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Molecular phylogenetics and the historical biogeography of dippers (*Cinclus*)

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I used combined sequences of mitochondrial cytochrome *b* and ND2 genes to determine the molecular phylogenetic relationships of all five extant species of dipper (C*inclus*), as well as the relationships of Cinclidae to postulated nearest relatives. All methods of analysis resulted in a single best tree of dipper relationships, uniting the two South American taxa (as sisters) with the single North American exemplar, and the two Eurasian taxa forming a sister clade to the New World taxa. Further, each tree identified thrushes (Turdidae) as the closest relative to Cinclidae. Based on relationships within C*inclus*, a Eurasian ancestral area is proposed, with subsequent movement into the New World. Dating of species divergences suggest that dippers arose approximately 4 mya, and achieved their present continental distributions soon after.

Dippers (genus C*inclus*: Cinclidae) are probably best known for their habit, unique among passerines, of foraging underwater in generally fast-moving streams and rivers. They are also of interest in that the genus is one of only a small number of passerine genera whose distribution includes North America and more than one other continent. Dippers are found in South America (Rufous-throated C*inclus schulzi* and White-capped C. *leucocephalus*), North America (American C. *mexicanus*) and Eurasia (Brown C. *pallasii* and White-throated C. *cinclus*) and even penetrate into Africa (populations of C. *cinclus*).

The distribution of C*inclus* has led to competing theories as to the continent of origin for the group, and has also obfuscated the identification of close relatives because such a widespread distribution provides a large number of candidate sister-families. Sibley (1972) proposed a North American origin for Cinclidae, from which the group proceeded to disperse into Asia and South America. Stejneger (1905) suggested an Asian origin for dippers, deciding dippers were closer to thrushes (Turdidae); he had previously suggested a closer relationship to wrens (Troglodytidae), and a South American origin.

Indeed, for most of the twentieth century, Cinclidae has been thought to be most closely related to either the Turdidae or Troglodytidae. Several morphological characters and egg-white protein data support a closer relationship to the former (Sibley & Ahlquist 1990), yet the AOU checklist (American Ornithologists' Union, 1998) places Cinclidae after the wrens. Several linear classifications (e.g. Wetmore 1960), place Cinclidae between wrens and accentors (Prunellidae). DNA–DNA hybridization evidence suggests placement of Cinclidae between thrushes and waxwings (Bombycillidae, Sibley & Ahlquist 1990).

In this paper, I use mitochondrial cytochrome *b* and ND2 sequence data to try to resolve the relationships among C*inclus* species, as well as to determine the relationships of Cinclidae to proposed nearest relatives. Based on these phylogenetic relationships, I propose a historical biogeographical scenario.

MATERIALS AND METHODS

DNA isolation, amplification and sequencing

I sequenced 1000 bp of cytochrome *b* (cyt *b*) and 1000 bp of ND2 from 11 C*inclus* specimens representing all five extant species, as well as from five outgroup taxa (Table 1). Each outgroup taxon represents an avian family previously thought to be closely related to Cinclidae. Mitochondrial DNA was isolated from these specimens using a caesium chloride gradient (Dowling *et al.* 1990).

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Table 1. Species, museum number and collecting localities for specimens examined.

Species	Museum number[a]	Collection locality
Cinclidae		
schulzi	UWBM 54513	Argentina: Prov. Tucumán; San Miguel de Tucumán, 15 km S, 40 km W, Rio Sosas
	MBM 6912	Argentina: Prov. Tucumán; Tafi del Valle, 15 km S, 4 km E
leucocephalus	LSU B-5936	Ecuador: Prov. Pichincha; Papallacta
	LSU B-8027	Peru: Dpto. Pasco; Playa Pampa, 8 km NW Cushi on trail to Chaglla
cinclus	UWBM 46430	Kazakhstan: Alma-Ata Oblys; Alma-Ata, 30 km S, 80 km W, Khrebet Zhetyzhoi
pallasii	UWBM 51144	Russia: Primorskiy Kray; Lazo, 3 mi N, 16 mi E, pass above Van-Chin River
mexicanus	UWBM 46757	Washington: Kittitas Co.; Ellensburg, 1 mi S, 13 mi W
	UWBM 56993	Washington: Whatcom Co.; Mt. Baker, 7 km W
	UWBM 72390	Washington: Yakima Co.; Naches, 12 mi W, 6.5 mi N
	LSU B-6425	California: Sierra Co.; 4.41 mi N Sierra-Nevada Co. line on HWY 89
	LSU B-6479	California: Sierra Co.; 4.4 mi N Nevada Co. line on HWY 89
Turdidae		
Catharus fuscescens	UWBM 56991	Washington: Kittitas Co.; Ellensberg, 1.5 mi N, 10 mi W, Robinson Canyon
Troglodytidae		
Salpinctes obsoletus	UWBM 56992	Washington: Grant Co.; Electric City, 2 mi S, 6.5 mi W, Barker Canyon
Bombycillidae		
Bombycilla garrulus	UWBM 53989	Alaska: Houston, 25 mi S, 5 mi W
Prunellidae		
Prunella atrogularis	UWBM 46573	Russia: Gorno-Altay Republic; Gorno-Altaysk, 95 km S, 20 km W
Motacillidae		
Anthus brachyurus	UWBM 52901	South Africa: Kwa/Zulu Natal Prov.; Melmoth, 2 km N, 4 km E

