflects the comparatively weak phylogenetic signal in the morphological data (185 vs. 192 steps; K-H test, $P = 0.33$). Just as importantly, however, the molecular phylogeny explained the molecular data set significantly better than the morphological phylogeny did (K-H and S-H tests, $P < 0.0001$). In sum, the two topologies are not significantly different hypotheses from the morphological perspective, but they

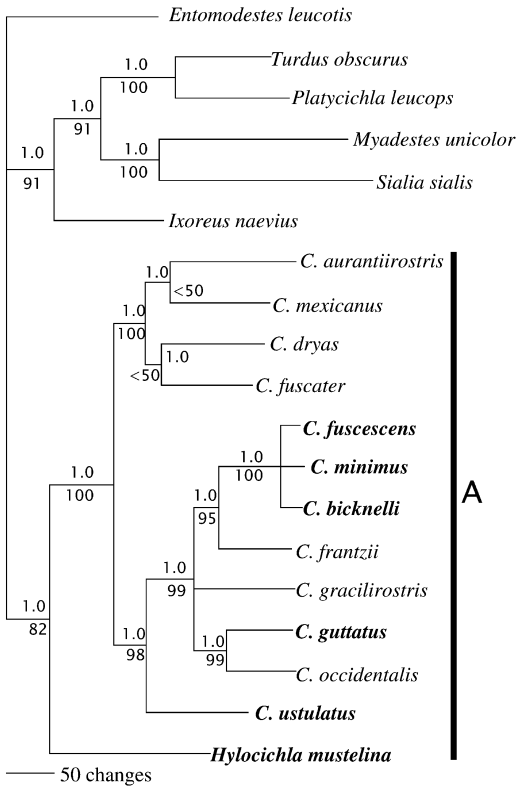

FIG. 2. Molecular phylogeny of the genus *Catharus sensu lato* (i.e., including *H. mustelina*) based on 2,920–3,027 bp from the cytochrome-*b* and ND2 genes and a β-fibrinogen intron, showing branch lengths and node support for nodes with >70% ML support (consensus of 1,000 heuristic bootstrap replicates) below, and 1.0 Bayesian posterior probability (consensus of 3,550 sampled trees) above. Within the ingroup (clade A), taxa in bold are obligate, long-distance seasonal migrants.

are strongly different when molecular data are mapped onto each tree. Given the weight of this evidence and prior suspicions of possible convergence in (yet unknown) morphological characters among the migrants, we consider the morphological phylogeny (Fig. 1) to be an inaccurate reconstruction of the evolutionary history of this group and choose instead the combined nuclear and mitochondrial DNA molecular phylogeny (Fig. 2).

Migration and morphology.—At the generic level, most species that our outgroups comprise are not long-distance migrants. Most of the species in our outgroup genera are considered resident, and only about one in five can be classified as seasonal migrants with sufficient nonbreeding distributional shifts to warrant description of wintering ranges (25 of 122 species; Sibley and Monroe 1990). The recognition that ~80% of species in our outgroup genera lack the trait of long-distance seasonal migration enabled us to polarize this character when mapping it onto the molecular phylogeny of the *Catharus–Hylocichla* clade, such that the ancestor of this clade lacked this trait (Fig. 3). This polarization involves the same number of changes (four) on this clade as would an ancestral condition of long-distance migration, and the situation is equally equivocal if we attempt to reconstruct the ancestral state of this clade without considering the outgroups. However, we consider the preponderance of evidence to indicate the likelihood of an ancestor lacking this trait. Under this framework, long-distance seasonal migration seems to have arisen independently four times in this clade (Fig. 3).

