

SYSTEMATICS, EVOLUTION, AND BIOGEOGRAPHY OF THE SOUTH AMERICAN OVENBIRD GENUS *CINCLODES*

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ABSTRACT.—Phylogenetic relationships within the genus *Cinclodes*, a group of South American furnariids, were studied using complete sequences of the mitochondrial genes COII and ND3. The 13 species of *Cinclodes* formed a monophyletic group consisting of three major lineages: (1) the southeastern Brazilian isolate *C. pabsti*, which was sister to the rest of the genus; (2) a clade of five primarily Patagonian or central Argentine highlands species; and (3) a clade of seven primarily north-central Andean or Pacific species. Biogeographic structure in the Patagonian–Andean taxa was consistent with the deep Patagonian and north-central Andean division previously noted in the similarly distributed genus *Muscisaxicola*. Evolutionary relationships among *Cinclodes* species were partially consistent with expectations based on plumage, behavior, and ecology. The phenotypically distinctive *C. antarcticus* was found to be sister to the widespread *C. fuscus* in the primarily Patagonian–Argentine clade, and the distinctive *C. palliatus* to be sister to *C. atacamensis* in the high Andean–Pacific clade. The central Argentine isolates *C. comechingonus* and *C. olrogi* formed a clade with *C. oustaleti* (*olrogi* sister to *oustaleti*, and *comechingonus* sister to those two) within the Patagonian–Argentine clade. The Pacific marine specialists *C. nigrofumosus* and *C. taczanowskii* were sisters within the Andean–Pacific clade and were distantly related to the southern maritime species *C. antarcticus*. Thus, marine ecological specialization apparently evolved twice within *Cinclodes*; behavioral and ecological data also support the nonhomology of the two character states. The two exclusively Pacific species were positionally apomorphic within the Andean–Pacific clade; ancestral area analysis indicated that the high Andes were the most likely area of origin for this clade, and that the Pacific coast was occupied secondarily. Received 30 May 2002, accepted 23 February 2004.

RESUMEN.—Se estudiaron las relaciones filogenéticas en el género *Cinclodes*, un grupo de furnáridos suramericanos, empleando secuencias completas de los genes mitocondriales COII y ND3. Las 13 especies de *Cinclodes* formaron un grupo monofilético compuesto por tres linajes principales: (1) *C. pabsti*, una especie aislada del sureste brasileño, que fue la especie hermana del resto del género; (2) un clado de cinco especies principalmente patagónicas o de las tierras altas del centro de Argentina; y (3) un clado de siete especies principalmente del centro y norte de los Andes o del Pacífico. La estructura biogeográfica en los taxa patagónicos-andinos fue consistente con la división profunda entre elementos patagónicos y de los Andes nor-centrales evidenciada anteriormente en el género *Muscisaxicola*, el cual tiene una distribución similar. Las relaciones evolutivas entre las especies de *Cinclodes* fueron parcialmente consistentes con lo esperado con base en plumaje, comportamiento y ecología. Se encontró que la especie fenotípicamente distintiva *C. antarcticus* es hermana de la ampliamente distribuida *C. fuscus* en el clado principalmente patagónico-argentino, y que la especie distintiva *C. palliatus* es hermana de *C. atacamensis* en el clado altoandino-Pacífico. Las especies aisladas del centro de Argentina, *C. comechingonus* y *C. olrogi*, formaron un clado con *C. oustaleti* (*olrogi* es hermana de *oustaleti* y *comechingonus* de estas dos) dentro del clado patagónico-argentino. Las especies especialistas marinas del Pacífico, *C. nigrofumosus* y *C. taczanowskii*, fueron hermanas dentro del clado andino-Pacífico y estuvieron lejanamente emparentadas con la especie marina del sur, *C. antarcticus*. Por lo tanto, la especialización ecológica en ambientes marinos parece haber evolucionado dos veces en *Cinclodes*; datos comportamentales y ecológicos también sugieren la no-homología de los dos estados de carácter. Las dos especies exclusivas del Pacífico fueron posicionalmente apomórficas en el clado andino-Pacífico; un análisis de áreas ancestrales indicó que los altos Andes fueron el área de origen más probable para este clado, y que la costa Pacífica fue ocupada de forma secundaria.

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THE 13 SPECIES of the genus *Cinclodes* (Aves: Passeriformes, Furnariidae; Table 1) are characteristic of the open country of the Andes and other highlands of South America, where they are typically found near mountain streams and other sources of water. Seven of those mainly terrestrial species breed in the highlands or along slopes of the Andes ranging from Venezuela south to Tierra del Fuego, and another three species are endemic to isolated highlands in southern South America—two to the highlands of Córdoba and San Luis in central Argentina, and another to the highlands of Rio Grande do Sul and Santa Catarina in southeastern Brazil (Table 1). Three *Cinclodes* species are restricted to the páramo, puna, or stunted *Polylepis* woodlands of the high Andes, but other Andean and highland species are found additionally or exclusively along lower montane slopes or seasonally in various open lowland habitats.

Although most *Cinclodes* species are found along freshwater streams, three species occur exclusively in coastal areas (Ridgely and Tudor 1994, Stotz et al. 1996): *C. nigrofumosus* and *C. taczanowskii* along the rocky Pacific coastlines of Chile and Peru, and *C. antarcticus* along rocky coasts and gravel beaches in southern Tierra del Fuego and the Falkland Islands. *Cinclodes nigrofumosus* and *C. taczanowskii* feed exclusively in the intertidal zone, hopping among rocks in the manner of Surfbirds (*Aphriza virgata*) or Purple Sandpipers (*Calidris maritima*), and are “almost certainly the most maritime of all passerine birds” (Paynter 1971). Those coastal specialists have been the subject of several physiological studies, including investigation of their nasal glands (Paynter 1971), intestinal biochemistry (Sabat 2000a), and renal function (Sabat and Martínez del Río 2002). The third coastal specialist, *C. antarcticus*, feeds in shoreline seaweed and kelp (*Macrocystis* spp.) mats and among tussock-grass (*Poa flabellata*) in peaty soil near the sea (Reynolds 1935, Cawkell and Hamilton 1961, Robbins et al. 2001). Three other species—*C. patagonicus*, *C. oustaleti*, and *C. fuscus*—occur in winter along the central or northern Chilean coast (Housse 1945, Goodall et al. 1946, Sielfeld et al. 1996, Jorge et al. 1998, Sabat 2000b), but those populations breed inland; *patagonicus* also breeds along seacoasts in southern Chile and Argentina, but even those southern populations are not as maritime as the specialists (Reynolds 1935, Robbins et al. 2001).