[a]UWBM, University of Washington Burke Museum; MBM, Barrick Museum, University of Nevada Las Vegas; LSU, Louisiana State University Museum of Natural Science.

The segment of cyt *b* considered here was amplified by PCR as a single unit using primers L14841 (Kocher *et al*. 1989) and H16065 (Helm-Bychowski & Cracraft 1993). For sequencing, these primers along with L15114, L15299, L15609, H15547 (Edwards *et al*. 1991), H15299 (Hackett 1996), H15915 (Edwards & Wilson 1990), and those described by Voelker and Edwards (1998) were used. Fragments were amplified in 100-μL PCR reactions. The amplification conditions were 30 s at 94 °C, 30 s at 50 °C, 30 s at 72 °C, for 35 cycles. Amplified products were prepared as templates for automated sequencing by purification and concentration in 22 μL of water after three passes through Ultrafree-MC filters by centrifugation (Millipore). Two microlitres of the purified and concentrated PCR product were used as a template in a 10-μL DyeDeoxy Cycle Sequencing reaction (ABI), along with one of the above primers, according to the manufacturer's instructions (PerkinElmer).

For all samples, the ND2 gene was amplified with L5215 (Hackett 1996) and H6313 (Johnson & Sorenson 1998). For sequencing, I used those primers with L5215, L5219, L5758, H5776, H5578 (Hackett 1996, Johnson & Sorenson 1998) and two primers designed specifically for this study (L5758.2, 5′-GGGTGAATGGGACTGAACCAAAC-3′; L5758.3, 5′-GGATGAATAGGCCTCAACCAAAC-3′) to obtain overlapping sequences. Fragments were amplified in 50-mL PCR reactions: conditions were an initial 10-min denaturation at 94 °C, followed by 40 cycles of 94 °C for 30 s, 55 °C for 45 s, and 72 °C for 30 s. The products went through a final extension of 72 °C for 10 min. Products were purified using Promega Wizard PCR Prep methodology. Five microlitres of the purified product were used in a 20-μL sequencing reaction with one of the above primers using ABI BigDye Terminator reaction mix, following manufacturer's instructions.

After cycle sequencing, cyt *b* and ND2 products were placed on coarse-grained Sephadex columns and cleaned of excess nucleotides by centrifugal passage through the columns. Both light and heavy strands of the entire 2000 bp were sequenced with an ABI model 373 (cyt *b*) or 377 (ND2) automated sequencer. Sequences were aligned unambiguously using SEQUENCHER software (Gene Codes Corporation).

Phylogenetic analysis

To determine whether all, or some major portion of, these two gene regions exhibited a significantly

different phylogenetic signal, I performed partition homogeneity tests in PAUP* (Swofford 1999), using 500 random partitions on the entire data set, and on each of the three codon positions.

All phylogenetic analyses were performed using PAUP*. I conducted parsimony and maximum likelihood (ML) analyses, generally following the methods of Voelker and Edwards (1998). For parsimony analysis, I began by generating initial trees using equal weights; subsequent trees were constructed using overall and codon-specific transition/transversion ratios estimated from the data set. Cladistic signal was determined for each clade by bootstrapping (500 replicates and 10 random additions). For ML analyses, I employed the successive approximations method of Voelker and Edwards (1998), with the HKY85 model of evolution (Hasegawa *et al*. 1985) to determine κ and α values for tree topologies, using successive values of these parameters until the tree topology stabilized. I conducted heuristic searches with 10 replicates and random additions to generate the trees. In response to the results of the partition-homogeneity test, I also conducted a ML analysis using site-specific rates and an estimated transition/transversion ratio. Site-specific rates were estimated for each of the six codon partitions (three cyt *b*, three ND2).