We next asked how morphological characters were associated with long-distance seasonal migration in the *Catharus–Hylocichla* clade. This comparison is independent of the polarization of the character of long-distance migration. Characters changing on the branch supporting the morphological monophyly of the Nearctic–Neotropic migratory clade (historically the subgenus *Hylocichla*; Fig. 1, clade B), are precisely those that, *a priori*, we wished to test for convergence or correlated evolution using the independently derived molecular tree. Importantly, we did not test all morphological characters scored; this would not represent *a priori* hypothesis-testing and, through control of experimentwise error, would lower statistical power over the questions posed.

Members of the traditional Nearctic–Neotropic migratory group share seven characters that changed unequivocally on the branch supporting the clade (Fig. 1, clade B). These characters included aspects of adult external morphology, song, and skeletal morphology (characters 3, 4, 9, 24, 26, 27, and 40; Appendix). Of these seven characters, three (3, 4, and 9) showed significant association with long-distance migration on the molecular phylogeny of the full *Catharus–Hylocichla* clade using a Bonferroni-corrected alpha for multiple pairwise comparisons ($P < 0.0005$ for each). These characters were spotting

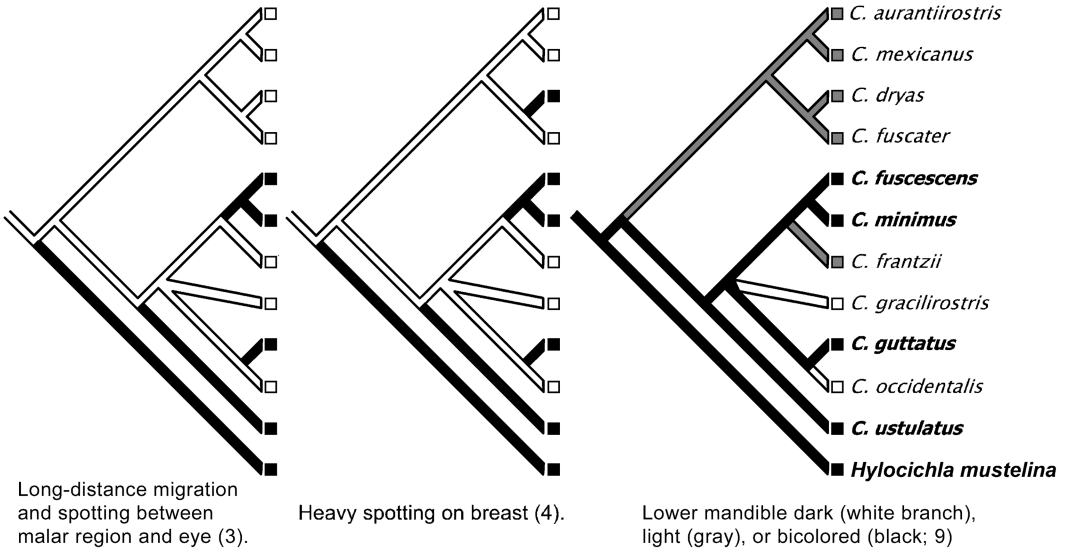

FIG. 3. Mapping morphological characters that showed unambiguous changes on the branch supporting clade B in Figure 1 onto the molecular phylogeny of *Catharus* revealed three that were significantly associated with long-distance seasonal migration. The first shown, character 3, is perfectly correlated with the presence of the character long-distance seasonal migration. Among the long-distance migrants in general, the adult facial and breast plumage spotting of characters 3 and 4 are derived, whereas the bicolored lower mandible of character 9 is ancestral.

between the malar region and eye (3), breast spotting (4), and a bicolored lower mandible (9; Fig. 3). Character 26, the presence of highly complex song, may also be associated with long-distance migration ($P = 0.016$). Bonferroni adjustment of alpha, in this case $\alpha = 0.00714$, is conservative and increases the probability of making a type II error, or accepting a null hypothesis (here, no association) that is false (Sokal and Rohlf 1995).

