

Evolution in the High Andes: The Phylogenetics of *Muscisaxicola* Ground-Tyrants

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Phylogenetic relationships within the genus *Muscisaxicola*, a primarily Andean group of tyrant-flycatchers, were studied using complete sequences of the mitochondrial genes *COII* and *ND3*. Relationships among *Muscisaxicola* species were found to differ substantially from those of previous views, suggesting convergence in traditional avian taxonomic characters within the genus. The 11 species of large, gray, "typical" *Muscisaxicola* flycatchers (including *M. grisea*, newly restored to species status) formed a distinct clade, consisting of two major groups: a clade of 6 species breeding primarily in the central Andes and a clade of 5 species breeding primarily in the southern Andes. The other 2 species traditionally placed in this genus, *M. fluviatilis*, an Amazonian species, and *M. maculirostris*, were both rather divergent genetically from the typical species, although *M. maculirostris* may be the sister taxon to the typical clade. The patterns of sympatry exhibited by *Muscisaxicola* species in the high Andes appear to be the consequence of speciation and secondary contact within regions of the Andes, rather than a result of dispersal between regions. Diversification of the typical *Muscisaxicola* species appears to have occurred during the middle and late Pleistocene, suggesting generally that taxa of the high Andes and Patagonia may have been greatly influenced by mid-to-late Pleistocene events. There were likely several independent developments of migration within this genus, but migration is probably ancestral in the southern clade, with subsequent loss of migration in two taxa. © 2000 Academic Press

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The Andes have provided exceptionally fertile ground for the study of biogeography, geographic variation, and speciation (e.g., Chapman, 1917, 1926; Vuilleumier, 1969; Vuilleumier and Simberloff, 1980; Remsen, 1984; Hillis, 1985; Fjeldså, 1985; Graves, 1985; Patton and Smith, 1992; Bates and Zink, 1994), due in large part to the patterns of elevational zonation shown by many Andean organisms and to the geogra-

phy of the mountains themselves, which occupy a narrow longitudinal but broad latitudinal range. Inhabitants of the páramo and puna, the distinctive open habitats of the high Andes, have been the focus of much of this research, numerous investigators having undertaken studies of the origins of high Andean organisms, their relationships to lowland faunas of the Neotropics, their adaptive strategies, or their diversification and radiation (see especially papers in Vuilleumier and Monasterio, 1986). Few of these studies, however, have adopted a phylogenetic approach.

Muscisaxicola ground-tyrants (Aves: Passeriformes, Tyrannidae) are a characteristic group of the high Andes and exhibit many of the features typical of high Andean organisms, including patterns of distribution suggestive of a complex speciation history and apparent adaptations to the high Andean environment. Eleven of the 12 traditional species (Hellmayr and Cory, 1927; Traylor, 1979) breed in open scrub and grassland in the high Andes and Patagonia (an isolate of 1 species occurs additionally on the Falkland Islands), but the other species (*M. fluviatilis*) is an exclusively lowland bird, occupying sandbars along watercourses in Amazonia. Although they occupy structurally simple habitats and are very similar behaviorally and morphologically, as many as 4–5 species of *Muscisaxicola* can be found breeding in sympatry in both the central Andes of Peru and Bolivia (Vuilleumier, 1971) and the southern Andes of Chile (Cody, 1970; R.T.C., pers. obs.). Several traits of *Muscisaxicola* species are thought to be adaptations to the extreme environments in which they occur, including inconspicuous plumage (all species are primarily gray or grayish brown, differing mainly in head markings; Table 1), relatively long legs, and simplified vocalizations (Vuilleumier, 1971); their highly terrestrial habits represent an extreme behavioral type among tyrant-flycatchers. *Muscisaxicola* is among the most migratory genera of South American birds (Chesser, 1994); 8 species are austral migrants, breeding in south temperate South America and migrating north, primarily in the Andes, for the southern winter (Chesser, 1995; Table 1).

TABLE 1
 Characteristics of Traditional *Muscisaxicola* Species

Species	Species group	Length and dorsal coloration	Distinguishing head markings	Breeding distribution	Migration
<i>Muscisaxicola maculirostris</i>	1	15 cm, Gray-brown	None	N, C, S Andes/Patagonia	Polymorphic
<i>Muscisaxicola fluviatilis</i>	1	13 cm, Gray-brown	None	Western Amazonia	Nonmigratory
<i>Muscisaxicola macloviana</i>	2	15.5 cm, Dark gray	Dark face	S Andes/Patagonia, Falkland Islands	Polymorphic
<i>Muscisaxicola capistrata</i>	2	16.5 cm, Pale gray	Dark face, chestnut crown patch	S Andes/Patagonia	Migratory
<i>Muscisaxicola rufivertex</i>	3	16.5 cm, Gray	Rufous crown patch	C Andes	Polymorphic
<i>Muscisaxicola juninensis</i>	3	16.5 cm, Gray	Rufous crown patch	C Andes	Nonmigratory
<i>Muscisaxicola albiflora</i>	3	16.5 cm, Gray-brown	Rufous crown patch	C, S Andes/Patagonia	Migratory
<i>Muscisaxicola alpina</i>	4	18 cm, Gray (C), gray brown (N)	None	N, C Andes	Nonmigratory
<i>Muscisaxicola cinerea</i>	4	16 cm, Gray	None	C Andes	Polymorphic
<i>Muscisaxicola albifrons</i>	5	20 cm, Gray	Conspicuous white lores	C Andes	Nonmigratory
<i>Muscisaxicola flavinucha</i>	5	18.5 cm, Gray	Yellow crown patch, conspicuous white lores	C, S Andes/Patagonia	Migratory
<i>Muscisaxicola frontalis</i>	5	18 cm, Gray-brown	Conspicuous white lores, dark forehead	C, S Andes/Patagonia	Migratory

Note. Species group designations follow Vuilleumier (1971). Length and dorsal coloration were taken from Fjelds  and Krabbe (1990). See Methods for further information.

Muscisaxicola is widely held to be closely related to such other ground-tyrant genera as *Agriornis* and *Xolmis* (Vuilleumier, 1971; Traylor, 1977; Lanyon, 1986), but little previous phylogenetic work has been done within the genus. Only Vuilleumier (1971) has published an explicit classification of the genus; this classification was based primarily on plumage patterns, size, shape, and proportions, and it divided the traditional genus *Muscisaxicola* into five groups of 2–3 species each (Table 1). In addition, Vuilleumier also merged the traditional *Muscisaxicola* with the monotypic genus *Muscigralla*, so that his *Muscisaxicola* was composed of the two subgenera *Muscisaxicola* (12 species) and *Muscigralla* (1 species).

