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RESEARCH ARTICLE

Morphological divergence in a continental adaptive radiation: South American ovenbirds of the genus *Cinclodes*

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ABSTRACT

Cinclodes is an ecologically diverse genus of South American passerine birds and represents a case of continental adaptive radiation along multiple axes. We investigated morphological diversification in *Cinclodes* using a comprehensive set of morphometric measurements of study skins. Principal component analysis identified 2 primary axes of morphological variation: one describing body size and a second capturing differences in wing-tip shape and toe length. Phylogenetic analyses of the first principal component suggest an early divergence of *Cinclodes* into 2 main clades characterized by large and small body sizes. We suggest that 2 morphological outliers within these main clades (*C. antarcticus* and *C. palliatus*) may be cases of island gigantism and that a third (*C. patagonicus*) may reflect ecological character displacement. Despite its ecological and physiological diversity, the genus *Cinclodes* does not appear to show morphological diversity beyond what is typical of other avian genera.

Keywords: adaptive radiation, ancestral character state reconstruction, Furnariidae, morphology, phylogenetic analysis

Divergencia morfológica en una radiación adaptativa continental: horneros de Sud América del género *Cinclodes*

RESUMEN

Cinclodes es un género ecológicamente diverso de aves paserinas de Sud América y presenta un caso de radiación adaptativa continental a lo largo de múltiples ejes. Investigamos la diversificación morfológica en *Cinclodes* usando un conjunto integral de medidas morfométricas de pieles de estudio. Un análisis de componentes principales identificó dos ejes principales de variación morfológica: el primero describe el tamaño corporal y el segundo captura las diferencias en la forma de la punta del ala y el largo del dedo del pie. Los análisis filogenéticos del primer componente principal sugieren una divergencia temprana de *Cinclodes* en dos clados principales caracterizados por tamaños del cuerpo grande y pequeño. Sugerimos que dos valores atípicos dentro de estos dos clados principales (*C. antarcticus* y *C. palliatus*) pueden ser casos de gigantismo en islas y un tercer caso (*C. patagonicus*) puede reflejar el desplazamiento de un carácter ecológico. A pesar de su diversidad ecológica y fisiológica, el género *Cinclodes* no parece mostrar diversidad morfológica más allá de lo típico de otros géneros de aves.

Palabras clave: análisis filogenético, Furnariidae, morfología, radiación adaptativa, reconstrucción de un carácter ancestral

INTRODUCTION

Adaptive radiation may be responsible for a large proportion of the observed diversity of life (Osborn 1902, Schluter 2000, Gavrillets and Losos 2009). To be considered an adaptive radiation, a group of closely related taxa must display rapid cladogenesis accompanied by significant adaptive phenotypic divergence (Schluter 2000). Pheno-

typic diversity has most often been documented by differences in morphology, and functional studies have described the adaptive value of these differences. For example, Galápagos finches vary in body size and bill dimensions (Grant 1986). Variation in bill dimensions among finch species correlates with the size and hardness of seeds that the birds are capable of opening (Schluter and Grant 1984, Grant 1986, Price 1987). Similarly, lizards of

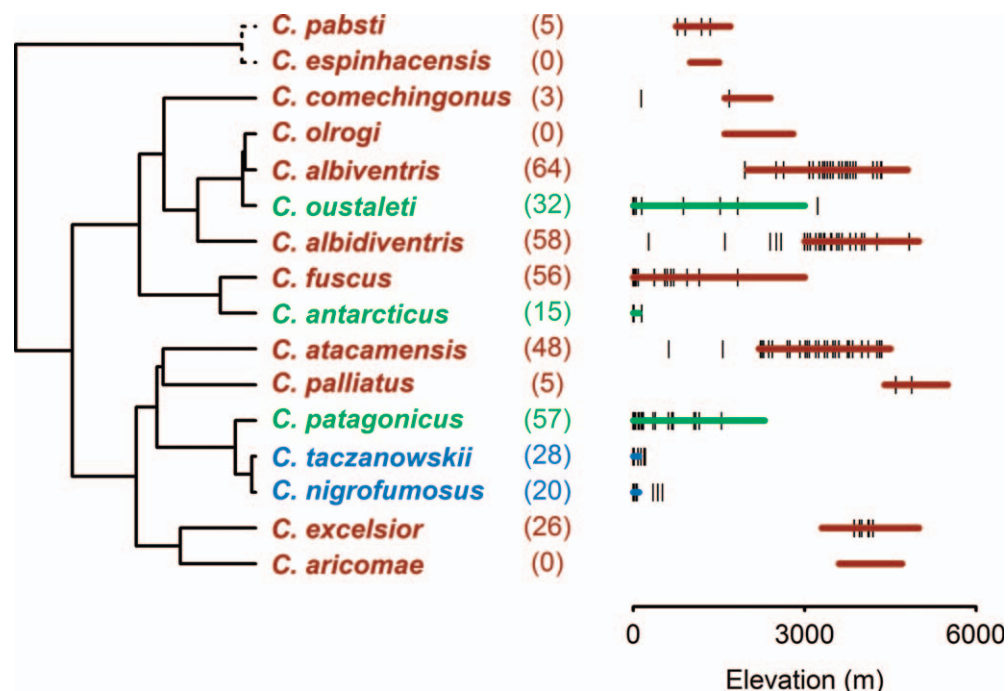


FIGURE 1. Ecological diversity and phylogenetic relationships (after Derryberry et al. 2011) within the genus *Cinclodes*. The phylogenetic hypothesis included the recently discovered *C. espinhacensis* (Freitas et al. 2012). Branch lengths represent relative divergence times. Although *C. pabsti* and *C. espinhacensis* (dotted lines) are very closely related, the branch lengths joining them are unknown and are shown for illustration only. Blue denotes species that feed exclusively in intertidal habitats, green denotes species that are seasonally or nonobligate intertidal feeders, and brown denotes species that do not occur in the intertidal zone. The horizontal bars on the right depict the estimated elevational ranges of each species (Remsen et al. 2003, Chesser 2004, Sanín et al. 2009), and the vertical hash marks represent the elevations of the specimens measured for this study. Numbers in parentheses are sample sizes for morphological measurements. Study materials of *C. espinhacensis*, *C. olrogi*, and *C. aricomae* were not available.

the genus *Anolis* have radiated on the islands of the Caribbean (Jackman et al. 1999, Losos 2009) and have diversified in limb and tail morphology, facilitating locomotion in alternative microhabitats (Irschick and Losos 1998, 1999). These classic cases of adaptive radiation, along with most other well-described cases, occurred on archipelagos. Continental radiations have received less attention (Claramunt 2010).