In addition to unambiguous character changes along the branch supporting monophyly of the Nearctic–Neotropic migratory clade (Fig. 1, clade B), six more characters showed ambiguous state changes. This ambiguity arises in part because we did not polarize characters and because of uncertainties in character-state reconstruction, but testing for the lack of an association with long-distance migration remains valid. Of these six characters (2, 15, 16, 33, 34, and 39; Appendix), which span all four of the phenotypic character groups examined, three (2, 33, and 39) were significantly correlated with long-distance migration using a Bonferroni-corrected alpha for multiple pairwise comparisons (all with $P < 0.0069$; Fig. 4). These characters were throat spotting between malar regions (2), heavy ventral spotting in the juvenal plumage (33), and moderate flaring of the *os maxillare* at the "latitude" of the vomer on the skull; these are maxillar bones in the upper jaw (39; Appendix). Character 15, a bold eye ring caused by contrasting pale feathers, may also be associated with long-distance migration ($P = 0.048$; see Bonferroni-related type II errors above).

DISCUSSION

Seasonal migration and speciation.—The genus *Catharus* (*sensu lato*; i.e., including *Hylocichla*) does not contain a simple five- or six-member subgenus that arose following the origin of long-distance migration and the subsequent colonization of new breeding areas at higher latitudes (this confirms the results of Outlaw et al. [2003] and Klicka et al. [2005]). Instead, among the full group of thrushes once considered members of the genus *Hylocichla* (the long-distance migrant thrushes [*Catharus* spp.] plus *H. mustelina*; AOU 1957), migration seems to have arisen independently four times (Fig. 2). Given its sister relationship to *Catharus*, it

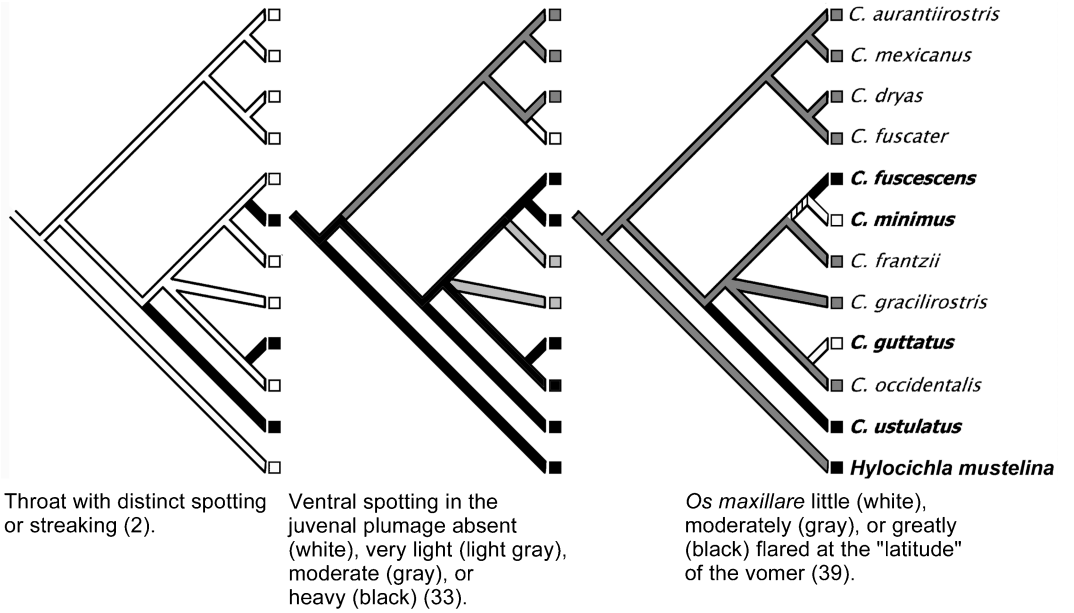

FIG. 4. Mapping morphological characters with ambiguous changes on the branch supporting clade B in Figure 1 onto the molecular phylogeny of *Catharus* showed that three were significantly associated with long-distance seasonal migration (see Fig. 3, character 3). Ancestral states in these characters were uncertain, but the best reconstructions possible suggested that among the long-distance migrants in general, throat plumage spotting (character 2) and departures from a moderately flared *os maxillare* (character 39) are derived and that ventral spotting in the juvenal plumage (character 33) is ancestral.

is taxonomically optional whether *H. mustelina* retains its monotypic generic name, but for clarity we continue to use it here. The unresolved but seemingly close relationship proposed between *Hylocichla* and the monotypic genus *Ridgwayia* by Klicka et al. (2005) requires further investigation with nuclear data.