Cinclodes is a fairly well-defined genus, distinguished by its habitat preferences, plumage, and songs and displays (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994). Except for several species only recently described—*C. comechingonus* (Zotta and Gavio 1944), *C. pabsti* (Sick 1969), and *C. olrogi* (Nores and Yzurieta 1979)—the constitution of the genus has remained nearly stable over the past 70 years; the *excelsior*–*aricomae* complex has been the only source of contention. *Cinclodes excelsior*, placed in *Cinclodes* by Sclater (1860), was later shifted to the genus *Upucerthia* (Sclater 1890, Cory and Hellmayr 1925), although its affinities with *Cinclodes* were also mentioned. When describing *C. aricomae*, Carriker (1932), noting the similarity of the new species to *excelsior*, accordingly named it *U. aricomae*, though he suggested that the affinities of both species were actually closer to *Cinclodes*. Bond (1945) returned *excelsior*, along with *aricomae*, to *Cinclodes*. Although Vaurie (1980) considered both taxa to be part of *Geositta*, other modern sources consider *excelsior* and *aricomae* to be typical members of *Cinclodes* (Vuilleumier in Vaurie 1980, Fjeldså et al. 1987, Fjeldså and Krabbe 1990, Sibley and Monroe 1990, Ridgely and Tudor 1994, Stotz et al. 1996).

Vaurie (1980) outlined four species groups within *Cinclodes* (Table 1); he did not include *olrogi* (it had not been described yet) or *excelsior*–*aricomae* (see above). Vaurie's species groups seem to have been based primarily on plumage (especially color of wing patch) and ecology. His first group (*fuscus*, *comechingonus*, *pabsti*) shared a cinnamon-buff or rufous wing patch, his second group (*oustaleti*, *patagonicus*) a buff wing patch, his third group (*taczanowskii*, *nigrofumosus*, *antarcticus*) a restricted coastal habitat, and his fourth group (*atacamensis*, *pal-liatus*) a white wing patch and chestnut back.

No other comprehensive classifications of *Cinclodes* have been proposed, but relationships among particular taxa, especially the restricted-range endemics, have attracted attention. For example, *C. pabsti* was originally described as a species similar to *fuscus* (Sick 1969, 1973), a position also adopted by Sibley and Monroe (1990). Mayr and Vuilleumier (1983), however, following Vaurie (1980), proposed that *pabsti* was also closely related to *comechingonus* and suggested that *pabsti* be considered part of a superspecies with *fuscus* and *comechingonus*—or perhaps, along with *comechingonus*, a subspecies

TABLE 1. Characteristics of *Cinclodes* species. Species group designations follow Vaurie (1980); *C. olrogi* was undescribed when Vaurie wrote his monograph, and he placed the *excelsior-aricomae* group in the genus *Geositta*. Number of subspecies follows Remsen (2003); wing-patch coloration and breeding elevational range were taken from Ridgely and Tudor (1994).

Species	Common name	Species group	Number of recognized subspecies	Color of wing patch	Breeding distribution	Elevation
<i>C. fuscus</i>	Bar-winged Cinclodes	1	9	Cinnamon-buff (strongly rufous in north)	Andes from Venezuela south; Patagonia	0–5,000 m
<i>C. comechingonus</i>	Cordoba Cinclodes	1	Monotypic	Deep rufous	Mountains of Córdoba and San Luis, Argentina	1,600–2,400 m
<i>C. pabsti</i>	Long-tailed Cinclodes	1	Monotypic	Cinnamon-buff	Highlands of southeastern Brazil	750–1,700 m
<i>C. oustaleti</i>	Gray-flanked Cinclodes	2	3	Buff	Chile and western Argentina; Juan Fernandez Archipelago	0–3,000 m
<i>C. patagonicus</i>	Dark-bellied Cinclodes	2	2	Buff	Chile and western Argentina	0–2,300 m
<i>C. taczanowskii</i>	Surf Cinclodes	3	Monotypic	Rufous buff	Central and southern Peruvian Pacific coast	0–100 m
<i>C. nigrofumosus</i>	Seaside Cinclodes	3	Monotypic	Rufous buff	Northern and central Chilean Pacific coast	0–100 m
<i>C. antarcticus</i>	Blackish Cinclodes	3	2	Faint rufescent	Southern coastal Argentina and Chile; Falkland Islands	0–100 m
<i>C. atacamensis</i>	White-winged Cinclodes	4	2	White	Andes of Peru south to central Argentina and Chile; mountains of Córdoba and San Luis, Argentina	2,200–4,500 m
<i>C. palliatus</i>	White-bellied Cinclodes	4	Monotypic	White	Andes of central Peru	4,400–5,500 m
<i>C. olrogi</i>	Olrog's Cinclodes	NA	Monotypic	White	Mountains of Córdoba and San Luis, Argentina	1,600–2,800 m
<i>C. excelsior</i>	Stout-billed Cinclodes	NA	2	Rufous buff	Andes of Ecuador and Colombia	3,300–5,000 m
<i>C. aricomae</i>	Royal Cinclodes	NA	Monotypic	Rufous	Andes of southern Peru and northwestern Bolivia	3,600–4,700 m

NA = not available

of *fuscus*. The recently described *C. olrogi* was originally compared with *fuscus* and *oustaleti* (Nores and Yzurieta 1979), and Olrog (1979a) himself considered it a subspecies of *oustaleti*, as did Navas and Bo (1987). Nores (1986), however, in describing a new subspecies of *C. fuscus* (*C. f. riojana*) very similar in plumage to *olrogi*, proposed that *olrogi* also was a subspecies of *fuscus*. Subsequent opinion has generally considered *olrogi* a species closely related to *oustaleti* (Vuilleumier and Mayr 1987, Sibley and Monroe 1990, Ridgely and Tudor 1994), though Sibley and Monroe (1990) also commented that it might be closely related to *fuscus*. Southern marine specialist *C. antarcticus* has been considered closely related to Pacific marine specialists *nigrofumosus* and *taczanowskii* (Vaurie 1980, Sibley and Monroe 1990), or perhaps sister to *patagonicus* (Robbins et al. 2001), but *antarcticus* is quite distinctive, and most sources have not speculated on its affinities. *Cinclodes patagonicus* has also been proposed to be sister to *aricomae* and *excelsior*, on the basis of similarities in coloration and wing and facial patterns (Fjelds  1992).