The genus *Cinclodes* (Passeriformes: Furnariidae) represents a case of an adaptive radiation centered in western South America wherein species have diverged along several phenotypic axes (Chesser 2004, Sabat et al. 2006a, 2006b, Sanín et al. 2009). Fourteen of the 16 *Cinclodes* species (Freitas et al. 2012) form 2 primary clades (Sanín et al. 2009), and 13 of those breed in western South America. *Cinclodes antarcticus*, the single exception, inhabits the Falkland Islands and the Tierra del Fuego archipelago. The other 2 species, *C. pabsti* and the recently discovered *C. espinhacensis* (Freitas et al. 2012; Figure 1), form a separate, more distantly related group found in inland grasslands of southern and eastern Brazil—geographic distributions that may reflect the ancestral range of the genus (Chesser 2004, Freitas et al. 2012).

Within the 2 main clades, species vary considerably in ecological and behavioral attributes. Three species (*C. nigrofumosus*, *C. taczanowskii*, and *C. antarcticus*) forage in the intertidal zone (Chesser 2004), and *C. nigrofumosus* and *C. taczanowskii* are among the most marine-dependent of all passerine birds (Sabat et al. 2006b). By contrast, *C. excelsior*, *C. aricomae*, and *C. palliatus* are restricted to high elevations (>3,300 m) in the Andes, and several other species range from middle to high elevations (Remsen et al. 2003; Figure 1). Most *Cinclodes* species are spatially sedentary, but migratory habits appear to have evolved multiple times in the genus (Chesser 2004). Figure 1 summarizes a few notable traits of *Cinclodes* species, including altitudinal range, migratory movements, and degree of dependence on marine habitats.

This ecological and physiological diversity has played out against a background of relatively rapid species diversification. Of 27 Neotropical genera surveyed by Weir (2006), *Cinclodes* was among the youngest, with all but 1 species known at that time having evolved during the Pleistocene. Weir (2006) attributed their rapid diversification to widespread habitat alteration and fragmentation due to glaciation in southwestern South America.

Morphological divergence has typically been used to delineate genera, so species within a genus tend to be morphologically similar. Although recent work has documented that *Cinclodes* species inhabit diverse habitats and show pronounced variation in physiological traits (Sabat et al. 2004, 2006a, 2006b, Martínez del Rio et al. 2009), little attention has been paid to morphological divergence within the genus. We hypothesized that species of this genus may also be morphologically diverse, given their documented ecological and physiological diversity. Many taxa have diverged primarily in body size (Ricklefs and Travis 1980, Beuttell and Losos 1999, Marroig and Cheverud 2005, Claramunt 2010), and therefore we predicted that body size would account for the majority of morphological diversity among *Cinclodes* species. However, because *Cinclodes* species also have diverse migratory habits (Sabat and Martínez del Rio 2005, Martínez del Rio et al. 2009) and vary in elevational range and diet (Chesser 2004, Sabat et al. 2006b, Martínez del Rio et al. 2009), we also expected variability in wing (Lockwood et al. 1998) and bill size and shape.

METHODS

Morphometrics

We measured morphology of study skins housed at the American Museum of Natural History (AMNH), the Field Museum of Natural History (FMNH), the Louisiana State University Museum of Natural History (LSUMZ), and the National Museum of Natural History at the Smithsonian Institution (USNM; see [Supplemental Material Table S1](#)). We measured 34 traits (see [Table S1](#)) from 418 individuals representing 13 of the 16 *Cinclodes* species (Figure 1). Study skins of species not represented in our sample either are not present in North American collections (*C. espinhacensis* and *C. olrogii*) or are represented only by the type specimen (*C. aricomae*). Species with low sample sizes (*C. comechingonus* and *C. palliatus*) represent the entirety of specimens available in the collections visited. We used digital calipers (Mitutoyo, Model CD-6''CX) interfaced with Microsoft Excel to measure bill, hind-limb, wing, and tail morphology, largely following Baldwin et al. (1931), with a precision of 0.5 mm. Bilaterally paired structures were measured once per individual, assuming no significant morphological variation between sides of the body. The measured side was selected opportunistically, so that all measurements of each body region were from the same side, while avoiding damaged or missing elements. Collecting localities and sex (male and female *Cinclodes* are not visibly dimorphic) were taken directly from specimen labels. Latitude and longitude values were taken from specimen labels (when available) or from searches for locality names on Google Earth. We recorded body mass

from specimen labels, where possible, but mass was available for only 84 of 418 specimens.

Bill metrics. We measured bill length from the anterior margin of the naris to the tip of the upper rhamphotheca. We measured the width of the upper rhamphotheca and the depth of both rhamphothecae (with the mandibles occluded) at 3 points along the length of the bill: at the anterior margin of the naris, near the tip (the edge of the calipers even with tip of the bill), and midway between these points. We calculated bill cross-sectional area as an ellipse, with bill depth and bill width serving as long and short axes, respectively.

Hind-limb metrics. We measured tibiotarsus and tarsometatarsus width mediolaterally, approximately at midshaft. The tibiotarsus and tarsometatarsus were covered by skin but lacked feathers below the knee joint in all species. Where necessary, body feathers were pushed aside to allow measurement of the tibiotarsus. We assumed a similar rate of shrinkage of the skin along these elements and among species. We measured the length of the tarsometatarsus from behind the middle of its junction with the tibiotarsus to the junction between the tarsometatarsus and the middle toe. We measured each digit along its long axis, from the proximal joint with the tarsometatarsus to the distal end of the ungual. When the digits were not preserved in a straight posture, we measured the length of each phalanx and summed to obtain a total digit length. We measured the claws across the curvature from the point where the upper surface of the claw emerges from the skin of the toes to their tips.

Wing and tail metrics. Preservation posture limited wing measurements to the hand-wing. We measured hand-wing length from the anterior edge of the wrist joint to the tip of the longest primary feather. The length of each of the 9 primaries was measured from the point of eruption from the skin to its tip, excluding birds with excessive feather wear. We used size-constrained component analysis to calculate indices of wing-tip pointedness and convexity from the primary feather lengths, following the methods of Lockwood et al. (1998). Tail measurements were limited to the lengths of the medial and most lateral rectrices, measured from skin eruption to the feather tip.