Questions regarding the origins of migration are inherently microevolutionary and are best addressed within species (see Zink 2002, Rappole et al. 2003). For example, of the seven species of nightingale-thrushes, only two are known to be truly resident (*gracilirostris* and *fuscater*), and at least three (*aurantiirostris*, *mexicanus*, and *occidentalis*) exhibit limited-distance movements such as seasonal withdrawals from higher elevations or from the northern parts of their ranges (Phillips 1991, K. Winker pers. obs.). These movements are not well understood, and they may represent facultative or hard-weather movements, which are difficult to distinguish from true migration (Lack 1944, Ramos 1988). Nevertheless, these types of movements are often considered the precursors to true seasonal migration, and they are rather common among Neotropical birds (Levey and Stiles 1992, Winker et al. 1997, Rappole et al. 2003). Our questions regarding the evolutionary consequences of long-distance seasonal migration are properly focused at the interspecific, macroevolutionary scale.

The multiple, evolutionarily independent occurrences of the presence and absence of the character of long-distance seasonal migration in *Catharus* spp. and *H. mustelina* come as a surprise, given the traditional understanding of relationships in this group. Long-distance seasonal migration arose independently among many avian lineages in the class Aves, and other molecular studies have confirmed this (e.g., Joseph et al. 1999, 2003). The phylogeny of these thrushes (Fig. 2) confirms the apparent ease with which this trait is gained or lost in evolutionary time, even within a genus. Although we believe the evidence points to the likelihood that the ancestor of the *Catharus–Hylocichla*

clade was not a long-distance seasonal migrant, our results may not be definitive. Thus, our question regarding the effects of migration on subsequent lineage differentiation is not strongly resolved. Long-distance migration in the *Catharus–Hylocichla* clade is not associated with an entire (albeit small) subgeneric species flock, but the trait is associated with continued differentiation regardless of the ancestral state. Given the surprising evolutionary history of this group (in sharp contrast to traditional hypotheses), this system does not provide a strong test of the competing hypotheses regarding migrant lineage differentiation. It is only clear that a migratory life history does not stop differentiation in evolutionary time; whether it might, in fact, stimulate differentiation is a question that must be resolved in other systems.

Morphological convergence.—The morphological data did not provide a strongly resolved phylogeny, and the best phylogeny reconstructed from these data was not congruent with the strongly resolved molecular phylogeny. Perhaps it should not be surprising that morphology has provided a misleading indicator of relationships in this group. For example, although birdwatchers often have difficulty distinguishing *C. minimus* from *C. ustulatus* outside of the breeding season, when they are not readily separable by song or forest type, these two species are quite distinct skeletally and have not been considered sister species by students of the genus (Marshall 2001). Helbig et al. (1996) also found phenotypic evidence to be a misleading indicator of relationships among a temperate, largely migratory group of Old World warblers (Sylviidae: *Phylloscopus*). However, the depths to which morphology may be misleading in *Catharus sensu lato* have not been fully appreciated.

