



## MOLECULAR PHYLOGENETIC RELATIONSHIPS AMONG THE GEOSITTA MINERS (FURNARIIDAE) AND BIOGEOGRAPHIC IMPLICATIONS FOR AVIAN SPECIATION IN FUEGO-PATAGONIA

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**ABSTRACT.**—Pleistocene glacial cycles have often been hypothesized to provide vicariant mechanisms leading to allopatric speciation in a wide range of southern South American (Fuegian and Patagonian) avian taxa. Few of those biogeographic hypotheses, however, have been rigorously tested using phylogenetic analysis. We examined sequence variation in three mitochondrial gene fragments (cytochrome *b*, ND2, and ND3) to construct a molecular phylogeny for the South American genus *Geositta* (Furnariidae) and to test the interrelated hypotheses that *Geositta cunicularia* and *G. antarctica* are sister species that originated from a common ancestor while isolated in glacial refugia during Pleistocene glacial events in Fuego-Patagonia. Sequence data were obtained for all 10 currently recognized species of *Geositta* as well as *Geobates poecilopterus* and two outgroup taxa (*Upucerthia ruficauda* and *Aphrastura spinicauda*). We found levels of sequence divergence among *Geositta* species to be high, ranging from 7.4% to 16.3%. Our phylogenetic reconstructions clearly indicate relationships among *Geositta* species that differ considerably from those of traditional *Geositta* phylogeny. These data also strongly suggest that *Geositta*, as currently defined, is paraphyletic, with *Geobates* being embedded within *Geositta*. Our data do not support the hypothesized sister relationship between *G. antarctica* and *G. cunicularia*. Instead, they suggest that *Geositta* consists of two distinct clades, with *antarctica* and *cunicularia* falling into different clades. The high levels of sequence divergence among *Geositta* species, lack of a sister relationship between *cunicularia* and *antarctica*, and placement of Fuego-Patagonian *antarctica* into a clade consisting of two high-Andean (*saxicolina* and *isabellina*) and one coastal–west-slope (*maritima*) species demonstrate that the evolutionary history of *Geositta* is much older and far more complex than a simple model of allopatric speciation in glacial refugia would suggest. Received 14 November 2003, accepted 28 August 2004.

**Key words:** biogeography, Furnariidae, *Geobates*, *Geositta*, glacial events, Patagonia, Pleistocene, sympatry, vicariant events.

### Filogenia Molecular del Género *Geositta* (Furnariidae) e Implicaciones Biogeográficas para la Especiación de las Aves en Tierra del Fuego y Patagonia

**RESUMEN.**—Se ha sugerido que los ciclos glaciales del Pleistoceno han causado eventos de vicarianza que han conllevado a procesos de especiación alopátrica en una amplia gama de taxa de aves del sur de América del Sur (Tierra del Fuego y Patagonia). Sin embargo, muy pocas de estas hipótesis han sido puestas a prueba rigurosamente por medio de análisis filogenéticos. En este estudio examinamos la

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variación en las secuencias de tres fragmentos de genes mitocondriales (citocromo *b*, ND2 y ND3) para construir una filogenia molecular del género suramericano *Geositta* (Furnariidae) y para poner a prueba la hipótesis de que *Geositta cunicularia* y *G. antarctica* son especies hermanas que se originaron de un ancestro común mientras estaban aisladas en refugios durante eventos glaciales del Pleistoceno en Tierra del Fuego-Patagonia. Obtuvimos secuencias para las 10 especies de *Geositta* reconocidas en la actualidad, así como para *Geobates poecilopterus* y para dos taxa considerados como grupo externo (*Upucerthia ruficauda* y *Aphrastura spinicauda*). Encontramos que los niveles de divergencia entre las secuencias de especies de *Geositta* son altos, entre 7.4% y 16.3%. Nuestras reconstrucciones filogenéticas claramente indican relaciones entre las especies de *Geositta* que difieren considerablemente de las sugeridas por la filogenia tradicional del género. Nuestros datos también sugieren fuertemente que como está definido actualmente, *Geositta* es un grupo parafilético, pues *Geobates* está anidado dentro de *Geositta*. Nuestros datos no apoyan la supuesta estrecha relación entre *G. antarctica* and *G. cunicularia*; en cambio, sugieren que *Geositta* comprende dos clados distintivos y que *antarctica* y *cunicularia* pertenecen a clados distintos. Los altos niveles de divergencia en las secuencias entre las especies de *Geositta*, la ausencia de una relación de especies hermanas entre *cunicularia* y *antarctica* y la ubicación de la especie fueguino-patagónica *antarctica* en un clado conformado por dos especies de los altos Andes (*saxicolina* y *isabellina*) y una de la vertiente costera occidental (*maritima*), demuestran que la historia evolutiva de *Geositta* es mucho más antigua y bastante más compleja que lo que sugeriría un modelo sencillo de especiación alopatrica en refugios glaciales.

THE GENUS *GEOSITTA* (Furnariidae), as traditionally recognized, includes 10 species (Cory and Hellmayr 1925, Peters 1951, Ridgely and Tudor 1994) that have a wide distribution in central, western, and southern South America; occurring along the Pacific coasts of Peru and northern Chile; along the western slopes and on the high plateaux of the central and southern Andes; and in the lowlands east of the Andes from central Argentina southward to Patagonia and Tierra del Fuego (Table 1). The taxonomy and phylogeny of the species that comprise the genus have been controversial for several decades. In the most extensive taxonomic treatment of the genus to date, Vaurie (1980) considered *Geositta* to consist of 12 species and placed 10 of them into 3 species groups (Table 1).

In addition to the 10 species traditionally included in *Geositta* (e.g. Peters 1951), Vaurie (1980) assigned to it 2 species of other genera: *poecilopterus* Wied 1831 (usually placed in *Geobates* Swainson 1837, a monotypic genus of the Brazilian cerrado) and *excelsior* Sclater 1860, of the Andes of central Colombia and Ecuador, previously considered to belong to either of the two Andean and Patagonian genera *Upucerthia* (e.g. Cory and Hellmayr 1925) or *Cinclodes* (e.g. Peters 1951, Meyer de Schauensee 1966).

Subsequently, the placement of *Geobates* has been controversial, with some workers supporting its inclusion in *Geositta* (Vuilleumier 1980, Remsen 2003a) and others maintaining *Geobates* as a genus separate from, though closely related to, *Geositta* (e.g. Ridgely and Tudor 1994). In the case of *Cinclodes excelsior*, many workers now agree that it should be placed within *Cinclodes* on the basis of plumage, behavioral, and molecular characters (Vuilleumier 1980, Fjelds  et al. 1987, Fjelds  and Krabbe 1990, Ridgely and Tudor 1994, Remsen 2003a, Chesser 2004).