Analyses

Principal component analysis. We used principal component analysis (PCA; JMP version 10; SAS Institute, Cary, North Carolina, USA) with a Varimax rotation to reduce dimensionality and to highlight axes of variation composed of >1 morphological variable. The linear metrics used to calculate bill cross-section and wing-tip shape were removed from the PCA to minimize multicollinearity. To determine the amount of variance accounted for by interspecific variation, rather than

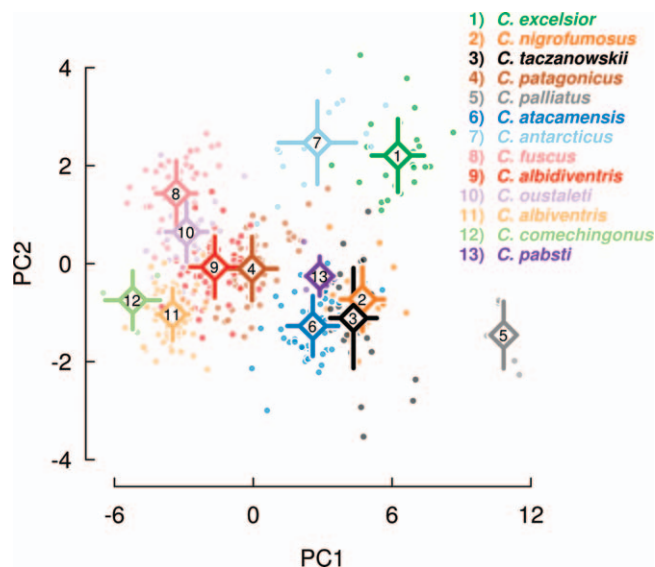


FIGURE 2. The first principal component (PC1: body size) plotted against the second (PC2: wing-tip pointedness and hallux length) for 13 species in the genus *Cinclodes*. Higher PC1 values indicate larger body size, whereas higher PC2 values equate to more pointed wing tips and longer halluces. PC1 and PC2 were the only axes showing significant interspecific morphological variation. Diamonds represent species means with error bars indicating 95% confidence intervals.

intraspecific variation, we conducted a one-way analysis of variance (ANOVA) of principal component (PC) scores and compared the species (among) sum of squares to the error (within) sum of squares. We emphasized the PC axes where among-species sums of squares exceeded within-species sums of squares because these are informative about interspecific, rather than intraspecific, variation.

Phylogenetic analyses and ancestral character reconstruction. Our phylogenetic analyses were based on a reconstruction of the family Furnariidae (Derryberry et al. 2011), including estimated branch lengths from that study, pruned to include only *Cinclodes* species. For the regression of body mass versus the first principal component (PC1), we used ordinary least squares (OLS), phylogenetically generalized least squares (PGLS; Martins and Hansen 1997, Freckleton et al. 2002, Blomberg et al. 2012), and standardized major-axis (SMA; Warton et al. 2006) regression approaches on species' mean values. We investigated the evolution of the 2 axes that accounted for most of the variation in morphology in our datasets, PC1 and PC2, using a 2-step approach (Pagel 1999, Claramunt et al. 2012). Following Claramunt et al. (2012), we used the “fitContinuous” function of the R package “geiger” (Harmon et al. 2008) to compare model fit and parameter estimates under 5 models of evolution: (1) constrained (Ornstein-Uhlenbeck) and (2) unconstrained constant-variance (Brownian-motion) random walks; (3) punctua-

tional evolution, with character divergence depending on speciation events (κ); (4) an exponentially accelerating or decelerating rate of evolution through time (δ); and (5) a Pagel's lambda model, which transforms the tree from a star phylogeny to the Brownian-motion model as λ varies from 0 to 1, respectively (Pagel 1999). We used estimates of standard errors (SE) of species (tip) morphology in all models (Claramunt et al. 2012) to account for the potential effect of intraspecific variation on model estimates. We compared among models using sample-size-corrected Akaike's Information Criterion (AIC_c) and Akaike weights (w_i ; Burnham and Anderson 2002). We then transformed the tree using the best model and reconstructed ancestral character states using a maximum-likelihood approach (Schluter et al. 1997) implemented with the “ape” package (Paradis et al. 2004) in R. We interpreted nonoverlapping confidence intervals (CIs) of adjacent tip and node values as instances of strong evolutionary changes in morphology. These analyses were implemented in R (R Development Core Team 2013) using the following packages: ape (Paradis et al. 2004), picante (Kembel et al. 2010), smatr (Warton et al. 2012), nlme (Pinheiro et al. 2013), and RColorBrewer (Neuwirth 2011).

RESULTS

Principal Component Analysis

The PCA, followed by a Bartlett's sphericity test (Jackson 1993), identified 21 statistically significant axes of variation (Appendix Table 3). The first 10 axes accounted for ~90% of the total variance (Appendix Table 3). PC1 and PC2 accounted for 56.7% and 7.9% of the variance in the dataset, respectively (Figure 2 and Table 1). Most of the variation in PC1 and PC2 (92.7% and 75.4% of total error variance, respectively) was the result of variation among, rather than within, species ($F_{12, 405} = 400.7$ and $F_{12, 405} = 103.0$, respectively; Table 1; all other F values were not significant at $P < 0.05$). Within-species variation was higher than among-species variation in all other PC axes (among-species variation was <30%; Appendix Table 4); given our interest in interspecific variation in morphology, we focused on PC1 and PC2 in subsequent analyses. The structure loadings on PC1 were nearly all strong and positive (Table 1). PC1 appeared to capture overall variation in size and was strongly and linearly correlated with body mass (OLS on species means, $n = 11$; mass = $4.83 * PC1 + 44.63$, $r^2 = 0.95$; $F_{1, 9} = 161.2$, $P < 0.001$). Phylogenetically generalized least-squares (PGLS; $r^2 = 0.94$; slope 95% CI: 4.2–5.8) and standardized major-axis regression (SMA; $r^2 = 0.95$; slope 95% CI: 3.9–5.6) yielded similar results, including broadly overlapping CIs for the slope of the relationship. We therefore used PC1 as a proxy for body size. The wing-tip shape indices were calculated to be size independent (Lockwood et al. 1998), which

TABLE 1. Results of principal component analysis of 13 species in the genus *Cinclodes*. Only the first and second principal component axes (PC1 and PC2) are shown because they are the only axes that captured significant among-species variation (92.7% and 75.4% of total error variance; $F_{12, 405} = 400.7$ and $F_{12, 405} = 103.0$, respectively). Complete results are presented in the Appendix Tables 3 and 4. Loadings on PC1 were largely positive and strong, such that PC1 can be viewed as a proxy for body size. Loadings on PC2 present a more complex pattern, indicating an inverse correlation between the wing-tip pointedness index (suggesting more pointed wings) and hallux length. Bold indicates significant loadings.