Species limits in *Muscisaxicola* have been generally agreed upon in most recent treatments (e.g., Vuilleumier, 1971; Traylor, 1979; Fjelds  and Krabbe, 1990; Ridgely and Tudor, 1994), although the taxa in the *alpina*–*cinerea* group (Vuilleumier, 1971) have been the subject of some controversy. Most detailed considerations of *Muscisaxicola* (e.g., Hellmayr and Cory, 1927; Vuilleumier, 1971; Traylor, 1979) and modern volumes on South American birds (e.g., Fjelds  and Krabbe, 1990; Ridgely and Tudor, 1994) have considered *M. alpina* and *M. cinerea* to be separate species, but in the past they were sometimes considered conspecific (e.g., Hellmayr, 1932; Goodall *et al.*, 1957; Meyer de Schauensee, 1970). Fjelds  and Krabbe (1990) recently suggested that the subspecies *M. cinerea argentina* may actually be conspecific with *M. al-*

pina, and Ridgely and Tudor (1994) noted that *M. alpina grisea* may be specifically distinct from the remainder of *M. alpina* (i.e., *M. a. alpina*, *M. a. columbiana*, and *M. a. quesadae*).

In this paper, I derive a molecular phylogenetic hypothesis for the genus *Muscisaxicola* and use this phylogeny to address the following questions:

(1) Does the traditional genus *Muscisaxicola* constitute a monophyletic group? Do the individual species of *Muscisaxicola* appear to be monophyletic? Do phylogenetic relationships among species conform to ideas of relationship based on plumage and morphometric characters? Is *Muscigralla* closely related to *Muscisaxicola*?

(2) In what geographical context did the patterns of sympatry arise among *Muscisaxicola* species? Is the Amazonian isolate *M. fluviatilis* sister to the rest of the genus? What do the molecular data suggest about the time scale over which *Muscisaxicola* species have evolved?

(3) How many times and under what circumstances did migration evolve among *Muscisaxicola* species? Were there many independent developments of migration, or was there a south temperate radiation of migratory taxa from a presumed migratory ancestor?

METHODS

Tissues were obtained for individual *Muscisaxicola* species and outgroups during personal fieldwork in

TABLE 2

List of Tissue Reference Numbers, Collecting Dates, and Localities for Sequenced Individuals of *Muscisaxicola* Species and Outgroups

Species	Tissue number	Date	Locality
<i>M. albifrons</i> 1	B-22575	4 July 1993	Bolivia: Depto. La Paz, Zongo Valley, 7 km by road N of summit, 4150 m
<i>M. albifrons</i> 2	B-22576	4 July 1993	Bolivia: Depto. La Paz, Zongo Valley, 7 km by road N of summit, 4150 m
<i>M. albilora</i> 1	RTC 420	20 Nov. 1996	Chile: Region Metropolitana, Prov. Cordillera, ca. 2 km ENE Embalse El Yeso, ca. 2500 m
<i>M. albilora</i> 2	RTC 421	20 Nov. 1996	Chile: Region Metropolitana, Prov. Cordillera, ca. 2 km ENE Embalse El Yeso, ca. 2500 m
<i>M. a. alpina</i>	ANSP 2797	19 Jan. 1991	Ecuador: Chimborazo Volcano
<i>M. alpina grisea</i>	B-103805	5 June 1983	Peru: Depto. Junín, 12 km N Chinchán on road to Marcapomacocha, 4600 m
<i>M. capistrata</i> 1	RTC 377	10 Feb. 1996	Argentina: Prov. Río Negro, Depto. Ñorquinco, ca. 5 km E Manuel Choique, Ruta Provincial 6, ca. 1100 m
<i>M. capistrata</i> 2	B-103896	5 July 1983	Peru: Depto. Puno, km 73 on Puno-Desquadero Road, ca. 5 km W Juli, 3800 m
<i>M. c. cinerea</i>	RTC 422	20 Nov. 1996	Chile: Region Metropolitana, Prov. Cordillera, ca. 2 km ENE Embalse El Yeso, ca. 2500 m
<i>M. cinerea argentina</i>	JAG 1792	4 Oct. 1995	Argentina: Prov. Tucumán, El Infiernillo, 7 km N, 60 km W San Miguel de Tucumán, 3370 m
<i>M. f. flavinucha</i> 1	RTC 362	8 Feb. 1996	Argentina: Prov. Río Negro, Depto. Bariloche, Cerro Perito Moreno, ca. 20 km N El Bolsón, ca. 1500 m
<i>M. f. flavinucha</i> 2	RTC 433	21 Nov. 1996	Chile: Region Metropolitana, Prov. Cordillera, ca. 15 road km ENE Embalse El Yeso, ca. 3400 m
<i>M. fluviatilis</i>	B-1188	6 July 1981	Bolivia: Depto. La Paz, Río Beni, ca. 20 km by river N Puerto Linares, 600 m
<i>M. frontalis</i> 1	RTC 416	20 Nov. 1996	Chile: Region Metropolitana, Prov. Cordillera, ca. 2 km ENE Embalse El Yeso, ca. 2500 m
<i>M. frontalis</i> 2	RTC 432	21 Nov. 1996	Chile: Region Metropolitana, Prov. Cordillera, ca. 15 road km ENE Embalse El Yeso, ca. 3400 m
<i>M. juninensis</i>	B-1203	19 July 1981	Bolivia: Depto. La Paz, 5.4 km by road W hydroelectric dam on Zongo Valley Road, 4600 m
<i>M. macloviana mentalis</i> 1	RTC 363	8 Feb. 1996	Argentina: Prov. Río Negro, Depto. Bariloche, Cerro Perito Moreno, ca. 20 km N El Bolsón, ca. 800 m
<i>M. macloviana mentalis</i> 2	PRS 1137	9 Feb. 1996	Argentina: Prov. Río Negro, Depto. Bariloche, Cerro Perito Moreno, ca. 20 km N El Bolsón, ca. 1500 m
<i>M. m. maculirostris</i> 1	B-103851	18 June 1983	Peru: Depto. Arequipa, Cerro Cosnatire, 5 km E Chala, 425 m
<i>M. m. maculirostris</i> 2	JAG 1793	4 Oct. 1995	Argentina: Prov. Tucumán, El Infiernillo, 7 km N, 60 km W San Miguel de Tucumán, 3320 m
<i>M. rufivertex pallidiceps</i>	PRS 1120	31 Jan. 1996	Argentina: Prov. Córdoba, Depto. Punilla, Pampa de Achala, El Condor, Ruta 20, ca. 2300 m
<i>M. rufivertex occipitalis</i>	B-7728	19 Aug. 1984	Peru: Depto. Arequipa, 37 km E Arequipa by road, 11700 ft
<i>Agriornis montana</i>	RTC 423	20 Nov. 1996	Chile: Region Metropolitana, Prov. Cordillera, ca. 2 km ENE Embalse El Yeso, ca. 2500 m
<i>Lessonia rufa</i>	RTC 456	29 Nov. 1996	Chile: Region IX (de La Araucanía), Prov. Malleco, ca. 2 km by road from SE end of Lago Gualletué, near origin of río Bío-Bío, 1050 m
<i>Muscigralla brevicauda</i>	ANSP 4244	18 June 1992	Ecuador: Depto. Guayas, 5 km N Playa, 50 m
<i>Xolmis pyrope</i>	RTC 393	15 Nov. 1996	Chile: Region Metropolitana, Prov. Chacabuco, ca. 4 km SSW by road from peak of Cerro de El Roble, ca. 1600 m
<i>Tyrannus melancholicus</i>	PRS 1090	24 Jan. 1996	Argentina: Prov. Buenos Aires, Partido Magdalena, 10 km SE Punta Indio

Note. Voucher specimens for RTC and PRS numbers are housed at the American Museum of Natural History; B- numbers at the Museum of Natural Science, Louisiana State University; ANSP numbers at the Academy of Natural Sciences of Philadelphia; and JAG numbers at the Burke Museum, University of Washington.