Even when sister relationships in the genus have been considered straightforward, species limits and species status have often been difficult to define. *Cinclodes aricomae*, for instance, was originally described as a species closely related to *excelsior* (Carriker 1932); that has been followed occasionally (Ridgely and Tudor 1994), but more often the two have been considered conspecific (Bond 1945; Peters 1951; Meyer de Schauensee 1966, 1970; Vaurie 1980; Fjelds  et al. 1987; Fjelds  and Krabbe 1990; Sibley and Monroe 1990; Stotz et al. 1996). *Cinclodes nigrofumosus* and *C. taczanowskii*, though generally thought to be sister species (Cory and Hellmayr 1925, Peters 1951, Vaurie 1980, Sibley and Monroe 1990, Ridgely and Tudor 1994), have sometimes been considered conspecific (Sclater 1890; Meyer de Schauensee 1966, 1970; Stotz et al. 1996). *Cinclodes comechingonus* was originally described as a species similar to *fuscus* (Zotta and Gavio 1944) and has since been considered either a subspecies of *fuscus* (Mayr 1957; Meyer de Schauensee 1966, 1970) or a species closely related to *fuscus* (Olrog 1979b, Vaurie 1980, Sibley and Monroe 1990, Ridgely and Tudor 1994).

Cinclodes species share a number of biogeographic and ecological characteristics with such furnariid genera as *Upucerthia* and *Geositta*, to

which they have been considered closely related (Sclater 1890, Cory and Hellmayr 1925, Peters 1951, Vaurie 1980, Zyskowski and Prum 1999), and to such tyrannid genera as *Muscisaxicola*. Those genera are also distributed chiefly in the Andes and Patagonia and are also characterized by open habitat, terrestrial habits, and inconspicuous plumage. Recent molecular evidence suggests that the primary division among typical *Muscisaxicola* species was biogeographic—between mainly central Andean and mainly southern Andean–Patagonian clades—and that *Muscisaxicola* species were the product of relatively recent radiations within those regions (Chesser 2000).

Here, I derive a molecular phylogenetic hypothesis for the genus *Cinclodes* and use it to address the following questions:

- (1) Do the 13 species of *Cinclodes* form a monophyletic group?
- (2) Do molecular phylogenetic relationships among species conform to ideas of relationship based on plumage and ecology?
- (3) What are the evolutionary relationships of the geographic isolates in the highlands of central Argentina (*C. comechingonus*, *C. olrogi*) and southeastern Brazil (*C. pabsti*)?
- (4) What are the biogeographic relationships among the Andean and Patagonian species? Is deep biogeographic patterning (cf. *Muscisaxicola*) evident?
- (5) What are the evolutionary relationships of the three marine ecological specialists (*C. nigrofumosus*, *C. taczanowskii*, *C. antarcticus*)? Do they constitute a monophyletic group?

METHODS

Tissues of *Cinclodes* species and outgroups were obtained during fieldwork in Argentina and Chile and from the frozen-tissue collections of the Museum of Natural Science, Louisiana State University; the Zoological Museum of Copenhagen University; and the Burke Museum, University of Washington (Table 2). Two individuals were sampled for each of the Argentine highland endemics (*C. comechingonus* and *C. olrogi*) and species thought to be closely related to them (*C. oustaleti* and *C. fuscus*); single individuals were sampled for the other species of *Cinclodes* and for all outgroups. Outgroups sampled were *Upucerthia dumeteria* and *U. validirostris*, members of the sister group to *Cinclodes* (R. T. Chesser unpubl. data; see also Sclater 1890); *Furnarius rufus*, member of a fairly closely related genus (Sclater 1890, Cory

TABLE 2. List of tissue reference numbers and collecting localities for sequenced individuals of *Cinclodes* species and outgroups. No tissue was available for *C. antarcticus*, *C. pabsti*, and *C. taczanowskii*; numbers in brackets refer to study skins from which DNA was extracted directly.

Species	Tissue number	Locality
<i>Cinclodes antarcticus</i>	[AMNH 817070]	Chile: Region XII (Magallanes), Bahía Inutil, Tierra del Fuego; sea level
<i>C. aricomae</i>	ZMCU 5186	Peru: Departamento de Apurímac, southeast of Abancay; 4,400 m
<i>C. atacamensis</i>	AMNH RTC 354	Argentina: Provincia de la Córdoba, Pampa de Achala; 2,000 m
<i>C. comechingonus 1</i>	AMNH RTC 356	Argentina: Provincia de la Córdoba, Pampa de Achala; 2,000 m
<i>C. comechingonus 2</i>	AMNH PRS 1123	Argentina: Provincia de la Córdoba, Pampa de Achala; 2,000 m
<i>C. excelsior</i>	LSU B-5935	Ecuador: Provincia de la Pichincha, west of Papallacta
<i>C. fuscus 1</i>	AMNH RTC 360	Argentina: Provincia de Río Negro, Cerro Perito Moreno; 1,500 m
<i>C. fuscus 2</i>	AMNH RTC 418	Chile: Region Metropolitana, ~2 km east-northeast of Embalse El Yeso; 2,500 m
<i>C. nigrofumosus</i>	AMNH RTC 413	Chile: Region V (Valparaíso), Roca Brava, ~2 km north of Zapallar; sea level
<i>C. olrogi 1</i>	AMNH RTC 353	Argentina: Provincia de la Córdoba, Pampa de Achala; 2,000 m
<i>C. olrogi 2</i>	AMNH RTC 355	Argentina: Provincia de la Córdoba, Pampa de Achala; 2,300 m
<i>C. oustaleti 1</i>	AMNH RTC 415	Chile: Region Metropolitana, ~2 km east-northeast of Embalse El Yeso; 2,500 m
<i>C. oustaleti 2</i>	AMNH RTC 417	Chile: Region Metropolitana, ~2 km east-northeast of Embalse El Yeso; 2,500 m
<i>C. pabsti</i>	[AMNH 813030]	Brazil: Rio Grande do Sul, Fazenda Baios de Fora, Bom Jesus; 1,350 m
<i>C. palliatus</i>	LSU B-103923	Peru: Departamento de Junín, ~14 km northwest of Chinchán; 4,600 m
<i>C. patagonicus</i>	AMNH RTC 453	Chile: Region VIII (Bío Bío), ~10 km by road southeast of Ralco; 500 m
<i>C. taczanowskii</i>	[AMNH 798898]	Peru: Departamento de Lima, Bujama Baja, 95 km south of Lima; sea level
<i>Upucerthia dumetaria</i>	AMNH RTC 368	Argentina: Provincia de Río Negro, Cerro Perito Moreno; 800 m
<i>U. validirostris</i>	UWBM 54396	Argentina: Provincia de Tucumán, El Infiernillo; 3,100 m
<i>Furnarius rufus</i>	AMNH RTC 389	Argentina: Provincia de Buenos Aires, ~8 km southwest of Loma Verde; sea level
<i>Synallaxis spixii</i>	AMNH RTC 349	Argentina: Provincia de Buenos Aires, ~15 km north of Belén de Escobar; sea level
<i>Geositta cunicularia</i>	AMNH APC 3280	Chile: Region XII (Magallanes), Tierra del Fuego, Estancia Los Tehuelches; 50 m

and Hellmayr 1925, Peters 1951, Zyskowski and Prum 1999, R. T. Chesser unpubl. data); *Synallaxis spixii*, a more distantly related member of the Furnariidae; and *Geositta cunicularia*, member of a genus often considered closely related to *Cinclodes* (e.g. Vaurie 1980), but which actually lies outside the main clade of the Furnariidae and Dendrocolaptidae (Chesser 2004).