	PC1	PC2
Percentage of total variance	56.7	7.9
Among-species sum of squares ^a	5,235.58	441.02
Within-species sum of squares ^b	537.12	175.93
Morphometric variable	Structure loadings	Structure loadings
Body length (mm)	0.88507	-0.06882
Head length (mm)	0.90824	-0.13721
Bill length (mm)	0.84197	-0.02677
Proximal bill cross-sectional area (mm ²)	0.87155	0.05260
Mid-length bill cross-sectional area (mm ²)	0.85251	0.17309
Wing length (mm)	0.83644	0.02095
Width of primary 1	0.72921	-0.22033
Width of primary 9	0.56787	-0.33569
Tibiotarsus width (mm)	0.82772	-0.05873
Tarsometatarsus length (mm)	0.82757	-0.20970
Tarsometatarsus width (mm)	0.30712	-0.01095
Digit 1 (mm)	0.61665	0.65462
Digit 2 (mm)	0.88798	0.03306
Digit 3 (mm)	0.88528	-0.00781
Digit 4 (mm)	0.90329	0.01239
Ungual 1 (mm)	0.50866	0.69050
Ungual 2 (mm)	0.87267	0.06606
Ungual 3 (mm)	0.86356	0.22778
Ungual 4 (mm)	0.87535	0.14420
Central rectrix (mm)	0.85965	-0.18149
Lateral rectrices	0.78193	-0.22205
Wing-tip pointedness index	0.32346	-0.55777
Wing convexity index	-0.21106	0.40321

^a df = 12.

^b df = 405.

appeared to be largely true in our analyses, as they loaded weakly on PC1. PC2 appeared to capture variation in the length of the hallux and in the convexity of wing tips (Table 1), given that these metrics both loaded strongly on this axis. Overall, birds with high PC2 had relatively longer halluces and more pointed wing tips (Table 1).

Ancestral State Reconstructions and Analyses

Phylogenetic analysis of PC1. We found significant variation in PC1. The unconstrained constant variance (Brownian-motion) model ($AIC_c = 76.92$, $w_i = 0.50$; Table 2) outperformed all other models ($\Delta AIC_c > 2.0$; Table 2). The reconstruction of ancestral body sizes (via PC1) identified an initial split into 2 primary *Cinclodes* clades. For clarity, and because PC1 is tightly correlated with body mass, we report results in grams by calculating body mass from PC1 values. The 2 groups identified in this initial split were a small-body-size clade (clade mean = 40.7 g; 95% CI: 29.6–51.9) and a large-body-size clade (clade mean = 63.1 g; 95% CI: 52.0–74.2) (Figure 3A). Within these clades,

body size was similar among species, with a few notable exceptions. *Cinclodes antarcticus* belonged to the small-body-size clade but was much larger (63.2 ± 15.9 g) than other members of the clade and than the reconstructed ancestor of the clade (40.7 ± 11.1 g; Figure 3A). This species was also significantly larger than the reconstructed ancestor (42.7 ± 8.0 g) that it shares with its sister species, *C. fuscus* (30.2 ± 11.2 g; Figure 3A). Two species also appeared to have diverged from the ancestral condition of the large-bodied clade. *Cinclodes patagonicus* was smaller (48.5 ± 14 g) than both the clade's ancestral node (63.1 ± 11.1 g) and the hypothetical ancestor (64.0 ± 2.8 g) that it shares with *C. nigrofumosus* and *C. taczanowskii* (Figure 3A). By contrast, *C. palliatus* (104.5 ± 20.3 g) was significantly larger than both the hypothetical ancestor of the large-bodied clade and that of its most recent ancestral node (66.0 ± 10.0 g; Figure 3A). Body size of the basal species *C. pabsti* was intermediate (54.5 ± 14.8 g; Figure 3A), overlapping with that of the large-bodied clade. Additionally, we found that 3 new species described in a

TABLE 2. Evolutionary models fit to first and second principal component (PC1 and PC2) scores, and their estimated parameters. Models were selected using AIC_c and Akaike weights (w_i).^a The number of parameters in each model is denoted by k . For definitions of evolutionary models, see text.

Model	Parameters	Log likelihood	k	ΔAIC_c	w_i
PC1					
Brownian ¹	$\sigma^2 = 5.35$	-35.86	2	0.00	0.50
Delta	$\sigma^2 = 3.06, \delta = 2.51$	-35.21	3	2.16	0.17
Ornstein-Uhlenbeck	$\sigma^2 = 8.57, \alpha = 0.18$	-35.29	3	2.32	0.16
Kappa	$\sigma^2 = 5.56, \kappa = 0.81$	-35.80	3	3.35	0.09
Pagel's lambda	$\sigma^2 = 5.35, \lambda = 1$	-35.86	3	3.47	0.08
PC2					
Ornstein-Uhlenbeck ²	$\sigma^2 = 1.73, \alpha = 0.52$	-20.54	3	0.00	0.29
Brownian	$\sigma^2 = 0.66$	-22.52	2	0.48	0.23
Delta	$\sigma^2 = 0.31, \delta = 3.00$	-20.92	3	0.75	0.20
Kappa	$\sigma^2 = 0.65, \kappa \approx 0$	-21.19	3	1.28	0.15
Pagel's lambda	$\sigma^2 = 0.33, \lambda = 0.76$	-21.41	3	1.73	0.12

^a AIC_c scores for the best-performing models: ¹76.92, ²49.75.

recent taxonomic split (Sanín et al. 2009) differed significantly in morphology (multivariate ANOVA [MANOVA], Wilks's $\lambda = 0.18$, approximate $F = 119.8$, $P < 0.001$; Figure 2). *Cinclodes albidiventris* was significantly larger (PC1) than *C. albiventris* and *C. fuscus* (Tukey's HSD, $P < 0.01$), although the latter two species did not differ significantly in PC1 (Tukey's HSD, $P > 0.1$; Figure 2); and *C. fuscus*, *C. albiventris*, and *C. albidiventris* all differed significantly in PC2 (Tukey's HSD, all $P < 0.05$; Figure 2).