Morphological convergence appears to be common among some swimming waterbirds (McCracken et al. 1999), for example, but aside from the development of more pointed wings (Kipp 1942, Rensch 1959, Winkler and Leisler 1992), evidence for phenotypic convergence among long-distance migrants has generally been lacking. However, as our study shows, this may be a consequence of not looking, for given other evidence (e.g., *zugunruhe*, hyperphagia) it seems likely. There is some evidence of ecomorphological convergence between New World warblers in the genus *Dendroica* (Parulidae) and Old World warblers in the genus *Phylloscopus* (Sylviidae; Price et al. 2000), but how these primarily mensural characters might be associated with long-distance migration, and whether nonmensural traits in these groups also show convergence, has not been determined.

The suite of characters showing significant association with long-distance migration clearly includes three of the four phenotypic character sets examined (adult external morphology, juvenal plumage, and skeletal morphology; Figs. 3 and 4), and it may include the fourth (song) as well (in highly complex song, character 26; see above). This full suite of characters is dominated by pattern contrasts in plumage and bill but includes one skull character and perhaps one song character. The six characters that are clearly significantly associated with long-distance migration (Figs. 3 and 4) include both derived characters (2–4) and differentially retained (9, 33) or lost (39) ancestral characters. Morphological convergence among the long-distance migratory lineages thus occurs through a somewhat complex process of intrageneric parallel evolution in which there is independent acquisition of similar characters among related lineages through similar developmental pathways (strict parallel evolution; Futuyma 1998) and the differential retention of ancestral characters.

Richman and Price (1992) and Richman (1996) found that major ecological and morphological shifts in an assemblage of *Phylloscopus* (Sylviidae) occurred early in the evolution of the group. Our evidence of morphological changes occurring repeatedly in association with long-distance migration may seem, on the surface, to be different from Richman's (1996) findings, but his study and Richman and Price (1992) did not examine similar questions or data sets. We did not assess ecological characteristics of thrushes in the genus *Catharus* or focus on ecomorphological characters that would provide an idea of how thrush bauplans changed through evolutionary time. Instead, we examined primarily traditional, largely nonmensural morphological characters such as plumage and skeletal characteristics to learn about possible associations with migration. In our study, plumage characters, long viewed as rather plastic among birds (e.g., owing to sexual selection), represented four of the six characters that clearly showed an association with migratory lineages.

The center of diversity within *Catharus sensu lato* is in the Neotropics, and we consider that migratory lineages in this group colonized breeding areas at higher latitudes, returning annually to what might be considered ancestral Neotropical ranges (Mayr 1946, Rappole 1995, Joseph 2005). Convergent adaptive change to a migratory life-history strategy in characteristics such as more pointed wings and *zugunruhe* (all of these migrants migrate at night) could be paralleled by adaptations to new environmental conditions in higher-latitude breeding areas. Most of the characters associated with migratory lineages in this group (considering the six that are clearly so and character 15) are on the head and venter, and they may be related in some manner to vision, feeding, and predator avoidance in the lower-statured, sun-dappled forests of higher latitudes. Field experience with most of these species (K.W.) suggests that general forest differences such as canopy height, forest composition, and light conditions at and near the forest floor could be a reasonable basis for the associations of these characters with the migratory lineages in this group. Further studies in ecomorphology are warranted.

Adoption of seasonal migration as a life-history strategy does not appear to diminish a propensity for differentiation in this group. At the same time, however, differentiation following the origin of migration is more limited than our traditional understanding of relationships suggested. The historical inaccuracy does have some morphological support (e.g., Fig. 1), but this is attributable to characters that have had a tendency to either develop or be retained among the migratory lineages. These characters tend to be on the head and venter, such as a bicolored lower mandible and head, throat, and breast spotting. This apparent morphological convergence may be related to environmental conditions in the higher-latitude forests in which the long-distance migrants breed, in which lower forest stature results in a more sun-dappled understory and forest floor, where individuals of these species spend most of their time.