Vaurie (1980) arranged *Geositta* species into groups on the basis of similarities in plumage and other morphological characters and, to a lesser extent, in habitat requirements (Table 1). Vaurie (1980) did not give names to those groups, but we have done so here for convenience in discussing them, according to similarity among the species that comprise each group. The first species group consists of five straight-billed lowland and Andean species, *antarctica*, *cunicularia*, *isabellina*, *poeciloptera* (= *Geobates poecilopterus*), and *saxicolina*. Within that group, Vaurie hypothesized that *poeciloptera* is closely related to *cunicularia*. The second group consists of two coastal species, *maritima* and *peruviana*, though note that Vaurie (1980) also suggested

TABLE 1. *Geositta* species groups recognized by Vaurie (1980).

Species group <sup>a</sup>	Species included	Geographic distribution, habitat, and migratory status <sup>b</sup>
Lowland–Andean straight-billed group	<i>Geositta antarctica</i>	Fuego-Patagonia; steppe; migrates to northern Argentina.
	<i>G. cunicularia</i>	Lowlands of southern Argentina, Chile, and southeastern Brazil; Andes of Chile, Argentina, Bolivia, and Peru; Patagonian steppes, Andean puna, coastal dunes; southern populations migratory.
	<i>G. isabellina</i>	Andes of central Chile; rocky slopes; altitudinal migrant.
	<i>G. poeciloptera</i> <sup>c</sup>	Southeastern Brazil and extreme northeastern Bolivia; cerrado; resident.
	<i>G. saxicolina</i>	Andes of central Peru; puna; resident.
Coastal straight-billed group	<i>G. maritima</i>	Coastal lowlands and Andean slopes of southern Peru and northern Chile; rocky desert; resident.
	<i>G. peruviana</i>	Coastal lowlands of southern Peru; sandy desert; resident.
Modified bill group	<i>G. crassirostris</i>	Western slope of Andes in central Peru; lomas; resident.
	<i>G. excelsior</i> <sup>c</sup>	Andes of central Colombia and Ecuador; páramo; resident.
	<i>G. tenuirostris</i>	Andes of northern Argentina and Peru; disjunct population in Andes of southern Ecuador; southern populations migratory.
	<i>G. punensis</i>	Andes of southern Peru, Bolivia, northern Chile and northern Argentina; puna; resident.
Unaffiliated <sup>d</sup>	<i>G. rufipennis</i>	Andes of Bolivia, Argentina and Chile; rocky slopes; partial migrant.

<sup>a</sup> Species groups were not named by Vaurie; those names were coined by the authors (see text).

<sup>b</sup> Species distributions adapted from Cory and Hellmayr (1925), Peters (1951), Vaurie (1980), Ridgely and Tudor (1994), and Rensen (2003a); habitat according to Vuilleumier (1991a, b) and unpublished field data (F. Vuilleumier); migratory status according to Fjeldså and Krabbe (1990), Chesser (1994), Ridgely and Tudor (1994), and unpublished field data (F. Vuilleumier).

<sup>c</sup> Taxonomy follows Vaurie (1980); *Geositta poeciloptera* = *Geobates poecilopterus* and *Geositta excelsior* = *Cinclodes excelsior*.

<sup>d</sup> Vaurie (1980) did not include these species in any of his species groups.

that morphological similarity between the two species may be largely superficial and, hence, that the grouping may be artificial. Vaurie's (1980) third group includes species with "specialized bills": *crassirostris*, *excelsior* (= *Cinclodes excelsior*), and *tenuirostris*. Vaurie (1980) placed those three species into a group because he felt that the greater length and overall higher degree of structural modification of their bills implied recent common ancestry. Both *G. crassirostris* and *C. excelsior* have thick, coarse, and slightly decurved bills; whereas the bill of *tenuirostris* is long, slender, and well decurved. However, we and others think that it is likely that those bill characters are under parallel selective influences, and thus particularly vulnerable to homoplasy (Bock 1964, 1985; Remsen 2003b). Vaurie (1980) made no suggestion regarding the phylogenetic affinities of *punensis* and *rufipennis*.

In addition to the phylogenetic difficulties encountered at the generic level, species-level taxonomy of *Geositta* is also somewhat unresolved, given that at least one widespread and polytypic species, *G. cunicularia*, with seven subspecies, may actually include at least three species-level taxa, a suggestion made on the basis of vocal differences among coastal, Andean, and Patagonian subspecies groups (Fjelds  and Krabbe 1990, Vuilleumier 1993). Given the controversies surrounding the intra- and interspecific taxonomic problems in *Geositta*, the need for a rigorous phylogenetic revision is evident. Furthermore, the biogeographic distribution of *Geositta* in diverse and historically unstable habitats of western (Andean) and Patagonian South America makes this group an excellent model genus for studies of speciation (Koepcke 1965, Vuilleumier 1993).

On the basis of their morphological, ecological, and some behavioral similarities, Vuilleumier (1991a, b) hypothesized that *G. cunicularia* and *G. antarctica* are sister species. *Geositta cunicularia* is widely distributed in southern South America, whereas the breeding range of *antarctica* is restricted to Fuego-Patagonia in extreme southern Chile and Argentina (Ridgely and Tudor 1994). The two species are entirely syntopic on Isla Grande of the Tierra del Fuego archipelago (Vuilleumier 1991a, b). Extrapolating from the hypothesis that *cunicularia* and *antarctica* are sister species and from their contemporary distributions, Vuilleumier (1991a, b) hypothesized further that

the two species diverged during a recent glacial event in Tierra del Fuego and Patagonia, which would have corresponded to the Llanquihue glaciation, approximately 20,000–14,000 years before the present.

Pleistocene glacial events, specifically the repeated, quasicyclical habitat perturbations resulting from glacial–interglacial episodes, have long been hypothesized to have acted as vicariant mechanisms leading to speciation in a wide range of vertebrate taxa (e.g. Mengel 1964; Macpherson 1965; Haffer 1969; Vuilleumier and Simberloff 1980; Vuilleumier 1985, 1991a, b; Avise and Walker 1998; Holder et al. 1999). North- and south-temperate-zone biotas are believed to have been particularly affected by those events. For example, speciation of many North American avian taxa has been hypothesized to have occurred during climatic fluctuations associated with that period (literature reviewed by Zink and Slowinski [1995]). However, the importance of Pleistocene glacial events to the speciation of temperate birds has become the subject of recent debate. Molecular studies have suggested that divergences among many North American species predate the Pleistocene (Zink and Slowinski 1995, Klicka and Zink 1997). Edwards and Beerli (2000), however, have shown that those divergence times are most likely overestimates because gene divergence estimates used by Klicka and Zink (1997) fail to correct for ancestral haplotype polymorphism present in ancestral populations prior to divergence, leading to an inflated estimate of the variable of interest (i.e. time since population divergence). In addition, Johnson and Cicero (2004) suggested that comparisons used by Klicka and Zink (1997) were made between closely related congeners that are not sister species and that, therefore, estimated divergence times reflect deeper splits.