Phylogenetic analysis of PC2. The constrained-constant-variance (Ornstein-Uhlenbeck) model ($AIC_c = 49.75$, $w = 0.29$; Table 2) performed marginally better than the Brownian-motion model ($\Delta AIC_c = 0.48$; Table 2). *Cinclodes oustaleti* had a significantly higher PC2 (0.65 ± 0.22 ; Figure 3B) value than the other members of its clade, *C. albiventris* (-1.04 ± 0.13 ; Figure 3B) and *C. albidiventris* (-0.07 ± 0.16 ; Figure 3B). The PC2 value for the clade that includes *C. fuscus* and *C. antarcticus* was also higher than that of its sister clade, as measured by the value of the reconstructed ancestral condition (1.67 ± 0.63 ; Figure 3B). In addition, *C. antarcticus* had a significantly higher PC2 value (2.47 ± 0.47 ; Figure 3B) than its sister species *C. fuscus* (1.43 ± 0.18 ; Figure 3B).

DISCUSSION

The genus *Cinclodes* appears to have diversified in morphology along 2 axes: size (PC1) and wing and hallux morphology (PC2). The primary axis (56.7% of the total variance) of morphological variation in the genus was body size (Figure 2), but PC2 also accounted for a significant fraction of variation (7.9%; Figure 2). Phylogenetically informed analyses revealed an early divergence in body size in the genus, with several subsequent changes in body size (Figure 3A). We also found a smaller, and difficult-to-

explain, component of interspecific variation in hallux length and wing morphology (Figure 3B). Here, we discuss the potential correlates of variation in size and form of *Cinclodes*, and we conclude by placing the evolution of external morphology in the broader context of ecological and phenotypic differentiation in the genus.

Body Size, Morphological Evolution, and Taxonomic Consequences

Divergence in body size among adaptively radiating taxa is relatively well documented and appears to be the primary axis of divergence in multiple systems (Nagel and Schluter 1998, Marroig and Cheverud 2005, Claramunt 2010). *Cinclodes* shows similarly strong divergence in body size. From *C. comechingonus* (body mass ≈ 21 g, estimated from PC1) to *C. palliatus* (104 ± 5.8 g), *Cinclodes* species varied fivefold in body size (Figure 3A). Furthermore, body size was not distributed randomly throughout the phylogeny. Instead, an early divergence appears to have generated 1 clade with mostly small species and another clade with mostly large species (Figure 3A). This pattern has 3 exceptions: *C. patagonicus* was a small-bodied member of the large-bodied clade and *C. antarcticus* was a large-bodied member of the small-bodied clade, and *C. palliatus* (at ~ 105 g, by far the largest *Cinclodes* species) was ~ 40 g heavier than *C. excelsior* (≈ 65 g), the next-largest member of the genus. *Cinclodes antarcticus* is found only on islands in southernmost Chile and Argentina and on the Falkland Archipelago (Chesser 2004). We hypothesize that the relatively large size of *C. antarcticus* is an example of island gigantism (or "the island rule"; Lomolino 1985, Palkovacs 2003). Tabak et al. (2014) reported that this species is driven to local extinction by invasive rats and suggested that it evolved in the absence of mammalian predators. A reduction in predation is one of the complementary explanations for