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APPENDIX: CHARACTERS USED IN THE MORPHOLOGICAL ANALYSES

ADULT EXTERNAL MORPHOLOGY (A)

1. Sexual plumage dichromatism. (Note: unless otherwise mentioned, scores were 0 = absent, 1 = present; and for species exhibiting dichromatism, only adult female traits were scored for characters 2–18.)
2. Throat with distinct spotting or streaking (strict throat: between malar regions).
3. Spotting between malar region and eye.
4. Breast spotting.
5. Abdominal spotting.
6. Throat and breast uniform in basal coloration (independent of spots, if present).
7. Basal breast coloration different from basal abdomen coloration.
8. Spotting on flanks.
9. Lower mandible dark (1), light (2), or bicolored (3).
10. Basal color of abdomen (*sensu stricto*) similar to undertail covert coloration.
11. Leg coloration light or dark.
12. Sharp contrast between cheek and throat in basal color.
13. Bold covert markings on greater wing coverts causing "wing bars."
14. Flank coloration differs from abdomen coloration.
15. Bold eye ring caused by a ring (or two semicircles) of contrasting (pale) feathers.
16. Bold eye ring caused by contrasting eyelid coloration.
17. Facial pattern resembles hood or mask.
18. Pattern of dorsal versus ventral coloration. Common "pale below, darker above" pattern, with a general lack of bright "advertising" coloration (0); venter with bright coloration exceeding brightness of dorsum (1); dorsum with bright coloration exceeding brightness of venter (2); dorsal coloration approximately same as ventral coloration (3).

19. Pale wing "windows" or pattern present on secondaries (visible mostly from the underwing; extends in one band into primaries in some species).

20. Crown coloration same as back coloration.

21. Dorsal surface of tail, upper tail coverts, or both with brighter coloration than rest of dorsum.

22. Upper mandible dark.

23. Upper mandible between nares sharply compressed, forming a pronounced ridge (1); moderately compressed (2), or rounded (3).

24. Primary emargination pattern: emargination shown in primaries 8 and 7 (1); 8, 7, and 6 (2); 8, 7, 6, and 5 (3); 8, 7, 6, 5, and 4 (4).

Song (B)

25. Clarity of notes: clear, flutelike (1); burry (2); both clear and burry (3).

26. Complexity of song: simple (1); moderately complex (2); highly complex (3).

27. Sonic "spiralling" absent (1); present in small amounts (2); much, or predominates (3).

28. Pace: slow or relaxed (1); moderate (2); rapid (3).

29. Song broken into distinct utterances (0); or more-or-less one continuous utterance (1).

30. Within song, distinct, separable phrases are strongly separable (1); somewhat separable (2); or distinctly separable phrases absent (3). (Note: this is different from complexity; for example, *H. mustelina* and *C. fuscescens* are both complex, but only the former has distinct phrases.)

Juvenal External Morphology (C)

31. Greater secondary covert spotting.

32. Lesser secondary covert spotting.

33. Ventral spotting absent (0), very light (1), moderate (2), or heavy (3).

34. Dorsal spotting absent (0), very light (1), moderate (2), or heavy (3).

Skeletal Morphology (D)

Skeletal characters were examined across several series to determine robustness of characters.

35. Posterior nostril rim on upper side, before apex of curve, smooth (0), or with small process causing nostril shape to be described by concave and convex curves (1).

36. Manner in which "stirrups" of nasal saddle join outer edge of mandible at posterior edges of nostrils: rather smoothly (0), or with slight or moderate projection or process protruding into open "nostril space" (1).

37. Pubis extends to (or very near to) caudal terminus of sternum (1), or ends more anteriorly (0).

38. Bill from anterior of vomer to tip of rostrum maxillare decidedly greater (3), equal to, or slightly greater (2), or shorter (1) than inter-quadratum distance (where inter-quadratum distance is taken between outer edges).

39. *Os maxillare* little (0), moderately (1), or greatly (2) flared at "latitude" of vomer.