Chile and Argentina and from the frozen tissue collections of the Museum of Natural Science, Louisiana State University; the Academy of Natural Sciences of Philadelphia; and the Burke Museum, University of Washington (Table 2). To reduce the possibility of phylogenetic errors due to incomplete lineage sorting, two

individuals of each *Muscisaxicola* species were sampled, with the exception of *M. juninensis* and *M. fluviatilis*, for which only single individuals were available. Conspecific individuals were selected from localities as distant as possible, and from different subspecies when available, to provide simple tests of

monophyly of individual species; however, in several instances conspecifics from distant localities were unavailable and individuals from the same or nearby localities were used (Table 2). Outgroups sampled included single individuals of *Muscigralla brevicauda*, *Xolmis pyrope*, *Agriornis montana*, and *Lessonia rufa*, members of ground-tyrant genera postulated to be closely related to *Muscisaxicola*, and a single individual of *Tyrannus melancholicus*, member of a tyrannid genus more distantly related to the ground-tyrants (Sibley and Ahlquist, 1985, 1990).

DNA was extracted using a 5% Chelex solution (Walsh *et al.*, 1991). Two complete, protein-coding mitochondrial genes, cytochrome oxidase II (*COII*; 684 bp) and NADH dehydrogenase subunit 3 (*ND3*; 351 bp), were amplified via the polymerase chain reaction, using standard protocols (Chesser, 1999). Primers used for *COII* were (1) L8263 (5'-GCCACTCATGCCTCTTCTTATGGG-3'; Chesser, 1999), (2) L8740 (5'-GGC-CACTTCCGACTACTAGAAGT-3'; Lee *et al.*, 1997), (3) H8856 (5'-ATGAAGGAGTTTTGATTTAGTCGTCC-3'; courtesy of J. Cracraft and J. Feinstein), and (4) H9085 (5'-CAGGGGTTTGGGTTGAGTTGTTGCAT-3'; Lee *et al.*, 1997). "H" and "L" refer here to the heavy and light strands of the mitochondrial genome, respectively, and reference numbers are for the 3' base corresponding to the chicken sequence of Desjardins and Morais (1990). Primers used for *ND3* were (1) L10755 (5'-GAC-TTCCAATCTTTAAAATCTGG-3'; Chesser, 1999), (2) H11151 (5'-GATTTGTTGAGCCGAAATCAAC-3'; Chesser, 1999), and (3) H11289 (5'-GATAGTATTATGCTTTCTAGGCA-3'; courtesy of G. Barrowlough and J. Groth). Sequencing was conducted using dye-terminator chemistry on an ABI 377 automated sequencer (Applied Biotechnologies Inc., Foster City, CA). Both heavy and light strands were sequenced for all analyzed sequences. Sequences were aligned using the computer program Sequencher 3.0 (GeneCodes, 1995). All sequences used in this study have been deposited in GenBank (Accession Nos. AF 132614–132640 for *COII* sequences; AF 132641–132667 for *ND3* sequences).

Analysis of sequence data was performed using the computer program PAUP* 4.0d64 (Swofford, 1998), with maximum-parsimony as the primary method of data analysis. *T. melancholicus* was designated the outgroup in all analyses. Parsimony analyses using branch-and-bound searches were conducted with equal character weighting and with downweighting of transitions (by 5:1, the observed transition/transversion ratio in the dataset, as estimated from the most-parsimonious tree). Character support for phylogenies was assessed via bootstrapping (Felsenstein, 1985), computed for 100 branch-and-bound replicates, and branch support (Bremer, 1988, 1994), calculated using the program TreeRot (Sorensen, 1996).

Sequence data were also analyzed using alternative

methods, because simulations have shown that agreement among phylogenies estimated using more than one method can be an index of the reliability of the resultant phylogenies (Kim, 1993). Data were analyzed using distance methods, which have been shown to find the proper tree in some instances in which parsimony fails (Hendy and Penny, 1989), and a simplified maximum-likelihood approach. Neighbor-joining analyses were conducted using uncorrected distance and Kimura two-parameter distance, and support was assessed using bootstrapping. The maximum-likelihood analysis was performed on the "typical" *Muscisaxicola* species (see below) as delineated by both parsimony and distance analyses, with *M. maculirostris* designated the outgroup. Heuristic searches were conducted with 10 random addition replicates, using a likelihood model employing empirical base frequencies, a transition/transversion ratio estimated from a neighbor-joining tree, and equal rates at all sites.

Two statistical tests were used to assess whether alternative topologies, in which *M. alpina grisea* and *M. a. alpina* were constrained to be sister taxa (see below), were significantly different from the best trees found using maximum-parsimony and maximum-likelihood, respectively. The single most-parsimonious tree was tested against the shortest constrained tree using the Wilcoxon signed ranks test (or Templeton test; Templeton, 1983). The single most likely tree was tested against the most likely constrained tree using the Kishino–Hasegawa test (Kishino and Hasegawa, 1989).

Biogeographic analysis of the genus was performed using DIVA 1.1 (Ronquist, 1996), a computer program that parsimoniously infers ancestral distributions based on phylogenetic and current distributional data, without making assumptions about general biogeographic patterns. DIVA is based on the variable assessment of costs for events such as vicariance, dispersal, and extinction. In brief, speciation events are assumed to divide ranges into vicariant components; DIVA reconstructs ancestral distributions based on minimizing the number of dispersal and extinction events implied by the ancestral distributions (see Ronquist, 1997 for complete details). Continental breeding distributions were classified as either northern Andean (from Ecuador north), central Andean (from central Argentina and Chile north to Peru), southern Andean/Patagonian (from central Argentina and Chile south), or some combination of these. Divisions between these areas correspond to natural barriers to gene flow proposed by Vuilleumier (1969): the "Northern Peruvian Low" (separating the Ecuadorian and Peruvian Andes) and the "Central Chilean–Argentine Andes" (separating the southern Chilean–Argentine Andes from the central Andes). The Falkland Islands, inhabited by *M. m. macloviana*, constituted a fourth area of classification. Because DIVA does not handle trees with polytomies,

TABLE 3

Mean Interspecific Divergence for *Muscisaxicola* Species and Outgroups Based on Complete Sequences of the Mitochondrial Genes *COII* and *ND3* (Uncorrected Distance above the Diagonal, Kimura Two-Parameter Distance Below)