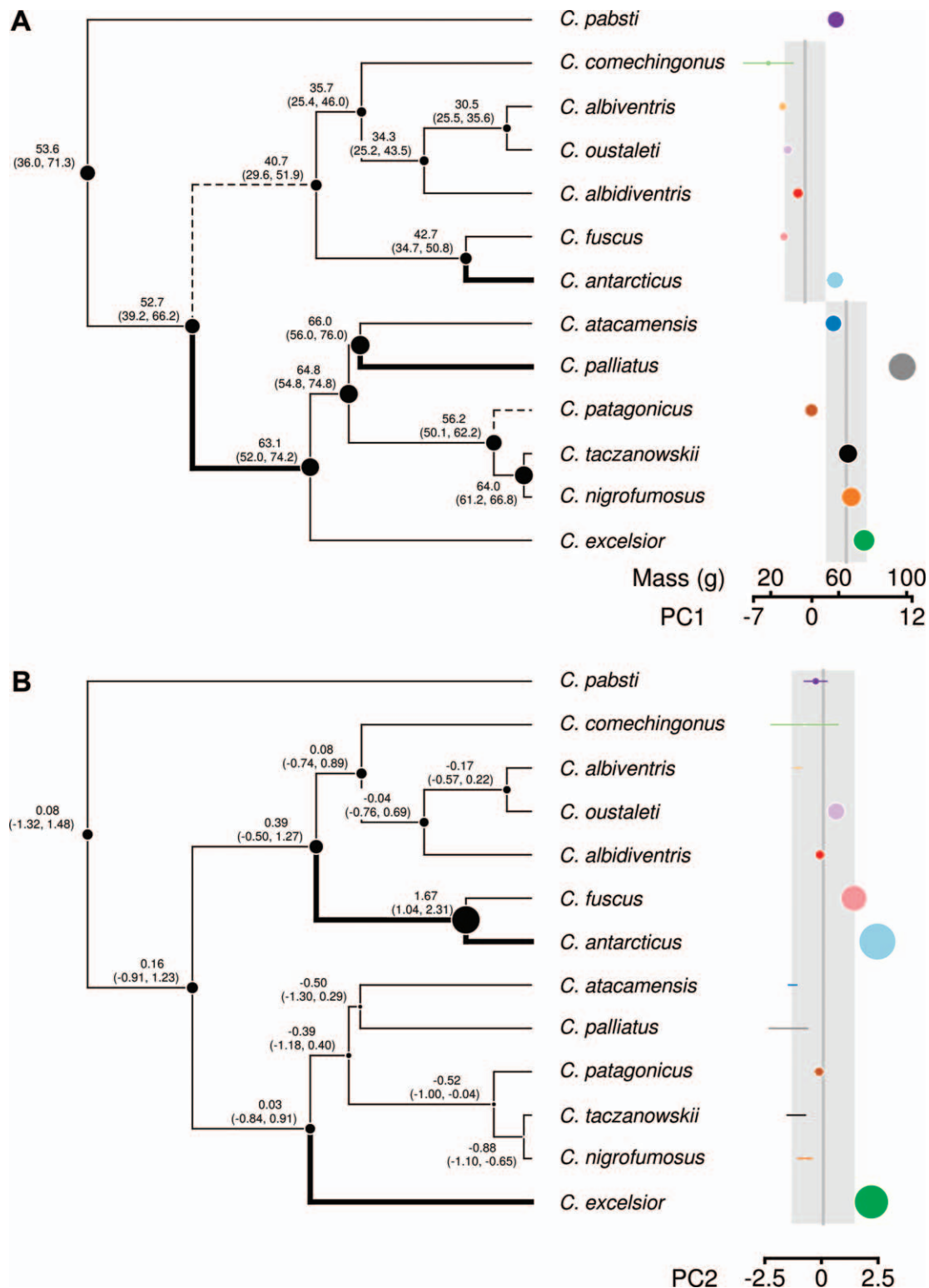


FIGURE 3. Morphological diversification in the genus *Cinclodes* as demonstrated by maximum-likelihood ancestral-character-state reconstructions of (A) the first principal component (PC1: body size), using a Brownian-motion model; and (B) the second principal component (PC2: wing-tip pointedness and hallux length), using an Ornstein-Uhlenbeck model. Species data points (tip values) are located on the x-axis and are sized in relation to the average (A) PC1 value or (B) PC2 value of the species. Error bars represent 95% confidence intervals (CIs) and are contained within the data points when not visible. Reconstructed node values are represented by point size, and CIs are provided to the left of each node. Significant evolutionary changes, inferred from nonoverlapping CIs, are denoted by bold lines (positive shifts in PC values) and dashed lines (negative shifts in PC values).

avian gigantism (Raia 2009). The large size of *C. palliatus* is likely partially related to its occurrence at high elevations in the Peruvian Andes (above 4,000 m) and adaptation to the resulting cold climate, in accordance with Bergmann's rule (Meiri and Dayan 2003). The relatively large size of both *C. antarcticus* and *C. palliatus* appears to be a derived condition; thus, these two species may represent cases of autapomorphic gigantism (*sensu* Gould and MacFadden 2004).

By contrast, *C. patagonicus* shows a phylogenetically derived reduction in body size within a large-sized clade. Possible causes of this evolutionary change are unclear, but the geographic distribution of *C. patagonicus* is partially sympatric with that of *C. nigrofumosus* and *C. oustaleti*. To our knowledge, this is the only case of 3-species syntopy within the genus. In northern and central Chile, where these species are sympatric, *C. nigrofumosus* inhabits and feeds almost exclusively in marine environments, and *C. oustaleti* inhabits and feeds in these environments seasonally, whereas *C. patagonicus* occupies a broad range of habitats and environments (Martínez del Rio et al. 2009, J. A. Rader personal observation). We speculate that the decrease in size of *C. patagonicus* in relation to its sister clade (*C. nigrofumosus* and *C. taczanowskii*) may have been shaped by ecological character displacement, construed broadly as the overdispersion in body size of potential competitors (Dayan and Simberloff 2005).

PC2 encompassed variation in the length of the reversed toe (hallux) and in the pointedness of the wing tips and accounted for ~8% of the total morphological variation. A higher value of PC2 appeared to have evolved twice within the genus: in *C. antarcticus* and in *C. excelsior*. Although the PC2 value for *C. oustaleti* was not large compared with that of the entire clade, it was significantly greater than that of its sister species, *C. albiventris*. Higher PC2 corresponds to more pointed wing tips and longer halluces (decreased wing-tip pointedness index indicates more pointed wings; Lockwood et al. 1998; Table 1). Migrant birds often have more pointed wing tips (Lockwood et al. 1998), which may reduce the energetic cost of migration (Bowlin and Wikelski 2008), and longer halluces may be related to ground-foraging habits (Fitzpatrick 1985). The higher PC2 value of *C. oustaleti* in relation to *C. albiventris* may reflect that *C. oustaleti* is a migrant (Remsen et al. 2003, Chesser 2004, Martínez del Rio et al. 2009) and *C. albiventris* is not (Remsen et al. 2003, Chesser 2004). However, *C. antarcticus* and *C. excelsior* are not migrants, nor are they arboreal. Therefore, the functional significance of these changes in PC2 is, as yet, difficult to explain.

The morphological data presented here not only reveal significant patterns in the evolution of size and morphology in the genus *Cinclodes*, but also support a recent taxonomic split. *Cinclodes fuscus* had traditionally been considered a single polytypic species, but using evidence

from mitochondrial DNA, Sanín et al. (2009) concluded that *C. fuscus* is paraphyletic and composed of 3 lineages (*C. albiventris*, *C. albidiventris*, and *C. fuscus*) more closely related to other *Cinclodes* species than to each other (Figure 1). Our results suggest that *Cinclodes albidiventris* was of larger body size than *C. albiventris* or *C. fuscus*, which were similar in size, and that *C. fuscus*, *C. albiventris*, and *C. albidiventris* all differed significantly in PC2 (Figure 2).

***Cinclodes*: Ecologically Diverse, Morphologically Conserved**

The genus *Cinclodes* includes species that differ dramatically in ecological habits (Sabat and Martínez del Rio 2002, Chesser 2004, Sabat et al. 2006a, Martínez del Rio et al. 2009, Sanín et al. 2009). Habitat use in *Cinclodes* ranges from the open grassland of the high Andes to the marine intertidal zone. Two species, *C. nigrofumosus* and *C. taczanowski*, are arguably the most marine-adapted of all passerine birds, and other species use the intertidal zone regularly or seasonally (Chesser 2004). Further, the genus contains ecological generalists as well as specialists (Martínez del Rio et al. 2009, J. A. Rader et al. personal observation).

Cinclodes species have also diversified physiologically, seemingly in response to their relative use of marine resources. Sabat and collaborators found a strong correlation between renal form and function and the relative reliance of *Cinclodes* species on marine resources (Sabat et al. 2004, 2006b). The relative size of the birds' kidneys, the fraction of kidneys composed of medullary tissue, and the capacity to concentrate urine increased with the reliance of each species on marine resources (Sabat et al. 2004, 2006a, 2006b).