Because of the analogous glacial histories of the regions, diversification among avian taxa of South American high Andean and temperate zones (especially Patagonia) has also been attributed largely to allopatric speciation in glacial refugia during Pleistocene glacial events (Vuilleumier and Simberloff 1980; Vuilleumier 1985, 1991a, b; Corbin et al. 1988). However, diversification among those taxa has not been studied as intensively as their northern-temperate counterparts, especially from a molecular perspective. Although several recent studies

(e.g. Garcia-Moreno et al. 1998, 1999; Chesser 1999, 2000, 2004) have added substantially to our understanding of patterns and processes of diversification among those taxa, the phylogenetic patterns of differentiation of many Andean and Patagonian taxa remain poorly understood. Analyses of phylogenetic patterns of speciose genera with complex distributions in Andean and Patagonian biomes have the potential to elucidate some of the historical aspects of speciation events within the Andean–Patagonian avifauna, especially their timing and spatial unfolding.

The objectives here were twofold: (1) to create a phylogenetic hypothesis for the interrelationships of *Geositta* species based on mitochondrial DNA (mtDNA) sequence variation, and (2) to use that phylogeny to test the hypothesis that *cunicularia* and *antarctica* are sister taxa and, if so, whether they diverged from a common ancestor in glacial refugia. Lack of a sister relationship between those two species would falsify the hypothesis of recent common ancestry, and thus also the biogeographical hypothesis of Pleistocene speciation (Vuilleumier 2004).

#### METHODS

*Taxon sampling.*—Twenty individuals were sampled, including at least one individual of each *Geositta* species, three individuals of *Geobates poecilopterus*, and two outgroup taxa (*Upucerthia ruficauda* and *Aphrastura spinicauda*) (see Appendix 1). Because of widespread agreement among ornithologists that the species does not belong in *Geositta* (Vuilleumier 1980, Fjeldsø et al. 1987, Fjeldsø and Krabbe 1990, Ridgely and Tudor 1994, Remsen 2003a, Chesser 2004), *C. excelsior* was not sampled here despite Vaurie's (1980) inclusion of *excelsior* in the genus *Geositta*. Tissue samples of *G. cunicularia*, *G. antarctica*, and one outgroup taxon (*A. spinicauda*) were collected by F.V. and A.P.C. using standard field collecting protocols. Tissue samples of all other taxa were obtained on loan from the Louisiana State University Museum of Natural Science (LSUMNS) and the American Museum of Natural History (AMNH) (Appendix 1).

*Extraction, amplification, and sequencing of DNA.*—Total genomic DNA was extracted from breast muscle using a DNeasy tissue extraction kit (Qiagen, Valencia, California). Fragments of the mitochondrial cytochrome-*b*,

ND2, and ND3 genes were amplified via polymerase chain reaction (PCR) using the following primers: for cytochrome *b*, H15149 and L14841 (Kocher et al. 1989); for ND2, H5578 and L5215 (Hackett 1996); and for ND3, H11151 and L10755 (Chesser 1999). All PCR reactions were performed in 50- $\mu$ L volumes using a model PTC-200 Peltier thermal cycler (MJ Research, Waltham, Massachusetts) and were conducted under the following conditions: (1) an initial denaturing step at 94°C for 7 min; (2) 35 cycles of the following: 1 min at 92°C, 1 min at 50°C, and 1 min at 72°C; and (3) a 7-min extension step at 72°C. After amplification, electrophoresis of a small aliquot of PCR product was carried out on an agarose gel to ensure correct fragment size and verify the presence of a single amplification product. We purified PCR products using a GeneClean II kit (Bio 101, Carlsbad, California). Cycle sequencing reactions were performed using a Big Dye Terminator kit (Applied Biosystems, Foster City, California) and the amplification primers listed above. Following cycle sequencing, the product was precipitated in ethanol, dried, resuspended in 15  $\mu$ L of template suppression reagent (Applied Biosystems, Foster City, California), and visualized using an ABI 310 Genetic Analyzer.

*Data analysis.*—With the exception of several unidirectional ND3 sequences, sequence data from both DNA strands were obtained for all individuals. Sequence data have been deposited in GenBank (ND2, AY694990–AY695009; cytochrome *b*, AY695010–AY695029; ND3, AY695030–AY695049). Heavy and light strands were aligned and differences between them reconciled using SEQUENCHER, version 4.1 (Genecodes, Madison, Wisconsin). To ensure that sequences were mitochondrial in origin, several precautions were taken: (1) sequences were aligned with the entire domestic chicken (*Gallus gallus domesticus*) mtDNA sequence (Desjardins and Morais 1990), translated to amino acid sequence, and analyzed for evidence of insertions, deletions, and stop codons that would render coding regions nonfunctional; (2) partition homogeneity tests were performed to ensure similar phylogenetic signal among data partitions; (3) sequences were expected to exhibit substitution patterns characteristic of mitochondrial rather than nuclear genes (Joseph et al. 2002); and (4) genetic distance



matrices were carefully examined for evidence of any obviously different sequences. Similar approaches have been used by other workers to check for presence of pseudogenes in other molecular phylogenetic studies of avian taxa (e.g. Sorenson and Quinn 1998, Bates et al. 1999, Aleixo 2002, Marks et al. 2002). Evidence of nuclear pseudogenes was not detected.

Three pairwise partition homogeneity tests were performed to assess congruence in phylogenetic signal among the protein-coding regions of the three gene fragments. Each of those tests was performed using 1,000 replicates and only informatively variable sites. Because phylogenetic signal did not differ significantly among data partitions, all three gene fragments were analyzed as a combined data set. Each gene fragment was examined for evidence of saturation at each codon position following the protocols outlined by Hackett (1996). Transitions at the third codon position revealed evidence of saturation (not shown) and were thus down-weighted in relation to all other substitutions in subsequent parsimony analyses.

Phylogenetic hypotheses were constructed using both maximum-parsimony (MP) and maximum-likelihood (ML) methods using PAUP\*, version 4.0b10 (Swofford 2002). Both weighted and equally weighted parsimony analyses were performed. To correct for observed saturation, transitions at the third codon position were downweighted in relation to all other substitutions by factors of 2, 5, 7, 10, 50, 100, and 1,000 via codon-specific step-matrices. Full heuristic searches were performed with all characters equally weighted and according to the aforementioned weighting scheme using tree bisection reconnection (TBR) branch swapping with 10 random-taxon-addition replicates. Confidence levels for each of the nodes in all MP analyses were evaluated using 1,000 nonparametric bootstrap replicates.