DNA was extracted from tissue samples using a

5% Chelex solution (Bio-Rad, Hercules, California) (Walsh et al. 1991). Tissue samples were unavailable for *C. antarcticus*, *C. pabsti*, and *C. taczanowskii*; for each of those species, a small (approximately 0.5 × 0.5 mm) piece of toe-pad was removed from a study skin in the American Museum of Natural History, and DNA was extracted using the QIAmp Tissue Kit (Qiagen, Valencia, California). Two complete protein-coding

mitochondrial genes—cytochrome oxidase II (COII; 684 base pairs [bp]) and NADH dehydrogenase subunit 3 (ND3; 351 bp)—were amplified via the polymerase chain reaction, using standard protocols (Chesser 1999). Primers used for samples extracted from tissue were those detailed previously (Chesser 1999, 2000). DNA extracted from study skins is particularly subject to contamination and can be expected to yield smaller pieces of DNA because of degradation over time. Therefore, *Cinclodes*-specific internal primers were designed and used to amplify 250- to 300-bp pieces of COII from study skins of *antarcticus*, *pabsti*, and *taczanowskii*. Primer pairs used were L8302 (5'-GCCTTGCAAGACTAAATCGCAGG-3') and H8566 (5'-CGTCTATTATGTAGAGGATTGAAGGG-3'), L8536 (5'-CTCGTCTGAACAATCTTACCTGC-3') and H8811 (5'-CGCCAAGACTTGGGACAGCTCAGGA-3'), and L8794 (5'-CCCCAATTCGAGTTATCGTAAACCGC-3') and H9036A (5'-CTTTCTCTAGCTTAAAGGCTAGTGC-3'). The primer pair used for ND3 was L10754 (5'-GACTTCCAATCTTAAAATCTG-3') and H11152 (5'-GATTTGTTGAGCCGAAATCAA-3'). Sequencing was conducted using dye-terminator chemistry on an ABI 377 automated sequencer (Applied Biotechnologies, Foster City, California). Complete heavy and light strands of both genes were sequenced for all taxa. Sequences were aligned using SEQUENCHER 4.1 (GeneCodes Corporation, Ann Arbor, Michigan). All sequences used here have been deposited in GenBank (accession numbers AY613370–AY613389 for COII sequences; AY613350–AY613369 for ND3 sequences).

Because previous studies of suboscine birds have revealed nuclear copies of the mitochondrial gene cytochrome-*b* (Arctander 1995), I investigated the possibility that nuclear copies were amplified in the present study. Sequences were examined for the following characteristics of nuclear copies (Sorensen and Quinn 1998): (1) ambiguous sequence resulting from co-amplification of the nuclear copy and the mitochondrial gene, noticeable at sites of divergence between the original and the copy; (2) substantial variation in measures of divergence between COII and ND3, indicating that sequence of one gene may be a nuclear copy; (3) mismatches in overlapping sequences amplified using different primer pairs, because of one primer pair amplifying a nuclear copy; (4) slower rate of evolution than in mitochondrial DNA, resulting in smaller divergences and shorter branch lengths; (5) evolution atypical of functional mitochondrial sequences, including excessive protein changes, length variation, or stop codons.

Data analysis was performed using PAUP* (Swofford 2001) and MACCLADE (Maddison and Maddison 2000). Data were analyzed using maximum-parsimony and maximum-likelihood (ML) approaches, with *G. cunicularia* designated as the outgroup in all analyses. Parsimony analyses were

conducted using heuristic searches, with equal character weighting and 100 random-addition replicates. Character support for parsimony-based phylogenies was assessed via bootstrapping (Felsenstein 1985), using 1,000 heuristic searches with 10 random-addition replicates each, and branch support (Bremer 1988, 1994), which was computed using TREEROT (Sorensen 1999).

Maximum-likelihood analyses were performed using heuristic searches with 10 random-addition replicates. The program MODELTEST (Posada and Crandall 1998) was used to evaluate a variety of models of sequence evolution for ML analysis. MODELTEST determines the model of sequence evolution that achieves the best fit given the data. Analysis of the data indicated that GTR+G+I was the best model, and the following settings were used in subsequent ML analyses: freqA = 0.30, freqC = 0.33, freqG = 0.13, freqT = 0.25; R[A-C] = 13.81, R[A-G] = 102.64, R[A-T] = 21.45, R[C-G] = 1.72, R[C-T] = 252.68, R[G-T] = 1.00; I = 0.62; G = 4.29. Support for ML phylogenies was assessed via bootstrapping (Felsenstein 1985), using 100 heuristic searches with 10 random-addition replicates each.

For biogeographic investigation, distributions of *Cinclodes* species were classified as northern Andes, central Andes, southern Andes–Patagonia, central Argentine highlands (of Córdoba and San Luis), southeastern Brazilian highlands, Pacific coast of Peru–Chile, Falkland Islands, Juan Fernandez Archipelago, or some combination of those. The Andes were subdivided at two apparent natural barriers to gene flow (Vuilleumier 1969): the “Northern Peruvian Low,” separating the northern and central Andes, and the “Central Chilean–Argentine Andes,” separating the central and southern Andes.

Biogeographic analyses were conducted using ancestral area (AA) analysis (Bremer 1992, 1995), which assumes that a group's original distribution was more restricted than its current distribution, and weighted AA analysis (Hausdorf 1998). A restricted ancestral distribution seems likely for the major clades (see below) of *Cinclodes* and has been assumed in previous historical analyses of the biogeography of all or part of the genus (e.g. Chapman 1926, Vaurie 1980, Vuilleumier 1986, Fjeldså 1992). Under AA analysis, the eight areas enumerated above were treated as single characters and optimized, using Camin-Sokal (irreversible) parsimony (Camin and Sokal 1965), onto an area cladogram derived from the parsimony-bootstrap consensus tree. Calculations of gains of areas were made under reverse Camin-Sokal parsimony, and calculations of losses of areas under forward Camin-Sokal parsimony (see Bremer 1992 for further details). Weighted AA analysis involves similar procedures, but reversible parsimony is used in character optimization. Calculations of gains and losses are weighted according to their position on the

area cladogram, with steps on positionally plesiomorphic branches receiving higher weight than those on positionally apomorphic branches (Hausdorf 1998).