After Voelker and Edwards (1998), I arbitrarily rooted all trees to a representative from a family (Motacillidae) that falls close to, but has not been proposed as a sister group of, dippers, and allowed the representative taxa from the remaining four outgroup families to 'float' in the phylogenetic analyses. Each of the other four outgroup families (Troglodytidae, Bombycillidae, Turdidae, and Prunellidae) have been suggested to be the sister group to Cinclidae.

I used the statistical test of Kishino and Hasegawa (1989), implemented in PAUP*, to compare the best maximum likelihood estimate to alternative tree topologies that reflect competing hypotheses as to the relationships among dippers, and the relationships between Cinclidae and wrens and thrushes (see above). MacClade (Maddison & Maddison 1992) was used to create alternative tree topologies, and ML branch lengths were enforced on these trees in PAUP* prior to comparisons.

Historical biogeography

I used dispersal-vicariance analysis (DIVA; Ronquist 1996, 1997) and the ancestral areas method of Bremer (1992) to determine the ancestral area of dippers (see Voelker 1999b for a brief overview of these methods). To test whether *Cinclus*, as a genus and between species, is evolving in a manner consistent with the idea of a molecular clock, I applied the two-cluster test (Takezaki *et al*. 1995), with Tamura-Nei distance, to the best estimate of *Cinclus* relationships.

If daughter lineages above nodes were determined to be evolving in a clocklike fashion, I used 2% sequence divergence per million years to apply dates to lineage splits, based on cyt *b* data only. Values near 2% have been inferred from a number of previous studies involving avian lineages (Shields & Wilson 1987, Tarr & Fleischer 1993, Fleischer *et al*. 1998).

RESULTS AND DISCUSSION

Sequence evolution

I first aligned 2000 bp without insertions or deletions. Because the entire cyt *b* and ND2 fragments considered here were isolated as a single unit for amplification, nuclear copies were unlikely to have been sequenced. Both the lack of difficulty translating sequences into amino acids, and the lack of alignment problems and stop codons, suggested that the genes amplified were most likely of mitochondrial origin.

For the 1000 bp of cyt *b*, 379 nucleotide sites were variable and of these, 233 would be considered parsimony informative. Of the variable sites, 93 were at first codon positions, 38 were at second codon positions, and 248 were at third codon positions. For ND2, 485 of 1000 sites were variable, with 132 variable at first codon positions, 51 at second codon positions, and 302 at third codon positions. Furthermore, 318 sites were considered parsimony informative. Mean base composition, and thus compositional bias, within both gene regions is similar across taxa, and these values are comparable to values found across many avian lineages (e.g. Hackett 1996, Voelker & Edwards 1998, Voelker 1999a). As expected for protein coding genes, there is substantial rate heterogeneity across codon positions (Table 2).

Results of the partition-homogeneity test, with equal weighting, suggest that cyt *b* and ND2 represent significantly different data partitions, and thus cannot be combined ($P < 0.02$; Bull *et al*. 1993). Within each gene region, codon positions did not differ significantly from one another, and were thus combinable. Partition-homogeneity tests of each

Table 2. Overall and codon-specific dynamics of the cytochrome *b* and ND2 genes estimated on the best ML trees for each gene across all taxa.

Dynamic	First position	Second position	Third position	All positions
Mean base composition[a]				
Cytochrome *b*	24, 25, 23, 28	13, 20, 41, 26	3, 43, 8, 46	13, 30, 24, 33
ND2	17, 35, 19, 29	10, 16, 38, 36	7, 40, 13, 41	12, 30, 23, 35
α				
Cytochrome *b*	0.332	0.141	1.606	0.329
ND2	0.513	0.099	2.149	0.326
κ				
Cytochrome *b*	3.621	4.709	21.218	7.655
ND2	6.062	11.006	20.969	9.172

[a]Base composition is presented as (%G, %A, %T, %C) averaged over all sequences.

codon position between the two regions suggest that second and third positions do not reflect significantly different data partitions ($P = 0.10$ and $P = 0.13$, respectively). The underlying difficulty is incompatibility between first codon positions ($P = 0.01$), which within C*inclus* have very different κ rates (Table 2).