40. Most caudal parapophysis (Howard 1929: 321) on pelvis narrow (0), moderately (1), or heavily (2) thickened.

41. Penultimate caudal parapophysis on pelvis narrow (0), moderately (1) or heavily (2) thickened.

42. Ratio of tibiotarsus to femur (tib:f): tib:f < 1.7 (0), 1.7 < tib:f < 2.0 (1), tib:f ≥ 2.0 (2). (Note: critical values here and in 43 and 44 were based on groupings of measurement ratios when graphed among all taxa.)

43. Ratio of tibiotarsus:tarsometatarsus (tib:tar): tib:tar < 1.4 (0), tib:tar > 1.4 (1).

44. Ratio of tarsometatarsus:femur (tar:f): tar:f < 1.35 (0), tar:f > 1.35 (1).

45. Raised (1) or depressed (0) bone surface in the center of the region just anterior to the occipital condyle. This is, essentially, the shape of the *lamina parasphenoidalis* and the *fossa subcondylaris* (after Baumel and Witmer 1993:117, 118).

Specimens Used

Letters A, C, and D refer to categories above. All specimens are from USNM, except as indicated.

Turdus migratorius: (A) 438,009 and 437,883; (C) 2218 and 566,596; (D) 556,870, 491,404, 491,365, 491,848, 610,518, 502,307, 432,587, 491,363, 554,025.

Ixoreus naevius: (A) 365,789 and 271,574; (C) 591,748 and 165,828; (D) 612,997.

Sialia sialis: (A) 382,780 and 141,555; (C) 596,983 and 596,984; (D) 613,952, 611,176, 611,174, 489,942, 611,175, 611,177.

Platycichla flavipes: (A) 374,592 and 374,593; (C) 403,216 and 374,596; (D) 612,081.

Myadestes melanops: (A) 459,009 and 485,978; (C) 33,294 and 198,455; (D) 613,338.

Hylocichla mustelina: (A) 437,504 and 480,767; (C) 118,442 and 175,832; (D) 488,677, 432,519,

556,939, 432,518, 490,112, 554,209, 498,742, 489,778, 502,003, 488,611, 432,517, 432,320, 561,092.

Catharus fuscescens: (A) 382,036 and 382,057; (C) 156,299 and 438,327; (D) 499,526, 560,095, 501,951, 560,098, 560,345, 429,830, 4,930, 560,099, 553,565, 4,929.

C. minimus: (A) 382,031 and 382,014; (C) 111,773; (D) 556,911.

C. ustulatus: (A) 382,045 and 382,042; (C) 438,150 and 418,516; (D) 492,810.

C. guttatus: (A) 397,059 and 397,062; (C) 591,780 and 591,773; (D) 558,041.

C. gracilirostris: (A) 208,983 and 208,980; (C) 198,445 and 198,444; (D) 613,334, 345,535, and UMMZ 131,363, 153,294, 153,295, 210,650, 210,651, 210,649, 214,057.

C. aurantiirostris: (A) 447,271 and 447,274; (C) 198,431 and 198,466; (D) 428,737 and 428,816.

C. fuscater: (A) 387,903 and 387,901; (C) 374,610, 273,314, and 369,692; (D) 432,604.

C. occidentalis: (A) 142,452 and 185,753; (C) 142,433 and 165,610; (D) 500,611.

C. frantzii: (A) 485,998 and 471,561; (C) 30,483; (D) 488,508 and 431,179.

C. mexicanus: (A) 360,052 and 360,053; (C) 476,108; (D) FMNH 343,308, 323,480, 343,306, 343,307.

C. dryas: (A) 486,567 and 486,568; (C) FMNH 294,480; (D) FMNH 323,480.

DATA MATRIX.