We hypothesized that *Cinclodes* might exhibit external morphological diversity similar to its ecological and physiological diversity. Our results suggest that *Cinclodes* species have diversified significantly on two morphological axes, primarily in body size but also in wing and foot morphology. Is this pattern of morphological variation typical of bird genera? This question is confounded by a paucity of data and by the tendency to define genera by morphological criteria, which constrains the amount of morphological variation in any particular genus. Nevertheless, the result for *Cinclodes* appears to be concordant with those for other avian genera. Most of the morphological variation in *Cinclodes* is the result of divergence in body size; body size accounted for 56.7% of the variance in our data. Harmon et al. (2010) found similar variation in size, in a survey of 13 avian genera, wherein the variance captured by PC1 ranged from 33% to 80.9% (mean = 62%). It also accords well with a study of the suboscine passerines as a group (Claramunt 2010), in which body size accounted for the majority of variation.

Our results suggest that although *Cinclodes* has experienced rapid cladogenesis and unusual ecological and physiological differentiation, morphological divergence has not been atypical for an avian genus. In this it contrasts with some well-known examples of adaptive radiation, such as *Anolis* lizards (Irschick and Losos 1998, 1999) and Galápagos finches (Schluter and Grant 1984, Grant 1986, Price 1987), in which rapid speciation has been accompanied by pronounced diversification along both ecological and morphological axes.

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LITERATURE CITED

- Baldwin, S. P., H. C. Oberholser, and L. G. Worley (1931). Measurements of Birds. Scientific Publications of the Cleveland Museum of Natural History 2.
- Beuttell, K., and J. B. Losos (1999). Ecological morphology of Caribbean anoles. *Herpetological Monographs* 13:1–28.
- Blomberg, S. P., J. G. Lefevre, J. A. Wells, and M. Waterhouse (2012). Independent contrasts and PGLS regression estimators are equivalent. *Systematic Biology* 61:382–391.
- Bowlin, M. S., and M. Wikelski (2008). Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. *PLOS One* 3:e2154.
- Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York, NY, USA.
- Chesser, R. T. (2004). Systematics, evolution, and biogeography of the South American ovenbird genus *Cinclodes*. *The Auk* 121:752–766.
- Claramunt, S. (2010). Discovering exceptional diversifications at continental scales: The case of the endemic families of Neotropical suboscine passerines. *Evolution* 64:2004–2019.
- Claramunt, S., E. P. Derryberry, J. V. Remsen, Jr., and R. T. Brumfield (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society of London, Series B* 279:1567–1574.
- Dayan, T., and D. Simberloff (2005). Ecological and community-wide character displacement: The next generation. *Ecology Letters* 8:875–894.
- Derryberry, E. P., S. Claramunt, G. Derryberry, R. T. Chesser, J. Cracraft, A. Aleixo, J. Pérez-Emán, J. V. Remsen, Jr., and R. T. Brumfield (2011). Lineage diversification and morphological evolution in a large-scale continental radiation: The Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution* 65:2973–2986.
- Fitzpatrick, J. W. (1985). Form, foraging behavior, and adaptive radiation in the Tyrannidae. *Ornithological Monographs* 36: 447–470.
- Freckleton, R. P., P. H. Harvey, and M. Pagel (2002). Phylogenetic analysis and comparative data: A test and review of evidence. *American Naturalist* 160:712–726.
- Freitas, G. H., A. V. Chaves, L. M. Costa, F. R. Santos, and M. Rodrigues (2012). A new species of *Cinclodes* from the Espinhaço Range, southeastern Brazil: Insights into the biogeographical history of the South American highlands. *Ibis* 154:738–755.
- Gavrilets, S., and J. B. Losos (2009). Adaptive radiation: Contrasting theory with data. *Science* 323:732–737.
- Gould, G. C., and B. J. MacFadden (2004). Gigantism, dwarfism, and Cope's rule: "Nothing in evolution makes sense without a phylogeny." *Bulletin of the American Museum of Natural History* 285:219–237.
- Grant, P. R. (1986). *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton, NJ, USA.
- Harmon, L. J., J. B. Losos, T. J. Davies, R. G. Gillespie, J. L. Gittleman, W. B. Jennings, K. H. Kozak, M. A. McPeck, F. Moreno-Roark, T. J. Near, A. Purvis, R. E. Ricklefs, et al. (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution* 64:2385–2396.
- Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger (2008). GEIGER: Investigating evolutionary radiations. *Bioinformatics* 24:129–131.
- Irschick, D. J., and J. B. Losos (1998). A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* 52:219–226.
- Irschick, D. J., and J. B. Losos (1999). Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *American Naturalist* 154:293–305.
- Jackman, T. R., A. Larson, K. de Queiroz, and J. B. Losos (1999). Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. *Systematic Biology* 48:254–285.
- Jackson, D. A. (1993). Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. *Ecology* 74:2204–2214.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Lockwood, R., J. P. Swaddle, and J. M. V. Rayner (1998). Avian wingtip shape reconsidered: Wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* 29:273–292.
- Lomolino, M. V. (1985). Body size of mammals on islands: The island rule reexamined. *American Naturalist* 125:310–316.
- Losos, J. B. (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, CA, USA.