	<i>Tyr.</i>	<i>Less.</i>	<i>Xol.</i>	<i>Agr.</i>	<i>M. br.</i>	<i>albif.</i>	<i>albil.</i>	<i>alp.</i>	<i>gris.</i>	<i>cap.</i>	<i>cinere.</i>	<i>flav.</i>	<i>fluv.</i>	<i>front.</i>	<i>junin.</i>	<i>macl.</i>	<i>macu.</i>	<i>ruf.</i>
<i>Tyrannus mel.</i>	—	0.133	0.137	0.134	0.152	0.143	0.143	0.143	0.139	0.143	0.140	0.140	0.155	0.143	0.144	0.143	0.133	0.142
<i>Lessonia rufa</i>	0.150	—	0.112	0.108	0.141	0.118	0.123	0.122	0.118	0.123	0.116	0.118	0.124	0.124	0.122	0.121	0.128	0.118
<i>Xolmis pyrope</i>	0.154	0.132	—	0.087	0.128	0.111	0.117	0.114	0.112	0.119	0.112	0.114	0.124	0.119	0.117	0.117	0.109	0.114
<i>Agriornis mont.</i>	0.152	0.120	0.094	—	0.129	0.102	0.113	0.110	0.103	0.108	0.103	0.105	0.107	0.111	0.106	0.111	0.102	0.106
<i>Muscigralla brev.</i>	0.173	0.160	0.142	0.145	—	0.126	0.127	0.126	0.129	0.127	0.128	0.130	0.135	0.130	0.133	0.128	0.133	0.131
<i>M. albifrons</i>	0.162	0.133	0.123	0.113	0.141	—	0.024	0.023	0.012	0.026	0.005	0.007	0.111	0.023	0.013	0.021	0.101	0.009
<i>M. albilora</i>	0.163	0.139	0.131	0.126	0.141	0.025	—	0.016	0.024	0.019	0.021	0.021	0.111	0.019	0.027	0.010	0.102	0.022
<i>M. alpina</i>	0.163	0.138	0.127	0.123	0.140	0.023	0.017	—	0.022	0.015	0.019	0.110	0.015	0.025	0.009	0.100	0.021	0.021
<i>M. (alp.) grisea</i>	0.158	0.132	0.125	0.114	0.145	0.012	0.025	0.023	—	0.024	0.008	0.010	0.110	0.023	0.014	0.020	0.105	0.012
<i>M. capistrata</i>	0.163	0.139	0.134	0.120	0.142	0.027	0.019	0.015	0.024	—	0.023	0.023	0.107	0.008	0.029	0.014	0.098	0.024
<i>M. cinerea</i>	0.159	0.130	0.125	0.114	0.144	0.005	0.022	0.020	0.008	0.023	—	0.003	0.107	0.020	0.010	0.017	0.100	0.005
<i>M. flavinucha</i>	0.158	0.133	0.128	0.116	0.147	0.007	0.021	0.019	0.010	0.023	0.003	—	0.108	0.019	0.010	0.017	0.100	0.007
<i>M. fluviatilis</i>	0.178	0.140	0.140	0.119	0.153	0.124	0.124	0.123	0.123	0.119	0.119	0.120	—	0.109	0.110	0.111	0.123	0.109
<i>M. frontalis</i>	0.165	0.141	0.134	0.123	0.146	0.024	0.019	0.016	0.023	0.008	0.020	0.020	0.121	—	0.026	0.015	0.100	0.021
<i>M. juninensis</i>	0.164	0.137	0.131	0.118	0.150	0.013	0.028	0.026	0.015	0.029	0.010	0.010	0.123	0.026	—	0.023	0.101	0.013
<i>M. macloviana</i>	0.163	0.136	0.131	0.124	0.143	0.021	0.010	0.009	0.021	0.014	0.018	0.017	0.124	0.015	0.024	—	0.101	0.019
<i>M. maculirostris</i>	0.149	0.144	0.120	0.112	0.149	0.112	0.112	0.110	0.116	0.107	0.110	0.110	0.138	0.111	0.111	0.111	—	0.102
<i>M. rufivertex</i>	0.162	0.133	0.128	0.117	0.147	0.009	0.022	0.021	0.012	0.025	0.005	0.007	0.121	0.022	0.013	0.019	0.113	—

reconstructions were conducted on all possible fully resolved most-parsimonious trees.

The evolution of migration was analyzed using the computer program MacClade 3.05 (Maddison and Maddison, 1993). Traditionally recognized species of *Muscisaxicola* either are migratory, are nonmigratory, or consist of multiple subspecies, some of which are migratory and some of which are nonmigratory (Table 1). Species in these groups were coded as “migratory,” “nonmigratory,” and “polymorphic” for the character migration, respectively. The phylogenies used for all character state reconstructions in DIVA and MacClade consisted of the clade of “typical” *Muscisaxicola* species (see below) as reconstructed by maximum-parsimony, with *M. maculirostris* as sister group. These trees were simplified by collapsing the two individuals of monophyletic species into a single taxon; however, both individuals of species not demonstrably monophyletic were included in the analyses.

RESULTS

Sequence variation. Of 1035 bp sequenced, 319 sites (30.8%) were variable, and 216 of these were phylogenetically informative. The *COII* and *ND3* sequences provided similar proportions of informative sites. First, second, and third positions varied greatly in their variability: 51 first position sites were variable (16.0% of variable sites), 19 second position sites (6.0%), and 249 third position sites (78.1%); these percentages are very similar to previous data on variability in these two genes in suboscine birds (Chesser, 1999). The two genes differed significantly ($\chi^2 = 8.69$, $df = 2$; $P = 0.013$) in their distribution of site changes, with relatively low first and especially second

position variability in *COII* (29, 6, and 161 variable sites, respectively, compared to 22, 13, and 88 in *ND3*). Ratio of synonymous to nonsynonymous substitutions was likewise significantly different (Fisher’s Exact test, $P = 0.001$), with relatively fewer nonsynonymous substitutions in *COII* (19 nonsynonymous and 177 synonymous substitutions in *COII*, and 26 and 97, respectively, in *ND3*), consistent with the known greater selective constraint on cytochrome oxidase genes (e.g., Simon *et al.*, 1994; Nachman *et al.*, 1996).

Uncorrected sequence divergence (Table 3) ranged from 10.2 to 15.5% in comparisons between ingroup (*Muscisaxicola*, as traditionally defined) and outgroup taxa. Mean interspecific sequence divergence within the traditional *Muscisaxicola* ranged from 0.3% (between *M. cinerea* and *M. flavinucha*) to 12.3% (between *M. fluviatilis* and *M. maculirostris*). Excluding *M. fluviatilis* and *M. maculirostris*, both of which were highly divergent from the rest of the genus, interspecific sequence divergence was low, varying from 0.3 to 2.9% (between *M. capistrata* and *M. juninensis*). Intraspecific sequence divergence was likewise low, varying from 0.0% between the two *M. albilora* individuals and between the two *M. macloviana* individuals to 0.5% between the two *M. rufivertex* individuals (excluding the 2.2% divergence between the two *M. alpina* individuals, which are actually representatives of two different species, as discussed below). Patterns of sequence divergence were similar for both *COII* and *ND3*, when analyzed separately.