For analysis of the evolution of ecological and behavioral specialization to coastal environments, species were classified according to degree of marine specialization, using the following three categories: marine specialist (obligate or predominantly marine), partially or seasonally marine, and nonmarine. Evolution of marine specialization was investigated using MACCLADE (Maddison and Maddison 2000); degree of specialization was mapped as both an ordered and an unordered character.

RESULTS

Sequence variation.—Of 1,035 bp sequenced, 318 (30.7%) were variable and 208 were phylogenetically informative. COII provided 195 of the variable and 122 of the phylogenetically informative sites, and ND3 provided 123 and 86, respectively. First, second, and third positions differed substantially in their distribution of site changes, as is consistent with other protein-coding genes: 54 first-position sites were variable (17.0% of variable sites), 18 second-position sites (5.7%), and 246 third-position sites (77.3%). Those figures differ little from previous data on variability in the two genes (Chesser 1999, 2000).

Mean uncorrected sequence divergence between *Cinclodes* and outgroups ranged from 8.4% to 15.0%. Sequence divergence within *Cinclodes* ranged from 0.0% between two individuals of *comechingonus* to 7.8% between *pabsti* and *antarcticus*. Interspecific divergence was as low as 0.2% between *nigrofumosus* and *taczanowskii* and 0.5% between *olrogi* and *oustaleti*. Patterns of sequence divergence were similar in separate analyses of COII and ND3. No instances of amplification of nuclear copies were detected.

Phylogenetics.—Parsimony analysis of the data resulted in two most-parsimonious trees (length = 650, consistency index [CI] = 0.59, CI excluding uninformative characters = 0.49, retention index [RI] = 0.63). The strict consensus of those trees revealed that the 13 *Cinclodes* species formed a strongly supported monophyletic group, with *C. pabsti*, the southeastern Brazilian endemic, sister to the other 12 species. The remaining species formed two well-supported monophyletic groups, one consisting of *antarcticus*, *fuscus*, *comechingonus*, *olrogi*, and *oustaleti*; the other of *aricomae*, *excelsior*, *atacamensis*,

palliatus, *nigrofumosus*, *taczanowskii*, and *patagonicus*. Within the first clade (“clade 1”), sister species *antarcticus* and *fuscus* were sister to a clade consisting of *olrogi* and *oustaleti* and of *comechingonus*, which was sister to *olrogi* and *oustaleti*. The second clade (“clade 2”) contained a 4-fold polytomy leading to *excelsior*, *aricomae*, a clade consisting of *atacamensis* and *palliatus*, and a clade consisting of *nigrofumosus* and *taczanowskii*, which were sister species, and *patagonicus*, which was sister to them.

The parsimony-bootstrap consensus tree (Fig. 1) was identical to the strict consensus tree, except that the polytomy in clade 2 was resolved, such that *excelsior* and *aricomae* were sister species and sister group to a clade consisting of *atacamensis*–*palliatus* and *patagonicus* (*nigrofumosus*–*taczanowskii*). Bootstrap support was strong or moderate for most nodes, but rather weak for the node supporting

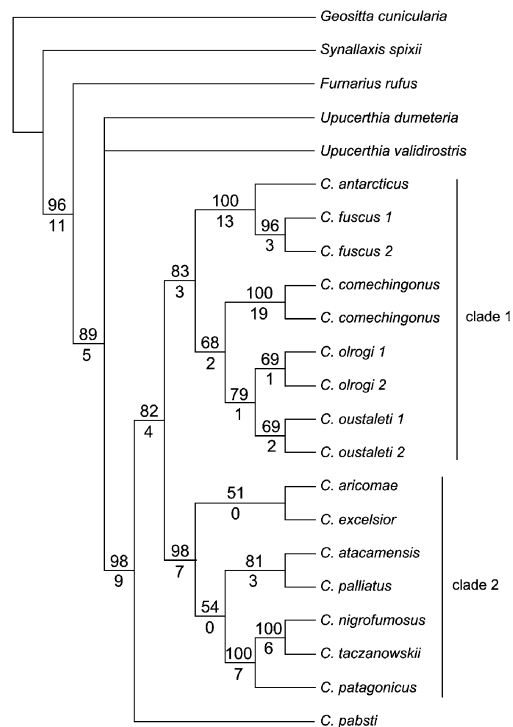


FIG. 1. Parsimony-bootstrap consensus tree based on combined sequences of COII and ND3. Numbers above branches are percentages of recovery of corresponding nodes in 1,000 heuristic bootstrap searches, and numbers below branches are Bremer support values.

sister-species status of *aricomae* and *excelsior* and for the node supporting the clade containing the other five species.

The best tree under the ML analysis (Fig. 2; $-\ln$ likelihood = 4260.411) was very similar to the parsimony-bootstrap consensus tree. *Cinclodes pabsti* was sister to the remaining *Cinclodes* species, which formed the two monophyletic groups recovered in the parsimony analyses. Clade 1 was identical in both analyses, but clade 2 differed somewhat: in the likelihood tree, *aricomae* and *excelsior* were successive sisters to the remaining five species in the clade. The relationships of the other five species were identical to those in the parsimony-bootstrap

consensus tree. Thus, *excelsior* and *aricomae* were not sister species in the most likely tree. Bootstrap support for the likelihood tree was generally strong, but the relationships of *aricomae* and *excelsior* received weak support.

All species for which more than one individual was sampled (*fuscus*, *comechingonus*, *olrogi*, and *oustaleti*) were monophyletic in all analyses.