C. gracilirostris	0 0 0 0 0 0 1 0 1 1 1 0 0 0 0 0 0 0 0 1 0 1 2 3 3 3 3 2 1 1 0 0 1 0 0 0 1 3 1 1 1 2 0 1 1
C. aurantiirostris	0 0 0 0 0 0 1 0 2 0 0 0 0 1 0 1 0 0 2 1 0 0 1 3 3 2 1 3 0 1 1 1 2 1 0 0 0 3 1 1 2 1 0 1 0
C. fuscater	0 0 0 0 0 1 1 0 2 0 0 1 0 1 0 1 0 0 0 0 1 0 0 1 4 1 2 1 1 0 1 0 0 0 0 0 0 0 3 1 1 1 1 0 1 0
C. occidentalis	0 0 0 0 0 1 1 0 2 1 0 0 0 1 0 0 1 0 3 1 0 1 1 3 3 2 2 3 1 2 1 1 3 1 0 0 0 3 1 0 2 1 0 1 0
C. frantzii	0 0 0 0 0 1 1 0 2 1 0 0 0 1 0 0 0 0 0 1 1 0 1 1 3 3 3 3 1 1 2 0 0 1 0 0 1 0 3 1 2 2 1 0 1 1
C. mexicanus	0 0 0 0 0 0 1 0 2 1 0 0 0 1 0 1 0 0 3 0 0 1 1 3 3 2 2 2 1 1 1 1 2 2 0 0 0 3 1 1 1 1 0 1 0
C. dryas	0 0 0 1 1 1 0 0 2 1 0 1 0 1 0 1 1 0 1 0 0 0 1 4 3 1 1 1 0 1 0 1 2 2 0 1 0 3 1 1 2 1 0 1 1
C. fuscescens	0 0 1 1 0 0 1 0 3 1 0 0 0 1 0 0 0 0 3 1 0 1 1 2 3 3 3 3 1 3 1 1 3 3 0 0 0 2 2 1 1 1 0 1 0
C. minimus	0 1 1 1 0 0 1 0 3 1 0 0 0 1 0 0 0 0 3 1 0 1 1 2 2 3 3 3 1 2 1 1 3 3 0 0 0 3 0 2 2 1 0 1 0
C. ustulatus	0 1 1 1 0 0 1 0 3 1 0 0 0 1 1 0 0 0 3 1 0 1 2 1 3 3 3 3 1 2 1 1 3 3 0 0 0 2 2 0 2 1 0 1 0
C. guttatus	0 1 1 1 1 1 1 0 3 1 0 0 0 1 1 0 0 0 3 1 1 1 1 3 3 3 3 2 1 1 1 1 3 3 0 0 0 3 0 0 2 1 0 1 0
Hylocichla mustelina	0 0 1 1 1 1 0 1 3 1 0 0 0 1 1 0 0 0 2 1 0 1 1 2 3 3 2 2 1 1 1 1 3 1 0 1 0 3 1 0 2 1 0 0 0
Ixoreus naevius	1 0 0 0 0 0 1 1 1 0 0 1 1 1 0 0 0 1 3 1 0 1 1 2 2 1 1 1 0 2 1 1 3 0 0 0 0 3 1 2 1 1 1 0 1
Sialia sialis	1 0 0 0 0 1 1 0 1 1 1 1 1 0 1 0 0 0 2 0 1 1 1 1 2 2 2 1 3 0 1 1 1 3 3 1 1 1 1 2 1 0 1 1 0 1
Platycichla leucops	1 0 1 0 0 1 0 0 1 1 0 0 0 0 0 1 0 3 0 1 0 1 2 2 3 3 1 3 0 1 1 1 3 3 0 0 0 3 1 0 1 0 1 0 0
Turdus migratorius	1 1 0 0 0 0 1 0 3 1 1 0 1 1 1 0 0 1 0 0 0 1 2 3 3 2 1 3 0 1 1 1 3 3 1 0 0 3 1 0 1 1 1 0 0
Myadestes melanops	0 0 0 0 0 0 0 0 2 1 0 0 1 0 0 0 1 3 3 1 0 0 3 4 3 2 1 1 0 1 1 1 3 3 1 0 1 1 0 1 2 0 1 0 1