An MP tree with all characters equally weighted and likelihood-ratio test implemented in MODELTEST (Posada and Crandall 1998) was used to select the best-fit model of molecular evolution based on the data set. A general time-reversible (GTR) model with empirical base frequencies, a proportion of invariant sites ( $I$ ), and gamma-distributed rate variation across sites ( $G$ ) with an estimated shape parameter ( $\alpha$ ) (GTR +  $I$  +  $G$ ) was selected as best fit. The following parameters were used in all ML analyses: (1) substitution rate matrix: [A–C] = 1.7115; [A–G] = 15.2023; [A–T] = 2.0377; [C–G] = 0.6142; [C–T] = 25.6006; [G–T] = 1.00; (2) empirical base frequencies: A = 0.3157; C = 0.3543; G = 0.1103; T = 0.2197; (3) proportion of invariant sites:  $I$  = 0.5797; (4)  $\alpha$  = 2.177. All ML analyses were performed using the “full heuristic” option in PAUP, with 10 random-addition replicates. Robustness of nodes in ML analyses was evaluated using 1,000 nonparametric bootstrap replicates.

## RESULTS

We obtained partial sequences of the mitochondrial cytochrome-*b* (262 base pairs [bp]), ND2 (298 bp), and ND3 (288 bp) genes for a total alignment of 848 bp for 18 *Geositta*–*Geobates* individuals and 2 outgroup genera (*Upucerthia* and *Aphrastura*). No insertions, deletions, or stop codons were observed in sequences of any gene fragment.

*Sequence variation.*—A summary of sequence variation is presented in Table 2. Percentages of sequence divergence values (uncorrected  $P$ ) among *Geositta*–*Geobates* species were high, ranging from 7.7% to 16.3% (Table 3). The lowest degree of divergence was between *cunicularia* and *tenuirostris*, and the highest was between *cunicularia* and *antarctica*, with a mean percentage of sequence divergence of 15.9% (Table 3). Generally, intraspecific divergence

TABLE 2. Variable and phylogenetically informative sites for each gene region.

Gene	Total	Variable sites (percentage of total)	Informative sites (percentage of total)	Informative sites by codon position		
				1st	2nd	3rd
Cytochrome <i>b</i>	262 bp	88 (33.6%)	71 (27.1%)	9	1	61
ND2	298 bp	119 (39.7%)	89 (29.7%)	17	6	66
ND3	288 bp	103 (35.8%)	82 (28.4%)	14	1	67
Total	848 bp	310 (36.4%)	242 (28.5%)	40	8	194

TABLE 3. Mean uncorrected (*P*) sequence divergence values among *Geositta*, *Geobates*, and outgroup taxa.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
1. <i>Geositta cunicularia</i>	—												
2. <i>G. antarctica</i>	0.1586	—											
3. <i>G. maritima</i>	0.1514	0.0974	—										
4. <i>G. saxicolina</i>	0.1448	0.0926	0.0912	—									
5. <i>G. isabellina</i>	0.1362	0.0843	0.0921	0.0790	—								
6. <i>G. punensis</i>	0.1417	0.1222	0.1158	0.1275	0.1181	—							
7. <i>G. rufipennis</i>	0.1310	0.1150	0.1050	0.1061	0.0991	0.0827	—						
8. <i>G. crassirostris</i>	0.1456	0.1150	0.1180	0.1144	0.1191	0.1057	0.0920	—					
9. <i>G. tenuirostris</i>	0.0767	0.1552	0.1536	0.1452	0.1372	0.1453	0.1428	0.1475	—				
10. <i>G. peruviana</i>	0.1047	0.1527	0.1558	0.1427	0.1344	0.1382	0.1498	0.1474	0.1231	—			
11. <i>Geobates poecilopterus</i>	0.1369	0.1183	0.1167	0.1143	0.1120	0.1178	0.0965	0.1082	0.1462	0.1496	—		
12. <i>Upucerthia ruficauda</i>	0.1640	0.1798	0.1794	0.1686	0.1686	0.1653	0.1663	0.1627	0.1759	0.1674	0.1697	—	
13. <i>Aphrastura spinicauda</i>	0.1622	0.1740	0.1690	0.1745	0.1675	0.1665	0.1639	0.1651	0.1617	0.1568	0.1613	0.1663	—

values were low, ranging from 0.0% to 4.7%. It should be noted, however, that the highest intra-specific divergence value is attributed to comparisons within the widespread *G. cunicularia*. Individuals sampled represent two subspecies, *G. c. cunicularia* (Tierra del Fuego) and *G. c. georgei* (Arequipa, southern Peru) (Appendix 1). If the individual collected in southern Peru is excluded from intraspecific comparisons, divergence values within *cunicularia* are all <1%. In all cases, intraspecific divergence values are one to two orders of magnitude less than inter-specific values. Phylogenetic analyses revealed two distinct clades (labeled A and B) within the genus (Fig. 1). Uncorrected divergence values between the two clades ranged from 11.8% to 16.3%; values within clades ranged from 7.4% to 14.5% (Table 3).

Partition homogeneity (ILD) tests did not reveal significant discordance in phylogenetic signal among data partitions (cytochrome *b* vs. ND2, *P* = 0.99; ND2 vs. ND3, *P* = 0.55; and cytochrome *b* vs. ND3, *P* = 0.33). Because of the overall congruence in phylogenetic signal among gene fragments, similarity in distribution of informative sites, and general topological congruence in phylogenies estimated using single gene fragments, all fragments were combined in subsequent phylogenetic analyses.