- Marroig, G., and J. M. Cheverud (2005). Size as a line of least evolutionary resistance: Diet and adaptive morphological radiation in New World monkeys. *Evolution* 59:1128–1142.
- Martínez del Río, C., P. Sabat, R. Anderson-Sprecher, and S. P. Gonzalez (2009). Dietary and isotopic specialization: The isotopic niche of three *Cinclodes* ovenbirds. *Oecologia* 161: 149–159.
- Martins, E. P., and T. F. Hansen (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* 149:646–667.
- Meiri, S., and T. Dayan (2003). On the validity of Bergmann's rule. *Journal of Biogeography* 30:331–351.
- Nagel, L., and D. Schluter (1998). Body size, natural selection, and speciation in sticklebacks. *Evolution* 52:209–218.
- Neuwirth, E. (2011). RColorBrewer: ColorBrewer palettes. <http://cran.r-project.org/web/packages/RColorBrewer/index.html>
- Osborn, H. F. (1902). The law of adaptive radiation. *American Naturalist* 36:353–363.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Palkovacs, E. P. (2003). Explaining adaptive shifts in body size on islands: A life history approach. *Oikos* 103:37–44.
- Paradis, E., J. Claude, and K. Strimmer (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team (2013). nlme: Linear and nonlinear mixed effects models, R package version. R Foundation for Statistical Computing, Vienna, Austria.
- Price, T. D. (1987). Diet variation in a population of Darwin's finches. *Ecology* 68:1015–1028.
- R Development Core Team (2013). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raia, P. (2009). Giantism. In *Encyclopedia of Islands* (R. G. Gillespie and D. A. Clague, Editors). University of California Press, Berkeley, CA, USA. pp. 372–376.
- Remsen, J. V., Jr. (2003). Family Furnariidae (ovenbirds). In *Handbook of the Birds of the World*, vol. 8 (J. del Hoyo, A. Elliott, and D. Christie, Editors). pp. 162–357.
- Ricklefs, R. E., and J. Travis (1980). A morphological approach to the study of avian community organization. *The Auk* 97:321–338.
- Sabat, P., K. Maldonado, M. Canals, and C. Martínez del Río (2006a). Osmoregulation and adaptive radiation in the ovenbird genus *Cinclodes* (Passeriformes: Furnariidae). *Functional Ecology* 20:799–805.
- Sabat, P., K. Maldonado, J. M. Fariña, and C. Martínez del Río (2006b). Osmoregulatory capacity and the ability to use marine food sources in two coastal songbirds (*Cinclodes*: Furnariidae) along a latitudinal gradient. *Oecologia* 148:250–257.
- Sabat, P., K. Maldonado, A. Rivera-Hutinel, and G. Farfan (2004). Coping with salt without salt glands: Osmoregulatory plasticity in three species of coastal songbirds (ovenbirds) of the genus *Cinclodes* (Passeriformes: Furnariidae). *Journal of Comparative Physiology B* 174:415–420.
- Sabat, P., and C. Martínez del Río (2002). Inter- and intraspecific variation in the use of marine food resources by three *Cinclodes* (Furnariidae, Aves) species: Carbon isotopes and osmoregulatory physiology. *Zoology (Jena)* 105:247–256.
- Sabat, P., and C. Martínez del Río (2005). Seasonal changes in the use of marine food resources by *Cinclodes nigrofumosus* (Furnariidae, Aves): Carbon isotopes and osmoregulatory physiology. *Revista Chilena de Historia Natural* 78:253–260.
- Sanín, C., C. D. Cadena, J. M. Maley, D. A. Lijtmaer, P. L. Tubaro, and R. T. Chesser (2009). Paraphyly of *Cinclodes fuscus* (Aves: Passeriformes: Furnariidae): Implications for taxonomy and biogeography. *Molecular Phylogenetics and Evolution* 53: 547–555.
- Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford, UK.
- Schluter, D., and P. R. Grant (1984). Determinants of morphological patterns in communities of Darwin's finches. *American Naturalist* 123:175–196.
- Schluter, D., T. Price, A. Ø. Mooers, and D. Ludwig (1997). Likelihood of ancestor states in adaptive radiation. *Evolution* 51:1699–1711.
- Simpson, G. G. (1953). *The Major Features of Evolution*. Columbia University Press, New York, NY, USA.
- Tabak, M. A., S. Poncet, K. Passfield, and C. Martínez del Río (2014). Invasive species and land bird diversity on remote South Atlantic islands. *Biological Invasions* 16:341–352.
- Warton, D. I., R. A. Duursma, D. S. Falster, and S. Taskinen (2012). Smatr 3—an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution* 3:257–259.
- Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby (2006). Bivariate line-fitting methods for allometry. *Biological Reviews* 81:259–291.
- Weir, J. T. (2006). Divergent timing and patterns of species accumulation in lowland and highland Neotropical birds. *Evolution* 60:842–855.

APPENDIX

TABLE 3. Principal component (PC) analysis yielded 21 significant axes of morphological variation within *Cinclodes*. The first and second PC axes are the only axes that captured significant among-species variation (92.7% and 75.4% of total error variance, $F_{12, 405} = 400.7$ and $F_{12, 405} = 103.0$, respectively).

PC axis	Eigenvalue	Percent variance	Cumulative percent variance	χ^2	df	$P > \chi^2$
1	13.6220	59.226	59.226	10,433.587	241.893	<0.0001
2	1.8058	7.851	67.077	3,782.907	244.924	<0.0001
3	1.0991	4.779	71.856	2,927.326	225.429	<0.0001
4	0.9253	4.023	75.879	2,494.098	205.182	<0.0001
5	0.7628	3.316	79.196	2,119.685	185.761	<0.0001
6	0.7023	3.054	82.250	1,818.680	167.490	<0.0001
7	0.6498	2.825	85.075	1,507.912	149.644	<0.0001
8	0.5549	2.413	87.487	1,176.641	133.434	<0.0001
9	0.4449	1.934	89.421	879.660	117.982	<0.0001
10	0.3412	1.483	90.905	657.636	103.197	<0.0001
11	0.2853	1.240	92.145	524.544	89.398	<0.0001
12	0.2524	1.097	93.242	432.250	76.558	<0.0001
13	0.2288	0.995	94.237	358.358	64.754	<0.0001
14	0.2211	0.961	95.198	294.456	53.864	<0.0001
15	0.1832	0.797	95.995	220.639	43.977	<0.0001
16	0.1667	0.725	96.720	176.909	34.909	<0.0001
17	0.1540	0.670	97.389	139.420	26.933	<0.0001
18	0.1372	0.596	97.985	103.965	19.974	<0.0001
19	0.1183	0.514	98.500	75.910	13.911	<0.0001
20	0.1150	0.500	99.000	58.862	8.913	<0.0001
21	0.1012	0.440	99.440	32.610	4.955	<0.0001
22	0.0712	0.310	99.749	4.398	1.936	0.1050
23	0.0577	0.251	100.000	0.000		

TABLE 4. Results of an analysis of variance (ANOVA) comparing treatment sum of squares (differences among species) with error sum of squares (intraspecific variation). Although principal component (PC) analysis revealed several significant PC axes, only PC1 and PC2 varied significantly among species (ANOVA, $F_{12, 405} = 400.7$ and $F_{12, 405} = 103.0$, respectively), with among-species variation explaining 92.7% and 75.4% of total axis variance, respectively. The remaining PC axes captured within-species variability.

	df	PC1	PC2	PC3	PC4	PC5
Among-species sum of squares	12	5,235.58	537.12	91.59	5.05	72.99
Within-species sum of squares	405	441.02	175.93	303.15	47.78	242.82