Phylogenetics. Parsimony analysis of the equally weighted data resulted in a single most-parsimonious tree (Fig. 1; length 637, CI excluding uninformative characters = 0.50, RI = 0.66). The traditional genus

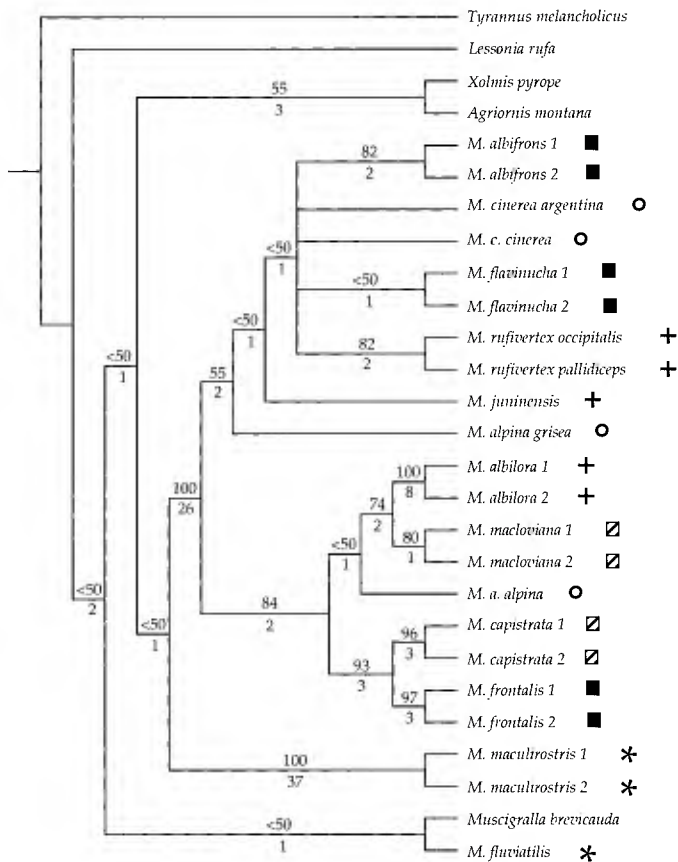


FIG. 1. Single most-parsimonious tree based on the equally weighted analysis of combined sequences of COII and ND3. Numbers above branches are percentages of time that the branch was recovered in 100 branch-and-bound bootstrap replicates, and those below branches are branch support values. Symbols following names of *Muscisaxicola* species (abbreviated using the generic initial *M.*) represent the species group designations of Vuilleumier (1971), as follows: asterisk, species group 1; striped square, species group 2; cross, species group 3; circle, species group 4; black square, species group 5.

Muscisaxicola formed a monophyletic group, with the exception of *M. fluviatilis*, which was the sister to *Muscigralla brevicauda* and only distantly related to the other *Muscisaxicola* species. Within *Muscisaxicola*, *M. maculirostris* was sister to the other 10 species (hereafter, the “typical” species or “typical” clade), which formed two monophyletic groups, a clade consisting of *albifrons*, *cinerea*, *flavinucha*, *rufivertex*, *juninensis*, and *alpina grisea* (hereafter, “clade 1”) and a clade consisting of *albilora*, *macloviana*, *alpina alpina*, *capistrata*, and *frontalis* (hereafter, “clade 2”). Relationships within clade 2 were fully resolved: *albilora* and *macloviana* were sister species, as were *capistrata* and *frontalis*, with *alpina alpina* sister to *albilora* + *macloviana*. Clade 1 contained a polytomy involving *M. albifrons*, *M. cinerea*, *M. flavinucha*, and *M. rufivertex*, with *juninensis* sister to this group and *alpina grisea* sister to *juninensis* + the polytomy species. All individual species were monophyletic, except for *M. alpina*,

which included individuals from clades 1 and 2, and possibly *M. cinerea*, for which the relationship of the two sequenced individuals was unresolved. Bootstrap support for and within the typical *Muscisaxicola* clade was strong for the most part, especially in clade 2, whereas support outside this clade was weak.

Differentially weighted parsimony analysis, with transversions weighted five times transitions, resulted in a single most-parsimonious tree (length 1071, CI excluding uninformative characters = 0.58, RI = 0.68). This tree was identical to the equally weighted tree, except that *Lessonia*, rather than *Muscigralla*, was the sister taxon to *M. fluviatilis*.

Both neighbor-joining analyses resulted in the same phylogeny (Fig. 2), which was consistent with the phylogeny obtained using equally weighted parsimony (Fig. 1), except for the positions of *M. fluviatilis* and the outgroups. Both clades of typical *Muscisaxicola* species

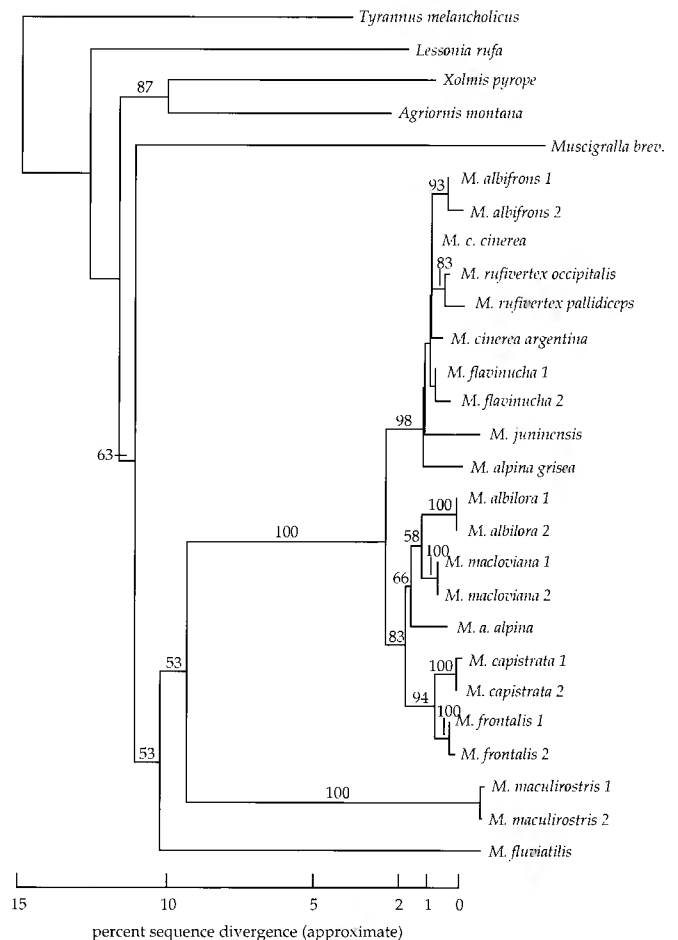


FIG. 2. Phylogram of the neighbor-joining tree constructed using combined sequences of COII and ND3. Numbers above branches are percentages of time that the branch was recovered in 1000 bootstrap replicates; branches lacking numbers were recovered less than 50% of the time. Branch lengths are proportional to the amount of character change along each branch. Approximate percentage sequence divergence is presented at the bottom of the phylogram.

were recovered in the neighbor-joining trees. Relationships within clade 2 were the same as those in the parsimony tree, and relationships within clade 1 were consistent with, although more fully resolved than, those in the parsimony tree. *M. maculirostris* was sister to the typical *Muscisaxicola* clade, and *M. fluviatilis* was sister to *maculirostris* + the typical clade.