*Maximum-likelihood analyses.*—Maximum-likelihood analyses resulted in a single most likely tree (likelihood score  $-\ln = 4313.66$ ) (Fig. 1), which revealed novel hypotheses of *Geositta* phylogenetic relationships. *Geositta* as defined by Cory and Hellmayr (1925), Peters (1951), and Ridgely and Tudor (1994) is paraphyletic (Fig. 1). Inclusion of *Geobates* within *Geositta* was supported with 100% bootstrap support. Within the enlarged genus *Geositta*, two distinct clades were recovered. The first (clade A in Fig. 1) includes *cunicularia*, *tenuirostris*, and *peruviana*; the second (clade B in Fig. 1) consists of *antarctica*, *isabellina*, *saxicolina*, *maritima*, *crassirostris*, *punensis*, *rufipennis*, and *Geobates poecilopterus*. Within clade A, *tenuirostris* was sister to *cunicularia* with 95% support, and *peruviana* was basal to that group with 92% support. Within clade B, two subclades are distinguishable. The first subclade—consisting of *antarctica*, *isabellina*, *saxicolina*, and *maritima*—was well supported, with 93% bootstrap support. Relationships within that subclade, however, were poorly supported. The second subclade consists of

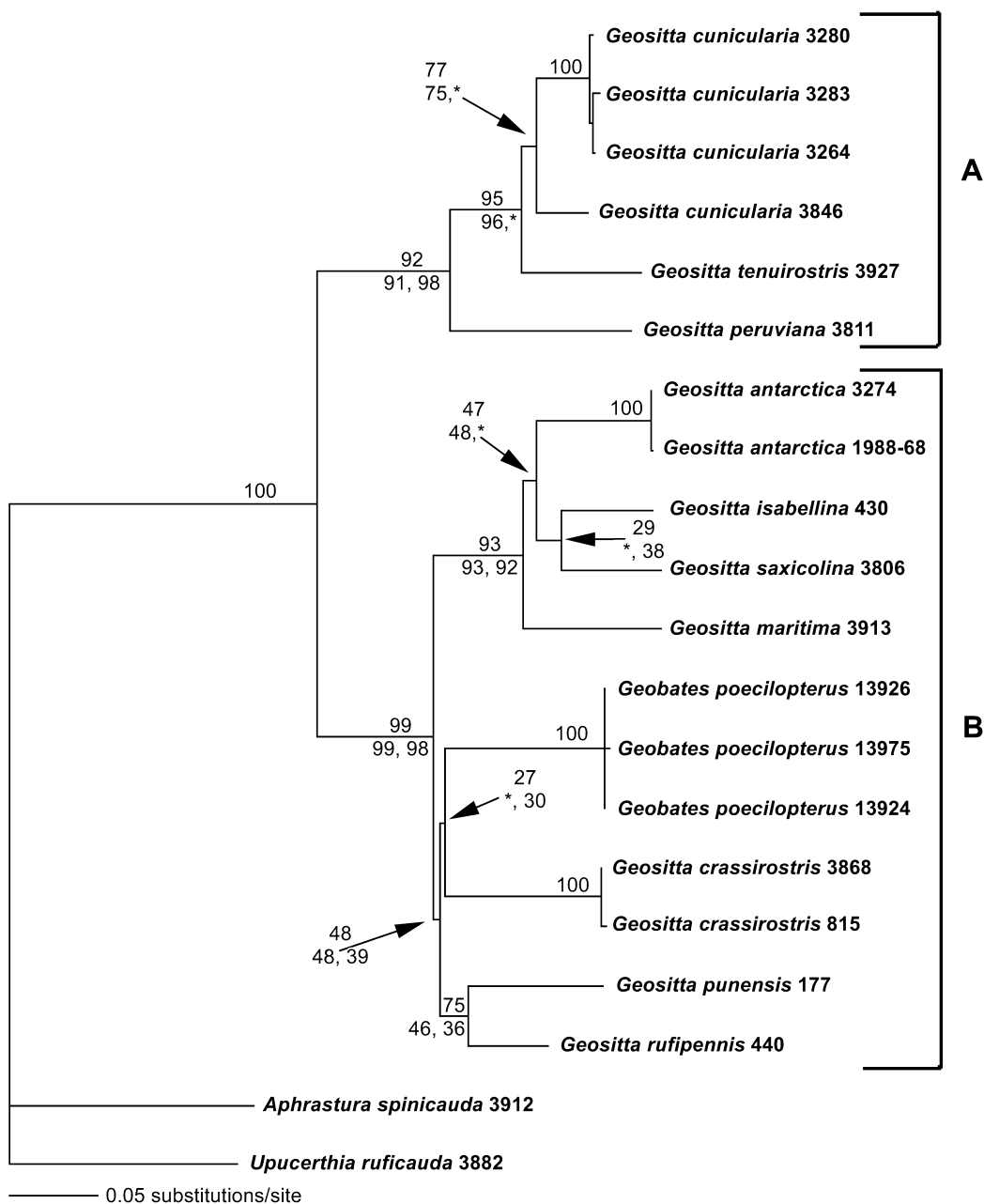


FIG. 1. Maximum-likelihood (ML) tree constructed under a GTR + I + G model of evolution (see text for substitution parameters). Numbers above nodes correspond to ML bootstrap values. Numbers below the nodes correspond to bootstrap values for MP and 10× weighted MP analyses, respectively, if they differ from those in the ML analysis. All bootstrap values are based on 1,000 replicates. Disagreement between ML and MP analyses is indicated by an asterisk (\*) (see text for details).



*Geobates poecilopterus*, *Geositta punensis*, *rufipennis*, and *crassirostris*. Again, relationships within the subclade were poorly supported, with the exception of *punensis* and *rufipennis*, which were inferred to be sister taxa with 75% bootstrap support.

**Maximum-parsimony analyses.**—Maximum-parsimony analysis with all characters equally weighted recovered six most parsimonious trees (length = 762, consistency index [CI] = 0.562, retention index [RI] = 0.664), the 50% majority rule consensus of which was nearly identical to the ML tree, in terms of both topology and levels of support (Fig. 1). Differences occurred at two poorly supported nodes. First, the equally weighted parsimony analysis did not support the sister relationship between *isabellina* and *saxicolina*. Instead, *isabellina* was placed sister to *antarctica*, with 33% bootstrap support. Second, the sister relationship between *Geositta crassirostris* and *Geobates poecilopterus* was not supported. Instead, *crassirostris* was sister to the *punensis* + *rufipennis* clade, with 56% bootstrap support, and *Geobates* was placed basal to that group, with 48% bootstrap support.

Despite observed saturation and high levels of interspecific sequence divergence, downweighting of third-position transitions had very little effect on overall topology as compared with the equally weighted parsimony and likelihood analyses, with all of the topological differences occurring at poorly supported nodes. Topologies for the 2× and 5× weighting schemes were identical to the equally weighted parsimony topology. Because topological differences were minor among the 10–1,000× weighted analyses (see below), only the 10× tree is discussed.