Biogeography and character evolution.— Considerable biogeographic structure was apparent when distributions were mapped onto the phylogenies (Fig. 2). The highland region of southeastern Brazil, inhabited by *pabsti* and >1,000 km from the next nearest *Cinclodes* breeding area, was sister to all other areas. Within the

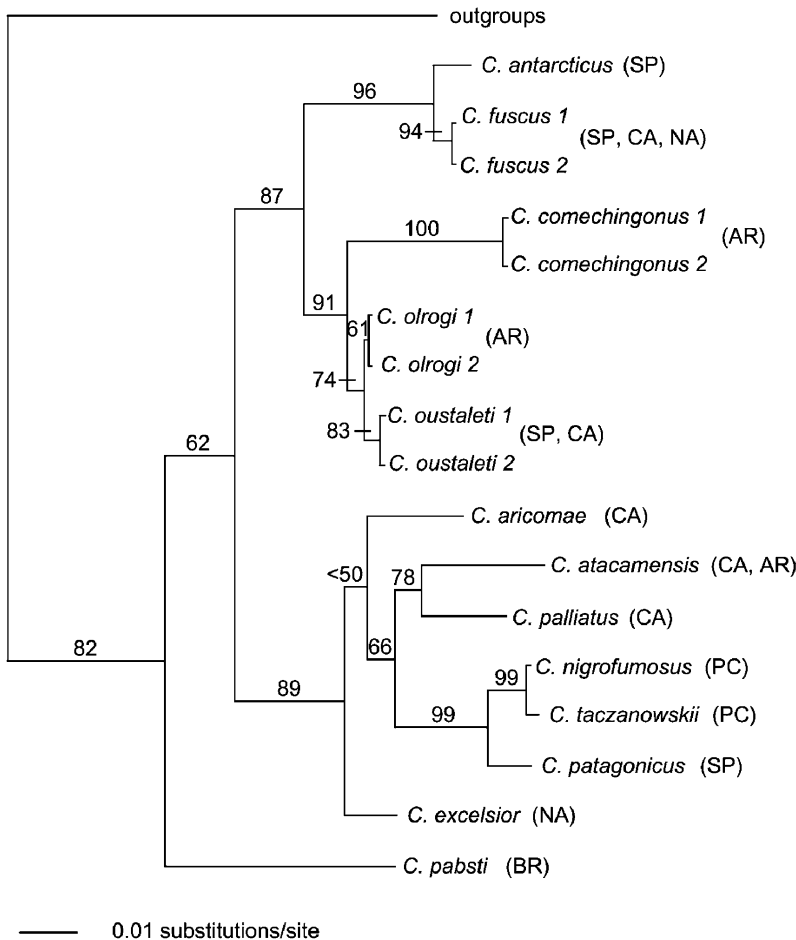


FIG. 2. Phylogram of the ML tree constructed using combined sequences of COII and ND3. Numbers above branches are percentages of recovery of corresponding nodes in 100 heuristic bootstrap searches. Branch lengths are proportional to the amount of character change along each branch. Letters following names of *Cinclodes* species represent continental breeding ranges of each species: SP = southern Andes–Patagonia, CA = central Andes, NA = northern Andes, AR = highlands of central Argentina, BR = highlands of southeastern Brazil, PC = Pacific coast.

two main clades, species in clade 1 occur primarily in the southern Andes, Patagonia, and the highlands of central Argentina; species in clade 2 occur primarily in the northern or central Andes or along the Pacific coast. Although the distribution of *fuscus* stretches from Patagonia to the northern Andes, ranges of all other species in clade 1 are restricted to Patagonia (*antarcticus*) or to the highlands of Córdoba and San Luis, Argentina (*comechingonus* and *olrogi*), or occur mainly within the southern Andes and Patagonia (*oustaleti*). Most members of clade 2, in contrast, are restricted to the high Andes of Bolivia, Peru, Ecuador, or Colombia (*aricomae*, *excelsior*, and *palliatu*), or to the coasts of Peru (*taczanowskii*) or northern and central Chile (*nigrofumosus*). The major exception is *patagonicus*, which breeds in Patagonia and along the lower slopes of the central Chilean and Argentine Andes. *Cinclodes atacamensis* occurs mainly in the high Andes of Peru, Bolivia, and northern Argentina and Chile, but its range also includes the highlands of central Argentina.

The AA analysis (Table 3) revealed that it was equally likely that the ancestor to clade 1 was

distributed in the southern Andes–Patagonia or in the highlands of central Argentina. The ancestor to clade 2 was most likely distributed in the central Andes, as was the ancestor to clades 1 and 2 combined. Results of the weighted AA analysis were the same for clade 2 and clades 1 and 2 combined, but indicated that the ancestor to clade 1 was more likely to have been distributed in the southern Andes–Patagonia than in the central Argentine highlands.

The phylogenetic tree revealed that two of the three coastal specialists (*nigrofumosus* and *taczanowskii*) were sister species and that the partially marine species *patagonicus* was sister to them; those species were part of clade 2. The other coastal specialist (*antarcticus*) was sister to a second partially coastal species (*fuscus*), but those species belonged to clade 1. The other partially marine species (*oustaleti*) was also part of clade 1 but was not closely related to *antarcticus* and *fuscus*. Reconstruction of ancestral states (Fig. 3) indicated that coastal specialization evolved twice within *Cinclodes* and that partial use of coastal habitats evolved three times, twice in sisters (*patagonicus* and *fuscus*) to coastal

TABLE 3. Ancestral area (AA) analyses (Bremer 1992, 1995) for the two major clades within the genus *Cinclodes*. Gains and losses are number of necessary gains and losses of areas under Camin-Sokal parsimony. G/L = number of gains divided by number of losses. AA scores = G/L scores rescaled to a maximum value of 1 within each of the three analyses. AA scores of 1 indicate the most likely ancestral area for each clade (southern Andes–Patagonia and central Argentine highlands for clade 1, central Andes for clade 2 and for clade 1 + 2).

Proposed ancestral area	Gains	Losses	G/L	AA score
Clade 1				
Northern Andes	1	2	0.50	0.50
Central Andes	2	3	0.67	0.67
Southern Andes–Patagonia	2	2	1.00	1.00
Central Argentine highlands	2	2	1.00	1.00
Pacific coast	2	3	0.67	0.67
Falkland Islands	1	2	0.50	0.50
Juan Fernandez Archipelago	1	3	0.33	0.33
Clade 2				
Northern Andes	1	2	0.50	0.50
Central Andes	2	2	1.00	1.00
Southern Andes–Patagonia	1	3	0.33	0.33
Central Argentine highlands	1	3	0.33	0.33
Pacific coast	1	2	0.50	0.50
Clade 1 + 2				
Northern Andes	2	4	0.50	0.62
Central Andes	4	5	0.80	1.00
Southern Andes–Patagonia	3	5	0.60	0.75
Central Argentine highlands	3	5	0.60	0.75
Pacific coast	3	5	0.60	0.75
Falkland Islands	1	3	0.33	0.41
Juan Fernandez Archipelago	1	4	0.25	0.31