The maximum-likelihood analysis resulted in a single most likely tree (not shown), which was similar to the phylogenies obtained using parsimony. The two clades of typical *Muscisaxicola* species were recovered in this tree, as well as sister species relationships in clade 2 between *M. albilora* and *M. macloviana* and between *M. capistrata* and *M. frontalis*; the position of *M. a. alpina* within this clade was unresolved. Relationships within clade 1 were again poorly resolved. *M. flavinucha* was found to be sister to a polytomy consisting of the following five taxa: *M. albifrons*, *M. rufivertex*, *M. juninensis*, *M. c. cinerea*, and *M. alpina grisea*/*M. cinerea argentina*, which were sisters in this tree.

Alternative topologies in which *M. alpina grisea* and *M. a. alpina* were constrained to be sister taxa were found to be significantly longer or less likely than the shortest and most likely trees, respectively ($P < 0.01$, Wilcoxon signed ranks test; $P < 0.05$, Kishino–Hasegawa tests).

Biogeography and the evolution of migration. Breeding ranges of *Muscisaxicola* species in clade 1 are primarily central Andean, whereas breeding distributions of species in clade 2 are primarily southern Andean and Patagonian (Table 1, Fig. 3). Reconstruction of ancestral distributions, using DIVA 1.1, suggested that the ancestor of clade 1 was central Andean in distribution and that *M. flavinucha* later dispersed to the southern Andes. It also suggested that the ancestor of clade 2 was southern Andean/Patagonian in distribution and that *M. albilora* and *M. frontalis* later dispersed to the central Andes, *M. macloviana* to the Falkland Islands, and *M. alpina alpina* to the northern Andes. The ancestor of the typical *Muscisaxicola* species, according to DIVA, was distributed in both the central and the southern Andes, and the ancestor of *M. maculirostris* (distributed throughout the Andes) and the typical species was distributed throughout the Andes.

Excluding *M. fluviatilis*, treating *M. alpina* and *M. grisea* as separate species, and separating *M. c. cinerea* from *M. c. argentina*, five *Muscisaxicola* taxa are migratory, five are nonmigratory, and three are polymorphic (Table 1, Fig. 4). Reconstruction of ancestral conditions using MacClade 3.05 (Fig. 4) suggested that the ancestor of clade 1 (the central Andean clade) was nonmigratory, with migration evolving independently in *M. cinerea argentina*, *M. flavinucha*, and *M. rufivertex*. The migratory condition of the ancestor of clade 2

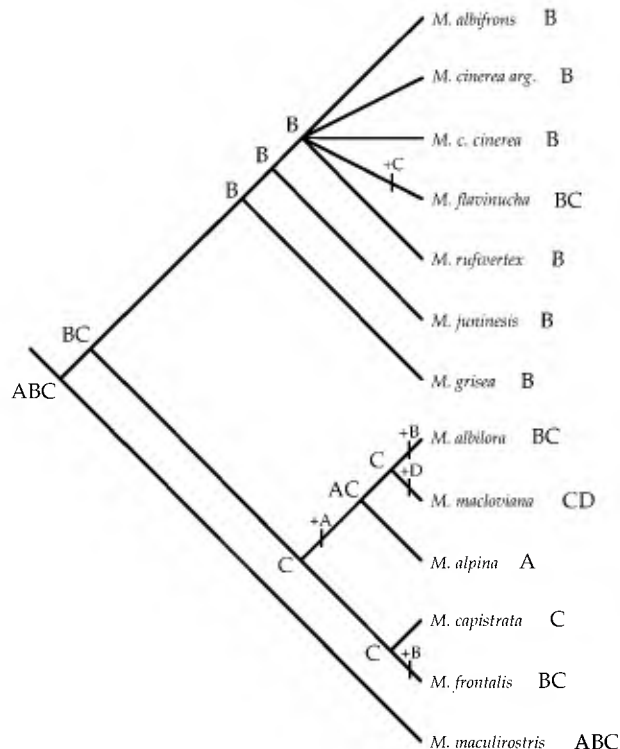


FIG. 3. Reconstruction of ancestral geographic ranges in the genus *Muscisaxicola*, based on dispersal–vicariance analysis (Ronquist, 1996). Key: A, northern Andes (from Ecuador north); B, central Andes (from central Argentina/Chile north through Peru); C, southern Andes (from central Argentina/Chile south) and Patagonia; D, Falkland Islands. Symbols beside taxon names represent current distributions and those on internal nodes ancestral distributions. Presumed dispersal events are noted on branches.

(the southern Andean clade) was equivocal, as was that of the ancestor of the entire typical *Muscisaxicola* clade. Resolving the character ambiguity to minimize the number of developments of migration resulted in migratory ancestors both to the entire typical clade and to clade 2, with the subsequent loss of migration in clade 2 in *M. a. alpina* and *M. m. macloviana*. Resolving the character ambiguity to maximize the number of developments of migration resulted in nonmigratory ancestors both to the typical clade and to clade 2, with three independent developments of migration in clade 2 (in *M. albilora*, *M. macloviana mentalis*, and the ancestor of *M. capistrata*/*M. frontalis*).

DISCUSSION

Phylogenetics. Although the genus *Muscisaxicola* is generally considered to consist of 12 species (Hellmayr and Cory, 1927; Traylor, 1979), 2 of these species, *M. maculirostris* and *M. fluviatilis*, differ phenotypically from the rest of the genus (they are smaller than other *Muscisaxicola* species, are browner overall, and show rufous wing edgings in adult plumage; Table 1) and