Two most parsimonious trees (length = 383.2, CI = 0.551, RI = 0.757) were obtained in the 10× weighted analysis. A 50% majority rule consensus of those trees was identical to the likelihood and equally weighted parsimony trees at the deeper nodes. Again, *Geobates* was embedded within *Geositta* with 100% bootstrap support, and the same two clades (A and B) within *Geositta* were recovered, both of which were well supported (98%). The taxa composing each clade were the same as those in the previous analyses, though some topological differences occurred at poorly supported nodes within clades A and B. First, *cunicularia* was polyphyletic in the 10× weighted analysis, with individuals collected in

Tierra del Fuego (*G. c. cunicularia*) being sister to *tenuirostris*, rather than the individual collected in Arequipa, Peru (*G. c. georgei*) (51%). Both ML and equally weighted MP analyses recovered the monophyly of *G. cunicularia* haplotypes. Second, the 10× weighted analysis supported a sister relationship between *saxicolina* and *isabellina* (38%), in agreement with the ML analysis, but differed from the ML analysis in that those two taxa, plus *maritima*, formed the sister clade to *antarctica* (36%). The 50–1,000× topologies differed from the 10× topology only by not supporting the sister relationship between *punensis* and *rufipennis*.

## DISCUSSION

**Phylogeny of *Geositta* and taxonomic recommendations.**—Although the mtDNA phylogeny presented here is not fully resolved, our data reveal novel hypotheses of phylogenetic affinities within the genus. Most notably, *Geobates* is embedded within *Geositta*, supporting previous hypotheses based on morphological and behavioral data (Vaurie 1971, 1980; Remsen 2003a). This result illustrates that the taxonomic significance of the morphological characters used to define *Geobates*—especially the underwing pattern of primaries, bill and tail length, and body size—was overemphasized. Intermediate levels of sequence divergence between *Geobates* and members of *Geositta* clade B suggest that those morphological characters do not imply higher levels of genetic differentiation as compared with other members of *Geositta*. Furthermore, placement of *Geobates* within clade B is well supported (Fig. 1). Thus, unless *Geositta* is split into two separate genera, separate generic status for *Geobates* is not warranted. Clearly, the simplest solution is to include *Geobates poecilopterus* within *Geositta* as previously suggested by Vaurie (1971, 1980) and Remsen (2003a). Remsen (2003a) proposed that plumage similarities and lowland distribution suggest that *Geositta poeciloptera* (= *Geobates poecilopterus*; rendered *poeciloptera* because of the feminine *Geositta*) and *cunicularia* are sister taxa; however, that relationship was not corroborated in the present study.

Our data also suggest that *Geositta*, thus enlarged, now consists of two distinct clades (here called clades A and B), with each of the previously proposed sister species, *cunicularia*

and *antarctica* (Vuilleumier 1991a, b), falling into different clades. *Geositta antarctica* belongs to a clade of primarily high Andean (*crassirostris*, *isabellina*, *rufipennis*, *saxicolina*), Andean and Pacific coast (*maritima*, *punensis*), and Brazilian (*poeciloptera*) species (Fig. 1). Within that clade, *antarctica* was most closely related to *isabellina*, *saxicolina*, and *maritima*; and that subclade was well supported in both 10× weighted and equally weighted MP and ML analyses, with 92%, 93%, and 93% bootstrap support, respectively. The second clade, which contained *cunicularia*, also included one Andean and one Pacific coast species. *Geositta tenuirostris* is widely distributed in the Andes of central Peru, Bolivia, and northwestern Argentina; whereas *peruviana* occurs along the northern and central coast of Peru. Within clade A, *cunicularia* was hypothesized to be most closely related to *tenuirostris* in all phylogenetic analyses. The well-supported phylogenetic relationships within clade A did not support any previous hypothesis. Remsen (2003a), however, has proposed that plumage similarities suggest that *tenuirostris* and *cunicularia* are closely related, and that an overemphasis on bill morphology had led previous workers to conclude that those two species did not share a recent common ancestor.

Neither of the two main mtDNA clades (A and B) was entirely consistent with the species groups proposed by Vaurie (1980). First, his modified bill group (*tenuirostris* and *crassirostris*) appears to be polyphyletic, because *crassirostris* and *tenuirostris* fall into different clades. The molecular data suggest that the similarities in bill structure used to define that group are attributable to homoplasy, which is most likely the result of the functional importance of bill morphology. *Geositta* species place their nests in underground burrows, and the substrate in which those burrows are dug may have a selective influence on bill morphology. Second, the lowland and Andean straight-billed group also appears to be polyphyletic, with *cunicularia* being only distantly related to other members of that group. However, with the exception of *cunicularia*, the molecular data support Vaurie's group. Finally, Vaurie's coastal group is also polyphyletic. The molecular result is consistent with Vaurie's (1980) suggestion that plumage characters defining that group are convergent, and those characters may reflect adaptation to substrate conditions (Koepcke

1965). These examples, as well as similarities between *cunicularia* and *antarctica* (see below), demonstrate that parallel selection pressures, such as background matching, are important factors leading to convergence in optimal bill and plumage types within *Geositta*. A parallel can be drawn between *Geositta* and other ground-dwelling birds, such as several genera of southern African larks, whose general plumage color matches the color of their substrate (Niethammer 1940, 1959; Maclean 1970). The evolutionary trends of morphological (bill structure) and plumage convergence among *Geositta* species will be discussed elsewhere.

Because *cunicularia* and *antarctica* fall into different clades, the previously proposed sister relationship between *cunicularia* and *antarctica* is clearly not supported by the molecular data. Moreover, in terms of percentage of sequence divergence (uncorrected *P*), *cunicularia* and *antarctica* are the most divergent of all pairwise comparisons of species-level taxa in the genus, with a mean divergence value of 15.9% (Table 3). All previous hypotheses (Vaurie 1980; Vuilleumier 1991a, b) have considered *cunicularia* and *antarctica* closely related.

The new data provided here suggest that plumage and behavioral similarities between *cunicularia* and *antarctica* are also the result of convergent evolution. Despite close similarity in plumage and behavior, the two species are clearly distinguishable vocally (Vuilleumier 1991b, 1993), which is often the most reliable means for distinguishing the two species in the field where they occur sympatrically (Vuilleumier 1991b, A. P. Capparella and F. Vuilleumier pers. obs.). The high degree of apparent morphological and plumage convergence within *Geositta* underscores the difficulty of assessing homology in those characters; whereas vocal differences, such as those highlighted between *cunicularia* and *antarctica*, may be more phylogenetically conservative. Further analyses of vocal and molecular characters are likely to reveal additional examples of plumage convergence in other furnariid taxa within which the emphasis has historically been placed on taxonomic significance of potentially plastic morphological characters (e.g. bill structure).