To determine the underlying cause of the first codon position incompatibility problem, I plotted cyt *b* first position transitions against ND2 first position transitions, as well as cyt *b* transversions against ND2 transversions, and both transitions and transversions against uncorrected *p*-distances. Plots that include transversions (not shown) reveal no clues to incompatibility, nor do plots in which transitions and transversions are plotted against their respective *p*-distances (not shown). However, in first codon position transition plots, cyt *b* first position transitions appear to accumulate much more slowly over time than do those in ND2 (Fig. 1), leading to the conclusion that the observed incompatibility between the two genes is a function of the differential accumulation rates.

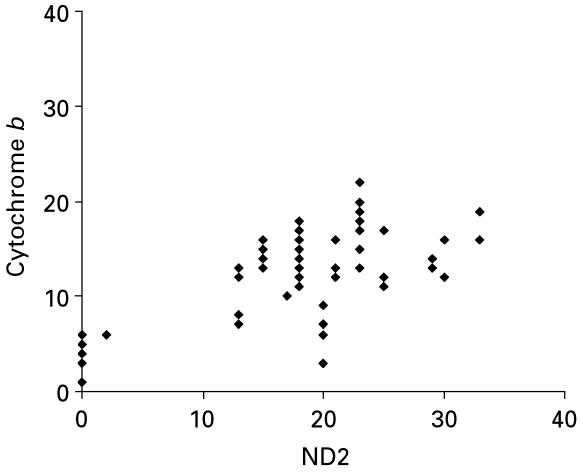

Figure 1. Pairwise comparisons of first codon position transitions between cytochrome *b* and ND2.

Phylogenetic analysis

Results of the partition-homogeneity test suggest that C*inclus* cyt *b* and ND2 genes are heterogeneous and thus non-combinable; in discussing non-combinability, most authors cite Bull *et al.* (1993) as the definitive source on the issue. However, Bull *et al.* (1993) clearly suggest that once heterogeneity is detected, the next step should be to identify the problem and modify the analysis. Furthermore, they state that it may be possible to accommodate heterogeneity by non-uniform weighting of characters. The logical conclusion then, is that if those heterogeneous data sets are not constrained to fit the same model, they are in fact combinable (T. Buckley pers. comm.; J. Sullivan pers. comm.). Therefore, I use the combined data set, and rely on non-uniform weighting strategies to resolve C*inclus* relationships.

All methods of combined analysis result in a single best tree (Fig. 2). Strong bootstrap support (> 70%) is given at all nodes within C*inclus*, under a parsimony analysis in which codon-specific transition/transversion rates were used. ML analysis using a single rate of α and a single rate of κ over all sites results in the same tree, as does the ML analysis using estimated site-specific rates (here, codon partitions).

Although all methods of analysis resulted in the same topology, the Kishino–Hasegawa test was unable to reject as significantly worse under ML criteria the most obvious topological variations, i.e. Asian taxa sister to *mexicanus*, or Asian taxa sister to South