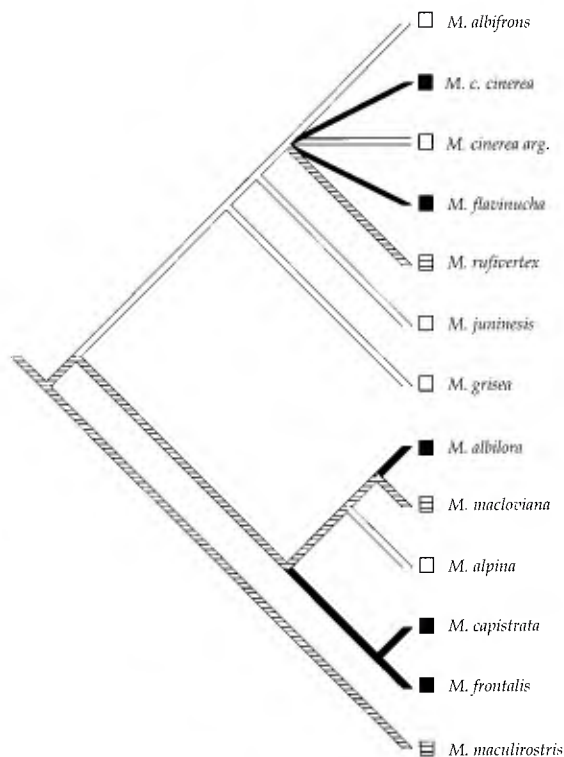


FIG. 4. Parsimonious reconstruction of the evolution of migration in the genus *Muscisaxicola*. Key: white boxes, nonmigratory taxa; black boxes, migratory taxa; striped boxes, polymorphic taxa (containing both migratory and nonmigratory subspecies); white branches, reconstructed as nonmigratory; black branches, reconstructed as migratory; striped branches, reconstructed equivocally.

have been singled out as distinctive. Ridgely and Tudor (1994), for example, explicitly segregated these two species from the other species of *Muscisaxicola*, referring to the other 10 species as the "typical ground-tyrants." Vuilleumier (1971) likewise separated them from the remainder of *Muscisaxicola* species in his *maculirostris* species group, and these 2 species are typically placed together at the beginning of the genus in other general works on South American birds (e.g., Fjeldså and Krabbe, 1990) and in standard reference works on tyrant-flycatchers (e.g., Traylor, 1979). The phylogenetic analyses presented above are partially consistent with this conventional wisdom, indicating strong support for the monophyly and genetic distinctiveness of the 10 typical *Muscisaxicola* species, but they offer no support for a close relationship between *M. fluviatilis* and *M. maculirostris* or between the typical species and *M. fluviatilis*. Although the data supported a sister relationship between the typical species and *M. maculirostris*, this support was not strong, and *M. maculirostris* was divergent from the typical species. *Muscigralla brevicauda*, merged by Vuilleumier (1971) into *Muscisaxicola*, was found to be only distantly related to any of the traditional *Muscisaxicola* species.

Relationships among typical *Muscisaxicola* species were found to differ substantially from previous ideas of relationship within the genus. Little support was found for the species groups of Vuilleumier (1971). Three of his four species groups (excluding species group 1) contain taxa from both major clades of typical *Muscisaxicola* species (Fig. 1). Species group 2, which consists of *M. macloviana* and *M. capistrata*, is wholly contained within the southern clade of *Muscisaxicola* species, but even here the two species are not sister taxa. Thus, the genetic data suggest that the plumage and other phenotypic characters used for designating the species groups have been subject to convergence. For example, rufous crown patches and conspicuous white lores have apparently evolved independently in both major clades of typical *Muscisaxicola* species (Fig. 1, Table 1). This finding is of potential importance because these types of characters are those that have traditionally been used in lower level avian taxonomic and systematic research, particularly in studies of passerine birds, which are notoriously conservative in morphology.

Sequences of two individuals of most species of *Muscisaxicola* were consistent with monophyly of those species (Fig. 1). However, *M. alpina* and *M. cinerea* were found to be somewhat problematic. *M. alpina*, as presently constituted, appears to be polyphyletic: *alpina grisea* is a member of the central Andean clade, whereas *alpina alpina* belongs to the predominantly southern Andean clade. The correlation of the genotypic differences with phenotypic differences (the dorsal plumage of *alpina grisea* is much grayer than that of *alpina alpina* or the other northern subspecies [*columbiana* and *quesadae*], which are grayish-brown) and the fact that the constrained topologies were significantly worse than the best trees strongly support the polyphyly of *M. alpina*. Ridgely and Tudor (1994) noted that *alpina grisea* differs phenotypically as much from the northern subspecies of *alpina* (*alpina*, *columbiana*, and *quesadae*) as it does from *M. cinerea* and suggested that it may warrant species status. This suggestion is supported by the data presented above, and it is recommended that *M. grisea* (Taczanowski, 1884) once again be recognized as a species distinct from *M. alpina* (which would continue to include *columbiana* and *quesadae*). Although not shown here to be polyphyletic, *M. cinerea* was not demonstrably monophyletic; that is, no synapomorphies were found to uniquely unite the two individuals sequenced. Fjeldså and Krabbe's (1990) suggestion that the species *M. alpina* should perhaps include the subspecies *M. cinerea argentina* receives some support from the data presented here (*M. alpina grisea* and *M. cinerea argentina* are sisters in the phylogeny based on the maximum-likelihood analysis), but it is recommended that these taxa be kept distinct pending more detailed studies.

Biogeography and radiation. Perhaps the most notable results of this study concern the spatial and temporal patterns of the radiation of the typical *Muscisaxicola* species. Members of the two major clades of *Muscisaxicola* occupy substantially different regions of the Andes, one clade being found primarily in the central Andes of Peru, Bolivia, and northern Argentina and Chile and the other breeding primarily in the southern Andes and Patagonian region of southern Argentina and Chile. Reconstruction of ancestral geographical ranges indicated that the ancestors of these two clades were likewise distributed in the central and southern Andes, respectively. Thus, the primary division among typical *Muscisaxicola* species is a biogeographic one, and the patterns of sympatry that we see among these species developed primarily within single biogeographic regions, rather than as the result of repeated extraregional invasions of taxa.

Although such patterns are seemingly consistent with nonallopatric modes of speciation, they are presumably the result of allopatric speciation and secondary sympatry, because the similarities among *Muscisaxicola* species in morphology, display behavior (Smith, 1971), and overall ecology (Vuilleumier, 1971), together with their homogeneous habitat, make them highly unsuitable candidates for sympatric speciation (to the extent that birds or other terrestrial vertebrates are candidates at all—cf. Futuyma and Mayer, 1980; Kondrashov and Mina, 1986; Grant and Grant, 1989). There presumably has been ample opportunity for allopatric speciation within *Muscisaxicola*, given the extensive glaciations, habitat change, and tectonic and volcanic activity in the high Andes over the past several million years (see Clapperton, 1993).

The precise location of the presumed former barrier between the central and the southern Andean regions is uncertain but would likely have been close to the current break in distribution between central and southern Andean species, at a latitude of roughly 38–40°S. This is the area in which the geological and topographic character of the Andes alters dramatically and mean elevation declines by some 2000 m (Rabassa and Clapperton, 1990), evidently coincident with a thinner and younger portion of continental crust (Clapperton, 1993). The elevational decline allows moist westerly winds to penetrate from the Pacific, the associated increased humidity favoring the development of glaciers (Rabassa and Clapperton, 1990). Evidence of former glaciations has been found in this area, in the Alumine Valley (Schleider, 1989; cited in Rabassa and Clapperton, 1990) and to the immediate south, extending east from Lago Nahuel Huapi and Cerro El Tronador (Rabassa and Clapperton, 1990). Although the exact dates and extents of the Alumine glaciations are not available, Mercer (1976) concluded that the most extensive glaciations further south in Patagonia probably occurred some 1–1.2 million years ago, which

agrees well with the estimated date of the divergence between the two major clades of *Muscisaxicola* species (see below).