Although the sampling design of the present study did not permit a rigorous analysis of the species status of subspecies and "subspecies groups" within *cunicularia*, some preliminary

assessment can be made. Here, individuals of lowland (*G. c. cunicularia*) and Pacific coast (*G. c. georgei*) subspecies groups were sampled. In the weighted parsimony analysis, the monophyly of *cunicularia* haplotypes was not recovered, with *tenuirostris* being sister to the individuals collected in Tierra del Fuego (*G. c. cunicularia*). The individual collected in southern Peru (*G. c. georgei*) was basal to those two taxa. However, those nodes were poorly supported (51% bootstrap support), and the equally weighted parsimony and likelihood analyses recovered the monophyly of *cunicularia* haplotypes with 75% and 77% bootstrap support, respectively (Fig. 1). Finally, although divergence values (uncorrected *P*) between *G. c. cunicularia* and *G. c. georgei* were relatively high (mean = 4.72%), they were only slightly more than half that between the least divergent species-level taxa, *cunicularia* and *tenuirostris* (mean = 7.44%). Further study is warranted to reassess the species status of *cunicularia* subspecies. A species-level linear sequence for *Geositta* based on our phylogenetic results is given in Appendix 2.

*Biogeographic implications.*—Hypotheses of diversification of Patagonian and Andean avian taxa generally focus on the importance of Pleistocene glacial events as vicariant mechanisms (e.g. Vuilleumier and Simberloff 1980; Vuilleumier 1985, 1991a, b; Corbin et al. 1988; Chesser 2000). For *Geositta* specifically, climatological and ecological correlates of a late Pleistocene glaciation event were hypothesized by Vuilleumier (1991a, b) to have led to the original isolation of an ancestral stock, eventually leading to diversification of modern

*cunicularia* (in Patagonia) and *antarctica* (in Tierra del Fuego). Though not explicitly stated as such, Vuilleumier’s (1991a, b) hypothesis referred to the Llanquihue glaciation, which took place approximately 20,000–14,000 years before the present. His biogeographic hypothesis was based on the proposed sister relationship between *cunicularia* and *antarctica* that is clearly not supported by the molecular data. Furthermore, the high levels of sequence divergence (7.7–16.3%) among *Geositta* species suggest that species-level divergences may be older than late Pleistocene in origin. Although we acknowledge the difficulties associated with estimating divergence times on the basis of single-locus gene trees (e.g. Edwards and Beerli 2000), the high levels of sequence divergence (7.7%) between proposed sister species *cunicularia* and *tenuirostris* suggest that all species-level divergences may predate the Pleistocene entirely. Unless, of course, rates of mitochondrial molecular evolution in *Geositta* are  $\geq 2.5\times$  as fast as those estimated in other avian taxa ( $\sim 2\%$  mya<sup>-1</sup>) (e.g. Fleischer et al. 1998).

Given the lack of well-supported resolution within clade B, we are reluctant to infer causal mechanisms or possible vicariant events leading to diversification among *Geositta* species. However, one important pattern emerging from the data is that pairs of sympatric species are generally distantly related (i.e. members of each of the two different clades), whereas allopatric species are generally closely related (i.e. members of the same clade). Table 4 identifies nine areas where at least two *Geositta* species occur sympatrically. The overarching pattern is one

TABLE 4. Areas of sympatry for *Geositta* species. (A) Clade A in Figure 1. (B) Clade B in Figure 1. Areas of sympatry are illustrated in Figure 2. Areas of sympatry adapted from Peters (1951), Fjelds  and Krabbe (1990), Ridgely and Tudor (1994), Remsen (2003a), J. Fjelds  and J. V. Remsen pers. comm., and F. Vuilleumier unpubl. data.

Area of sympatry	Taxon 1 (clade)	Taxon 2 (clade)
1. Central Peru coast	<i>peruviana</i> (A)	<i>maritima</i> (B)
2. Southern Peru coast	<i>cunicularia</i> (A)	<i>maritima</i> (B)
3. Central Peruvian Andes	<i>tenuirostris</i> (A)	<i>saxicolina</i> (B)
4. Central Peru to northwestern Argentina	<i>cunicularia</i> (A) <sup>a</sup>	<i>tenuirostris</i> (A) <sup>a</sup>
5. Altiplano of Bolivia	<i>punensis</i> (B) <sup>a</sup>	<i>rufipennis</i> (B) <sup>a</sup>
6. Altiplano of southern Peru and Bolivia	<i>cunicularia</i> (A)	<i>punensis</i> (B)
7. Central Chile	<i>rufipennis</i> (B) <sup>a</sup>	<i>isabellina</i> (B) <sup>a</sup>
8. Chubut, Argentina	<i>cunicularia</i> (A)	<i>rufipennis</i> (B)
9. Tierra del Fuego, Chile	<i>cunicularia</i> (A)	<i>antarctica</i> (B)

<sup>a</sup> Indicates sympatry between members of the same clade.

of dichotomous sympatry between distantly related species (Table 4). In six of the nine areas ( $P > 0.05$ , nonparametric sign test) identified in Table 4, sympatric species are distantly related. The three exceptions occur in the Andes of central Peru and northwestern Argentina where proposed sister species *cunicularia* and *tenuirostris* occur sympatrically, the altiplano of Bolivia where *punensis* and *rufipennis* are sympatric, and central Chile where *rufipennis* and *isabellina* are sympatric (Table 4 and Fig. 2). However, in those cases, sympatry does

not necessarily imply syntopy. Circumstantial evidence suggests niche separation in foraging habitat and nest-site selection in all those cases (F. Vuilleumier pers. obs., J. V. Remsen pers. comm.). Alternatively, complete syntopy has been documented in at least one case of distantly related taxa, *cunicularia* and *antarctica*, which are often found nesting in the same rodent burrow system (Vuilleumier 1991b).

Not surprisingly, little work has been done to investigate the ecological dynamics of *Geositta* species in those areas. The present study