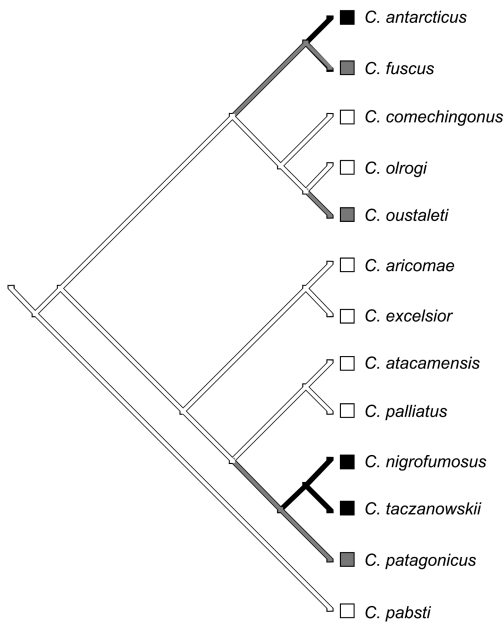


FIG. 3. Parsimonious reconstruction of the evolution of marine specialization in the genus *Cinclodes* (marine specialization treated as an ordered character). Shading of boxes represents character states in *Cinclodes* taxa: white boxes = nonmarine, gray boxes = partially or seasonally marine, black boxes = marine specialist. White branches were reconstructed as nonmarine, gray branches as partially or seasonally marine, and black branches as marine specialist.

specialists and once in an unrelated species (*oustaleti*). When degree of marine specialization was considered an ordered character, partial use evolved in the ancestor to the *nigrofumosus*–*taczanowskii*–*patagonicus* clade and in the ancestor to the *antarcticus*–*fuscus* clade, and obligate use in the ancestor to *nigrofumosus*–*taczanowskii* and in *antarcticus* (Fig. 3). The character state of the ancestors was equivocal (between partial and obligate use) when degree of marine specialization was considered an unordered character, which indicates that partial use of marine habitat evolved either in the ancestor to *nigrofumosus*–*taczanowskii*–*patagonicus* and *antarcticus*–*fuscus*, as in the ordered character analysis, or that it evolved solely in *patagonicus* and in *fuscus*.

DISCUSSION

Phylogenetics.—All phylogenetic analyses revealed a monophyletic *Cinclodes* consisting of three major lineages: the southeastern

Brazilian endemic *C. pabsti*, a clade of five primarily Patagonian–Argentine highlands species, and a clade of seven primarily north-central Andean or Pacific species. Those results contrast with previous ideas of relationships within *Cinclodes*. *Cinclodes pabsti* had been consistently considered closely related to or conspecific with *C. fuscus* (Sick 1969, 1973, 1985; Vaurie 1980; Mayr and Vuilleumier 1983) or *C. comechingonus* (Vaurie 1980, Mayr and Vuilleumier 1983); instead, genetic data indicated that this geographically isolated species was also very distinct phylogenetically. The subdivision of the remainder of the genus into clades 1 and 2 was likewise unexpected. Although those clades included several pairs of species previously thought to be closely related, other sister relationships were novel (e.g. *nigrofumosus*–*taczanowskii* and *patagonicus*), as were the overall groupings (e.g. inclusion of *nigrofumosus*–*taczanowskii*–*patagonicus* in a clade with the high-Andean species).

The first clade contained *olrogi* and *oustaleti*, two species generally considered closely related; *fuscus* and *comechingonus*, two other species thought to be closely related; and *antarcticus*. The genetic data supported sister-taxon status for *olrogi* and *oustaleti*, but indicated that *comechingonus* was sister to those species and that *fuscus* and *antarcticus* were sister species. Thus, *comechingonus*, which along with *pabsti* phenotypically resembles *fuscus*, was not particularly closely related to either species; and the enigmatic *antarcticus*, one of the most phenotypically distinctive *Cinclodes* species (Ridgely and Tudor 1994), was related not to fellow marine specialists *nigrofumosus* and *taczanowskii*, as has been suggested (Vaurie 1980, Sibley and Monroe 1990), nor to *patagonicus* (Robbins et al. 2001), but to the dissimilar *fuscus*.

The second clade of *Cinclodes* species contained two pairs of taxa consistently considered sister species or conspecifics (*aricomae*–*excelsior* and *nigrofumosus*–*taczanowskii*), along with *patagonicus*, *atacamensis*, and the phenotypically distinctive *palliatus*. The genetic data supported sister-taxon status for coastal specialists *nigrofumosus* and *taczanowskii*, and in some analyses for the high-Andean pair *aricomae* and *excelsior*. *Cinclodes patagonicus*, phenotypically similar to *oustaleti*, was found instead to be sister to the *nigrofumosus*–*taczanowskii* pair. The high-Andean species *palliatus* and *atacamensis*

(which also occurs in the highlands of central Argentina) were sister species in the genetic analyses, as had been suggested by Vaurie (1980) on the basis of plumage characters.

Biogeography and radiation.—The southeastern Brazilian endemic *C. pabsti*, geographically isolated from all other *Cinclodes* species, was sister to the rest of the genus, which, according to the biogeographic analyses, most likely originated in the central Andes. The southeastern Brazilian–Andean distribution pattern is exhibited by a number of birds (e.g. *Scytalopus tapaculos*, *Anabacerthia* foliage-gleaners) and other taxa, especially plants (e.g. Smith 1962, Moran 1991); frequently, however, the Andean component of the distribution also extends north into the highlands of Central America. Sick (1969, 1973, 1985) postulated that *pabsti* was a Pleistocene ice-age relict geographically isolated from *fuscus* of the Andes and Patagonia, which Sick considered to be its closest relative. Sequence data instead indicated that *pabsti* likely predates the Pleistocene considerably and that its speciation probably resulted from an event that isolated ancestral southeastern Brazilian populations from Andean populations, which subsequently evolved into the diverse group of species currently inhabiting the Andes, Patagonia, the central Argentine highlands, and the Pacific coast.

Vuilleumier's (1986) hypothesis that the genus *Cinclodes* originated in highland areas of South America and secondarily invaded the Pacific coast (and perhaps Patagonia) from the high Andes was based on patterns of species diversity and the ecological specialization of the coastal species. Vaurie (1980) and Fjeldså (1992), however, also considering patterns of species diversity, found it more probable that differentiation began in Patagonia and was followed by dispersal north into the high Andes and along the Pacific coast. The phylogenetic data and biogeographic analyses for clade 2, which contains the four primarily high-Andean species and both Pacific species, are consistent with Vuilleumier's hypothesis. Those analyses indicated that the most likely area of origin for that clade was the central Andes; and that the Pacific coast and Patagonia, inhabited by *nigrofumosus*, *taczanowskii*, and *patagonicus*, were occupied secondarily. Nevertheless, the biogeographic analyses indicated that the ancestor to clade 1, which contains primarily Patagonian and

Argentine highlands species, was most likely distributed in Patagonia or in both areas; that populations of *fuscus* are present in the northern and central Andes is consistent with the suggestion of northward dispersal of that species into the high Andes (see Chapman 1926).