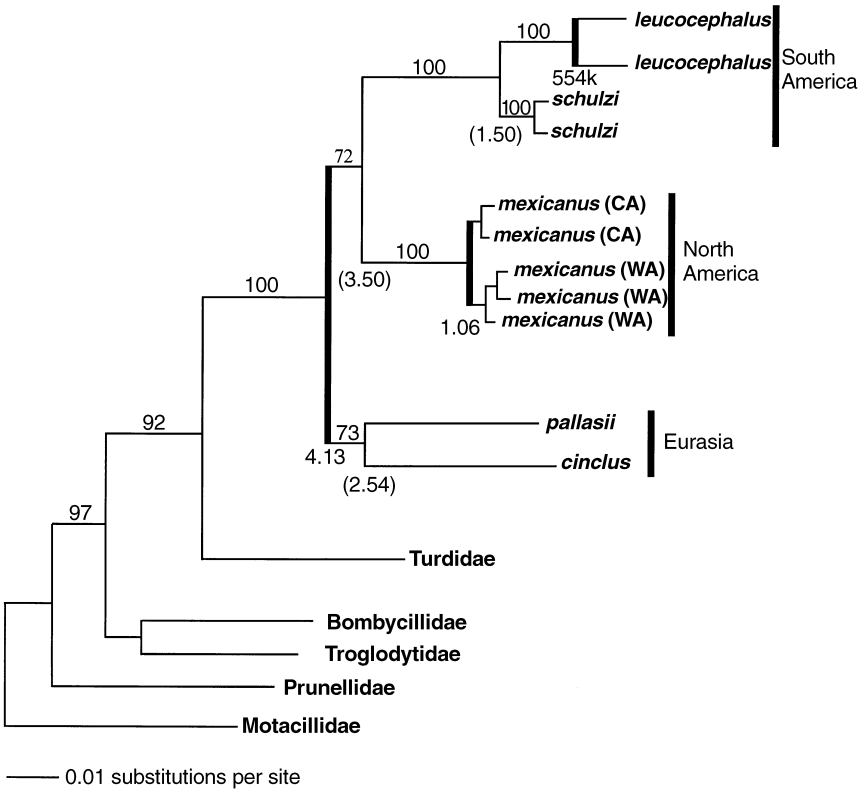

Figure 2. Maximum likelihood tree of *Cinclus* relationships. Numbers above internodes are frequencies of occurrence (> 50%) of groups in 500 maximum parsimony bootstrap replicates with 10 random additions. Thick bars indicate nodes determined to be evolving in a clocklike manner according to the two-cluster test; numbers below these nodes are dates in millions of years, unless otherwise denoted. The value for non-clocklike nodes (in parentheses) were determined via mean ML branch lengths. Continental distribution for each *Cinclus* species is also shown.

Table 3. Kishino and Hasegawa (1989) tests of competing hypotheses of dipper relationships. Values were obtained using the HKY85 model, using site-specific rates estimated from the data.

Tree topology	– ln L	*P*
Best ML tree	10 249.822	best
(South American taxa; *mexicanus* + Asian taxa)	10 251.018	0.835
(*mexicanus*; South American taxa + Asian taxa)	10 254.970	0.230
Troglodytidae as closest outgroup	10 303.875	0.0017
Bombycillidae as closest outgroup	10 301.197	0.0036
Troglodytidae + Bombycillidae as closest outgroup	10 294.880	0.0014
Prunellidae as closest outgroup	10 357.138	< 0.0001

American taxa (Table 3). This failure to reject alternative topologies is probably a function of comparatively short branch lengths near the basal *Cinclus* splits (Fig. 2).

The most obvious morphological and behavioural differences among dippers are diving to forage, wing-flicking, possession of a white wing patch, and a colour patch on the body. However, because the first three of these characters only serve to separate the South American taxa from the other species, these characters provide no clues to a more likely topology. However, it is intriguing that only the two South American taxa have white patches in their wings, using wing-flashing to expose these white patches as often as they perform dipping behaviour, and, that these two species are not known to dive for prey (Tyler & Ormerod 1994). White wing patches may serve as an additional means of communication

(Tyler & Tyler 1996), especially when considering that, much more so than the other three *Cinclus* species, the two South American taxa live in a generally darker habitat. However, it may also be that white wing-patches serve as a means to flush prey, as has been suggested for several other species (Selander & Hunter 1960, Monroe 1964). Indeed, when wading in streams to forage, *schulzi* often flicks its wings (Tyler & Tyler 1996). In either event, the possession of these traits does not help to resolve *Cinclus* relationships.

Despite the inability to reject alternative topologies, or to use morphology or behaviour to lend support to one topology over another, ML and parsimony did identify the same, single best tree. Therefore, I suggest that this best tree is the best current estimate of *Cinclus* relationships.

Turdidae was, in all analyses, the closest family to Cinclidae; alternative tree topologies placing other included families closest to Cinclidae were all rejected as significantly poorer explanations of the data (Table 3).

This close relationship between Cinclidae and Turdidae is also supported by morphological and egg-white protein data (Sibley & Ahlquist 1990).

Historical biogeography

Overall, *Cinclus* does not seem to be evolving in a clocklike manner. Indeed, daughter-lineages above just three of 10 nodes are evolving in a manner consistent with a molecular clock, according to the two-cluster test (Fig. 2). Using mean ML branch lengths, I was able to assign dates to non-clocklike nodes; the mean ML branch length method, although unable to determine clocklike behaviour, does generate dates that are reasonably consistent with the two-cluster test, when those dates are less than about 3–4 mya (Voelker 1999b).