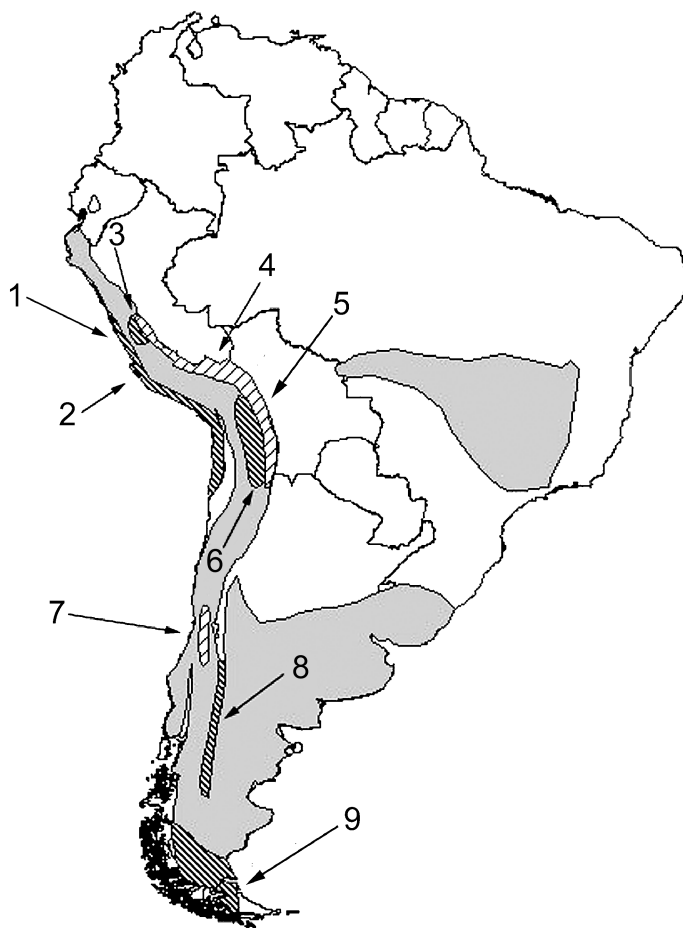


FIG. 2. Areas of sympatry among *Geositta* species. Distribution of all *Geositta* species is illustrated in gray. Light cross-hatched areas are areas of sympatry between closely related species (members of the same clade). Dark cross-hatched areas are areas of sympatry between distantly related species (members of different clades). Numbers refer to areas listed in Table 4. Distributions are based on Peters (1951), Vaurie (1980), Fjelds  and Krabbe (1990), Ridgely and Tudor (1994), and Remsen (2003a).

provides ornithologists with a phylogenetic framework for addressing many unanswered questions regarding patterns of sympatry within the genus. Future research focused on the following questions may prove fruitful. Are distantly related species entirely syntopic in areas of sympatry, as is the case with *cunicularia* and *antarctica*? Conversely, are closely related species segregated in their niche specialization in areas where they overlap? These questions must await further investigation, but their answers may provide important insights into our understanding of the development of sympatric distributions between closely related species. Finally, our study demonstrates that speciation within *Geositta* (and probably other Andean–Patagonian birds) is more complex than a simple model of allopatric speciation in Pleistocene glacial refugia would suggest and highlights the need for further research, both phylogenetic and ecological, of the understudied and intriguing Andean–Patagonian avifauna.

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APPENDIX 1. Taxa sampled, sampling locality, and tissue voucher numbers.

Species	Locality	Voucher number
<i>Geositta cunicularia</i>	Chile: Magellanes; Tierra del Fuego, Estancia "Los Tehuelches," ~4 km northeast of Puerto Nuevo, ~50 m above sea level	AMNH APC3264, APC3280, APC3283
<i>G. c. georgi</i>	Peru: Arequipa; Cerro Coscautire, ~5 km east of Chaia, 425 m above sea level	LSUMNS B-103846
<i>G. antarctica</i>	Chile: Magellanes; Tierra del Fuego, Estancia "Los Tehuelches," ~4 km northeast of Puerto Nuevo, ~50 m above sea level	AMNH 1988-68, APC3274
<i>G. tenuirostris</i>	Peru: Lima; 11.5 km west of Milloc, 3,750 m above sea level	LSUMNS B-103927
<i>G. peruviana</i>	Peru: Ica; ~5 km of west-northwest Pozo Santo, 300 m above sea level	LSUMNS B-103811
<i>G. maritima</i>	Peru: Ayacucho; 35 km on Nazca-Puquio road, 2,075 m above sea level	LSUMNS B-103913
<i>G. saxicolina</i>	Peru: Junin; ~12 km north of Chinchán on road to Marcapomacocha, 4,600 m above sea level	LSUMNS B-103806
<i>G. crassirostris</i>	Peru: Arequipa; 54 km on Div. Arequipa-Juliaca road, ~10 km west of Chinguata, 2,900 m above sea level	LSUMNS B-103868
<i>G. crassirostris</i>	Peru: Ayacucho; 52 km on Nazca-Puquio road, 2,800 m above sea level	LSUMNS B-103815
<i>G. rufipennis</i>	Chile: Región Metropolitana, Prov. Cordillera, ~2 km east-northeast of Embalse El Yeso, 33°38'04"S, 70°00'44"W, ~2,500 m above sea level	AMNH RTC440
<i>G. isabellina</i>	Chile: Región Metropolitana, Prov. Cordillera, ~15 km east-northeast of Embalse El Yeso, 33°36'42"S, 69°55'38"W, ~3,400 m above sea level	AMNH RTC430
<i>G. punensis</i>	Argentina: Jujuy; 23°43'21"S, 65°41'47"W	LSUMNS B-17177
<i>Geobates poecilopterus</i>	Bolivia: Santa Cruz; Serranía de Huanchaca, 45 km east of Florida, 725 m above sea level	LSUMNS B-13924, B-13926, B-13975
<i>Upucerthia ruficauda</i>	Peru: Tacna; 116 km on Tacna-Ilave road, ~25 km northeast of Tarata, 4,050 m above sea level	LSUMNS B-103882
<i>Aphrastura spinicauda</i>	Chile: Magallanes; Brunswick Peninsula, near mouth of Río Santa Maria, ~2 km south of San Juan, approximately sea level	AMNH APC3219

Abbreviations: LSUMNS = Louisiana State University Museum of Natural Science, AMNH = American Museum of Natural History.

APPENDIX 2. Linear sequence of species-level taxa in the genus *Geositta*.

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Genus *Geositta* Swainson 1837 (type species *Geositta cunicularia*)

Subgenus *Geositta* Swainson 1837 (type species: *Geositta cunicularia*)

*Geositta cunicularia* (Vieillot, 1816)

*Geositta tenuirostris* (Lafresnaye, 1836)

*Geositta peruviana* Lafresnaye, 1847

Subgenus *Geobates* Swainson 1837 (type species: *Geositta poeciloptera*)

*Geositta antarctica* Landbeck 1880

*Geositta isabellina* (Philippi and Landbeck, 1864)

*Geositta saxicolina* Taczanowski 1874

*Geositta maritima* (Lafresnaye and d'Orbigny, 1837)

*Geositta poeciloptera* (Wied, 1831) [= *Geobates poecilopterus* (Wied, 1831)]

*Geositta crassirostris* Sclater 1866

*Geositta punensis* Dabbene 1917

*Geositta rufipennis* (Burmeister, 1860)

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The linear sequence of species in the genus *Geositta* is based on the phylogeny in Figure 1. Species in the subgenus *Geositta* correspond to the species in clade A of Figure 1. Species in the subgenus *Geobates* are those included in clade B of Figure 1. However, because the phylogenetic arrangement of species in clade B is not yet fully resolved, the present linear arrangement of species in the subgenus *Geobates* remains tentative. Nomenclature follows Cory and Hellmayr (1925). According to Vaurie (1971), priority is given to *Geositta* because it was described in July 1837, whereas *Geobates* was described in December 1837.