Distributional patterns in clades 1 and 2 were consistent with the deep north-central Andean and southern Andean–Patagonian biogeographic division previously noted in *Muscisaxicola* (Chesser 2000). However, large differences in average between-clade sequence divergence (2.4% in *Muscisaxicola* vs. 5.7% in *Cinclodes*) suggest that different events separated the clades within *Muscisaxicola* and *Cinclodes*. Maximum intrageneric sequence divergence of 7.8% also suggests that *Cinclodes* has undergone a fairly recent radiation relative to most other avian genera of similar species-richness, although presumably not as recent as the 11 typical species of *Muscisaxicola* (Chesser 2000). Maximum sequence divergence in the mitochondrial gene cytochrome-*b*, a protein-coding gene with an average evolutionary rate similar to the protein-coding mitochondrial genes used in the present study (R. T. Chesser unpubl. data), ranged from 8% to 22% in 19 avian genera for which 6 or more species were sequenced (Johns and Avise 1998).

Perhaps the most remarkable aspect of the *Cinclodes* radiation is that sister species *fuscus* and *antarcticus*, which differ greatly in plumage and behavior and which breed sympatrically (although apparently not syntopically) in extreme southern Patagonia, were genetically differentiated by only 1.0%. That is similar to the situation in *Muscisaxicola*, in which sympatric species were differentiated by as little as 0.3% (Chesser 2000); however, phenotypic differentiation between *C. fuscus* and *C. antarcticus* exceeds that among all typical *Muscisaxicola* species, which are extremely conservative in morphology and behavior (Smith 1971, Vuilleumier 1971).

Marine specialization.—Few passerine birds are restricted to the maritime zone, presumably because of their lack of functional salt glands (Shoemaker 1972) and the consequent physiological difficulties of subsisting on mainly marine diets (Mahoney and Jehl 1985, Nyström and Pehrsson 1988). *Cinclodes* is an exceptional genus in that regard, containing three species specialized to the coastal environment and others that occur seasonally in coastal habitats.

Phylogenetic analyses indicated that marine specialization evolved twice among *Cinclodes* species, once in *nigrofumosus-taczanowskii* and once in *antarcticus*. The specializations shown by *nigrofumosus-taczanowskii* and *antarcticus*, respectively, are thus non-homologous and are the result of independent developments of a maritime existence. Although marine specialization has sometimes been used as a character uniting *nigrofumosus-taczanowskii* and *antarcticus* (e.g. Vaurie 1980, Sibley and Monroe 1990), their behavioral, ecological, and physiological similarities are more appropriately considered in the context of convergent or parallel evolution.

Differences in behavior and ecology are also apparent. *Cinclodes nigrofumosus* and *C. taczanowskii* are restricted to rocky coastlines, feeding mainly in the rocky intertidal zone but also along the beaches. Although *antarcticus* also generally feeds along the rocky intertidal zone and beaches, and its natural diet consists of marine invertebrates and insects taken from kelp mats, it also feeds among tussock-grass in nearby peaty soil, thus earning the common name Tussock Bird, and *antarcticus* individuals on the Falklands have been known to take food from humans (Cawkell and Hamilton 1961). This species is also closely associated with colonies of various seabirds and marine mammals (Reynolds 1935, Olrog 1950, Ridgely and Tudor 1994, Robbins et al. 2001); it feeds among birds and seals and has been considered a commensal of those colonial animals (Robbins et al. 2001). Neither feeding away from the intertidal zone nor a close association with colonial birds and mammals has been reported in either *nigrofumosus* or *taczanowskii*.

Although Paynter (1971) noted the absence of a functional salt gland in *C. taczanowskii*, he considered its large Harderian gland an adaptation to its maritime habitat. Recent physiological studies of its sister *nigrofumosus* revealed other apparent adaptations to a maritime existence, including enlarged kidneys with a higher-than-normal proportion of medullary tissue, and thus higher-than-normal osmoregulatory capacity (Sabat 2000b, Sabat and Martinez del Río 2002). Whether *antarcticus* possesses similar physiological features is unknown.

Reconstruction of degree of coastal specialization on the phylogenies suggested that marine specialization and seasonal use of marine habitats are closely associated evolutionarily.

It seems probable that those character states are ordered, and that seasonal use may be an intermediate state between lack of use of marine resources and coastal specialization. Physiological evidence is consistent with that position. Two species that are present only seasonally along the central and northern Chilean coast, *patagonicus* and *oustaleti*, differ substantially from coastal specialist *nigrofumosus* in their osmoregulatory capacity (Sabat 2000b). *Cinclodes nigrofumosus* is apparently better able to concentrate its urine than *patagonicus* or *oustaleti*, which enables it to feed on more salt-rich prey and to subsist in areas with no dilute saltwater or freshwater (Sabat 2000b). Inland migrations undertaken by *patagonicus* and *oustaleti* during the breeding season may result from their inability to maintain water balance in a coastal environment during the dry, hot summer months (Sabat 2000b).

Species limits and comparisons with other data.—Species status of many taxa of *Cinclodes*—including *comechingonus*, *aricomae*, *taczanowskii*, and *olrogi*—has been open to question (e.g. Sclater 1890, Bond 1945, Mayr 1957, Mayr and Vuilleumier 1983, Nores 1986). All those taxa are morphologically distinguishable and are valid phylogenetic species. Biological species status is more complex, and application of the biological species concept to allopatric populations is problematic. Phylogenetic analyses indicated that *comechingonus* is sister to *oustaleti-olrogi*; thus, its breeding range overlaps with that of its sister group in the central Argentine highlands, providing *prima facie* evidence of the biological species status of *comechingonus*. *Cinclodes aricomae* and its proposed conspecific (*excelsior*) differ in habitat and plumage and are probably best considered separate biological species (see Collar et al. 1992). Molecular support for those taxa as sister species was weak, and genetic divergence between the two was 2.4%, which is consistent with other closely related species in the genus.

Cinclodes taczanowskii and *C. olrogi* present more difficult cases. *Cinclodes taczanowskii* has often been considered conspecific with *nigrofumosus* (Sclater 1890; Meyer de Schauensee 1966, 1970; Stotz et al. 1996), and *olrogi* with *oustaleti* (Olrog 1979a, Navas and Bo 1987). Genetic differences between *taczanowskii* and *nigrofumosus* (0.2%) and between *olrogi* and *oustaleti* (0.5%) were quite low, which is consistent with the

small degree of morphological and behavioral differentiation between those sister pairs. Given the similarity between *taczanowskii* and *nigrofumosus* and between *oustaleti* and *olrogi*, it seems likely that they are potentially interbreeding taxa, and they are perhaps best considered biologically conspecific, pending further study. As such, they would be known as *C. nigrofumosus* and *C. oustaleti*, respectively.

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