DIVA suggests that if the possible *Cinclus* ancestral area is restricted to be composed of just two areas (the minimum allowable option), then Eurasia plus North America, or Eurasia plus South America can be inferred as ancestral, with one dispersal being required to explain those ancestral distributions. Bremer's (1992) ancestral area method suggests that Eurasia alone is the most likely ancestral area for *Cinclus*. From the combined results of these two methods, *Cinclus* probably originated in the Old World (and not the New World) as postulated by Stejneger (1905).

The assigned dates suggest that *Cinclus* arose approximately 4 mya in Eurasia, and was present in North America and South America shortly after. Movement into North America can be explained plausibly to have occurred during a Beringian interglacial period. The split between the ancestral North and South American species, estimated at roughly 3.5 mya, may be the result of early Pliocene (5–3 mya) climatic and habitat shifts in coastal Colombia due to the primary uplift of the northern Andes and the emergence of coastal lowlands in the same region (De Vries 1987; Mégard 1992). Indeed, the coastal lowlands of north-western Colombia appear to form a modern-day barrier to the southern expansion of *mexicanus* (which occupies mountains in Panama), and the northern expansion of *leucocephalus* (which occupies high mountains in Colombia).

Much of the range of *pallasii* (found only in eastern Eurasia) is overlapped by eastern populations of *cinclus*; *cinclus* also has an extensive range in central Eurasia and Europe (Tyler & Ormerod 1994). Given an extensive overlap in ranges, and the lack of continuous mountain barriers, it seems virtually impossible to identify a mechanism clearly by which speciation of the ancestral species occurred to result in these two modern species about 2.5 mya.

One possible mechanism, which was postulated to explain somewhat similar distributions of Eurasian pipits (Voelker 1999b), is that the ancestral species was split as a result of the climatic shifts associated with well-recorded glacial events in northern Eurasia (Frenzel 1968, Kukla & An 1989, An *et al*. 1991). If this mechanism is correct, then we can infer that *cinclus* has simply extended its range eastward to overlap that of *pallasii* in the intervening time period. Range extension by *cinclus* must in any case be inferred to explain its northernmost range in Scandinavia, most of which was glaciated in recent times (Frenzel 1968). A dispersal into northern Africa, possibly facilitated by a pre-Pleistocene land bridge that existed across the Mediterranean (Moreau 1952), is necessary to explain the toehold of *cinclus* in the Atlas Mountains.

The two South American taxa (*leucocephalus* and *schulzi*) are thought to have diverged from a common ancestor approximately 2.5 mya (Fig. 2). The age of this split, as well as obvious morphological differences, particularly in coloration, leave little doubt that these taxa are best treated as separate species, rather than as a potential superspecies as has been suggested (Sibley & Monroe 1990).

Leucocephalus can be found from Colombia to central Bolivia, and *schulzi* from southernmost Bolivia to northernmost Argentina; both are associated with fast mountain streams. The region in southern

Bolivia that serves as a disjunction between the ranges of these two species is also a northern or southern range terminus for a large number of South American passerine birds (Ridgely & Tudor 1989, 1994). This region has a long history of vicariant events (Gansser 1973, van der Hammen & Cleef 1986, Sébrier *et al.* 1988, Seltzer 1990), which are thought to be driving speciation in pipits and probably other taxa with similar distributions (Voelker 1999b).

Ridgely and Tudor (1989) questioned why some dipper species had not moved further south into the Chilean/Argentine Andes. With respect to *schulzi*, the answer seems to be that there is a fairly specific need for well-forested river courses. Also, within these river courses, only upper stretches have the stable channels with waterfalls, large rocks and rapids, which are preferred during breeding (Tyler & Tyler 1996). The extensive Andean glaciation may also have affected southward movements/speciations. Indeed, most of Chile and Patagonia were entirely covered by glaciers about 1.2 mya (Rabassa & Clapperton 1990), and these glaciers, coupled with narrow habitat preferences may have precluded southward movement by dippers through time.

Determining the extent of the role played by late Pleistocene events in generating modern species has long been a focus of historical biogeography (e.g. Mengel 1970). It is of course impossible to know whether Pleistocene events have driven some *Cinclus* to extinction. However, with respect to the evolution of extant species, *Cinclus* represents another example of a group of birds that appears to have diverged near the Pliocene–Pleistocene boundary, or earlier. Along with several other recently studied groups (Klicka & Zink 1997, Voelker 1999b) this implies that Pleistocene events may have had little effect in generating modern species.

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