The most striking deviation from the simple biogeographical pattern outlined above is the presence of *M. a. alpina*, a taxon restricted to the Ecuadorian Andes, in the clade breeding predominantly in the southern Andes. According to the dispersal–vicariance biogeographic reconstruction (Fig. 3), this represents a dispersal event in the ancestor to the *albilora/macloviana/alpina* clade, because the ancestor of the southern clade occurred only in the southern Andes (an alternative reconstruction, not favored by DIVA, is dispersal on the terminal branch leading to *M. a. alpina*). Because one of the current taxa in this clade, *M. albilora*, regularly winters as far north as Ecuador, a likely explanation for this colonization event would be the establishment of a sedentary breeding population on the wintering grounds of the migratory ancestral species, followed by differentiation and speciation. Beginning stages of this phenomenon have been observed in other passerine birds in recent times (e.g., the establishment of breeding populations of the wintering migrant *Hirundo rustica* in Argentina; Martinez, 1983).

Levels of sequence divergence among the 11 typical *Muscisaxicola* species (including *M. grisea* as a separate species) do not exceed 2.9%, with individuals of different species differentiated by as little as 0.1%. There can be no question of the species status of these taxa, all of which occur sympatrically with other *Muscisaxicola* species, with no evidence of interbreeding. Although birds in general are recognized as having low levels of genetic variability, these figures are low even among birds. Surveys of mitochondrial sequence divergence between avian sister species and between other congeners (Avice and Zink, 1988; Seutin *et al.*, 1993; Klicka and Zink, 1997; Johns and Avice, 1998) have found levels of sequence divergence as great as 10–15% or more and place *Muscisaxicola* species at the extreme low end of avian interspecific sequence divergence.

Although Pleistocene events have long been proposed as significant contributors to present biodiversity in both temperate and tropical regions (e.g., Rand, 1948; Haffer, 1969), the importance of Pleistocene events has been challenged in recent years (e.g., Zink and Slowinski, 1995; but see Avice and Walker, 1998). My results suggest that middle and late Pleistocene events greatly influenced the diversification of *Muscisaxicola* species and that taxa of the high Andes and Patagonia may be prime candidates in general for mid-to-late Pleistocene effects on biodiversification. Assuming that the mitochondrial genes used in this study are evolving at roughly 2% per million years, an estimate converged upon by avian mitochondrial studies involving RFLP and cytochrome *b* sequence data (e.g., Shields and Wilson, 1987; Tarr and Fleischer, 1993; Zink and Blackwell, 1998), the deepest split among

typical *Muscisaxicola* species, separating the two major clades, occurred roughly 1.2 million years ago (2.4% mean divergence between members of the two clades), and all other speciation events occurred during the past million years, during the middle to late Pleistocene (Fig. 2). The central Andean radiation has been particularly recent, with divergences averaging less than 1%, speciation likely having occurred within the past half-million years. Thus, although my results are not consistent with Vuilleumier's (1971) *Muscisaxicola* species groups, they accord well with his earlier (1969, p. 1180) broader analysis of the Andean avifauna: "one bird species having colonized the páramo-puna vegetation before the onset of the [Pleistocene] glaciations might thus have been isolated enough, in optimal conditions, to have given rise to five or even more new species." The results are also consistent with current estimates of a Pliocene origin of high Andean habitats (Van der Hammen and Cleef, 1986).

Migration. It seems clear that the migratory species of *Muscisaxicola* do not reflect a radiation from a single migratory ancestor, due to the independent development of migration in the two major clades of typical species (if the ancestor to the typical clade was nonmigratory) or to the loss and subsequent independent development in the central Andean clade (if the ancestor was migratory). Reconstruction of migration in the central Andean clade, consistent with the biogeographic reconstruction, indicated independent development of migration in three species (*cinerea*, *rufivertex*, and *flavinucha*), two of which contain a sedentary northerly subspecies and a migratory more southerly subspecies (although, depending on the resolution of the polytomy, there could have been a single development of migration, followed by the loss of migration in the northern subspecies of *cinerea* and *rufivertex*).

In the southern clade, parsimonious reconstruction of the evolution of migration differs depending on whether the number of developments of migration is minimized or maximized. Minimizing gains of migration results in the evolution of migration in the ancestor to the clade, with the subsequent loss of migration in *M. m. macloviana* and *M. a. alpina* (as in Fig. 4), whereas maximizing number of gains results in three independent evolutions of migration (in *albilora*, *macloviana mentalis*, and the ancestor of the *capistrata frontalis* clade). Although there are no *a priori* expectations for favoring gains or losses of migration among *Muscisaxicola* species, the reconstruction favoring a single development of migration, with two subsequent losses, seems more likely, for three reasons. First, this reconstruction is consistent with the biogeographic reconstruction, which postulates a southern ancestor. In contrast, the alternative reconstruction would presumably involve three separate colonizations of the tem-

perate zone from the north. Second, in the case of *M. macloviana*, which consists of a migratory subspecies on the South American continent (*M. m. mentalis*) and a sedentary subspecies restricted to the Falkland Islands (*M. m. macloviana*), it seems more likely that a sedentary island taxon evolved from a migratory continental ancestor than that a migratory continental taxon evolved from a sedentary island ancestor (as would presumably have occurred under the alternative scenario, involving a gain of migration in *M. m. mentalis*). This has been demonstrated in other avian taxa (e.g., the paraphyletic migratory continental species *Anas platyrhynchos* has apparently given rise to sedentary island species, rather than the opposite; Cooper *et al.*, 1996; Omland, 1997). Finally, as mentioned above, the establishment of a sedentary breeding population from wintering individuals of a migratory species, as would presumably have happened to establish the northern *M. a. alpina* from the migratory ancestor of the southern clade, has been observed in other passerine birds in recent times.

The only previous phylogenetic analysis of the evolution of migration in a New World genus appears to be that of Burns (1998), who found that migration evolved only a single time in the tanager genus *Piranga* (Passeriformes, Thraupidae). In contrast to the south temperate breeding migrants of the genus *Muscisaxicola*, most migration in *Piranga* involves Nearctic–Neotropical migrants, species that breed in North America and winter in the Neotropics. Although *Muscisaxicola* is unusual among South American genera in being so highly migratory, the difference between the multiple evolutions of migration in *Muscisaxicola* and the single evolution in *Piranga* is perhaps representative of general differences between the Neotropical–Nearctic migration system and the South American austral system. Most Nearctic–Neotropical migrant species are wholly migratory and belong to genera that are exclusively or primarily migratory; it is likely that many of these taxa represent Nearctic radiations from migratory ancestors. In contrast, many South American austral migrants have sister species or subspecies resident in northern South America (Chesser, 1995); presumably migration evolved independently in many of these taxa.

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