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ADAPTIVE MODIFICATION OF TAIL STRUCTURE IN RELATION TO BODY MASS AND BUCKLING IN WOODCREEPERS

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Abstract. We assessed the relationship between function and tail structure of woodcreepers (Dendrocolaptidae) and Neotropical ovenbirds (Furnariidae) using a comparative analysis of independent contrasts. Because woodcreepers are scansorial (they use their tail for body support), we predicted that the structure of the rectrix rachis should be reinforced both at the tip and at the base, whereas the nonscansorial Neotropical ovenbirds should lack reinforcement of the rectrix tips. For each species, we measured the length of the rachis of the medial rectrix and its diameter both at the tip and base of the feather. Rachis diameters were positively associated with body mass in both groups as expected if tail structure were a simple allometric product of body size. However, woodcreepers had larger rachis diameters for a given body mass and higher slopes in the allometric regressions than Neotropical ovenbirds. In addition, we found positive relationships between rachis width at both the tip and base of the rectrix and tail length in woodcreepers, but in Neotropical ovenbirds only rachis width at the base was associated with tail length. These results considered together are consistent with the hypothesis that the tip of the woodcreeper tail rachis is adapted to both support body mass and to prevent Euler buckling failure.

Key words: *Dendrocolaptidae, Euler buckling, Furnariidae, scansorial, tail morphology.*

Modificaciones Adaptativas de la Estructura de la Cola en Relación a la Masa Corporal y al Pandeo en Pájaros Trepadores

Resumen. Se evaluó la relación entre la función y la estructura de la cola en los trepadores (Dendrocolaptidae) y los furnáridos (Furnariidae) usando un análisis comparativo de contrastes independientes. Debido a que los trepadores son escansoriales (es decir que usan su cola para el soporte del cuerpo), se predijo que la estructura del raquis de la rectriz debería estar reforzada tanto en la punta como en la base mientras que la de los furnáridos que no son escansoriales debería carecer del reforzamiento en la punta. Para cada especie se midió el largo del raquis de la rectriz medial y su diámetro, tanto en la punta como en la base de la pluma. Los diámetros del raquis estuvieron positivamente asociados con la masa corporal en ambos grupos, tal como se esperaría si la cola fuera el simple producto de una relación alométrica con el tamaño corporal. Sin embargo, los diámetros del raquis para una dada masa corporal y las pendientes de las regresiones alométricas fueron mayores en los trepadores que en los furnáridos. Además, se encontraron relaciones postivas entre el ancho del raquis en la punta y en la base de la rectriz y el largo de la cola en trepadores, pero solamente el ancho del raquis en la base estuvo asociado con el largo de la cola en furnáridos. Estos resultados considerados en su conjunto son consistentes con la hipótesis de que la punta del raquis en la cola de los trepadores está adaptada para soportar la masa corporal y prevenir el pandeo de Euler.

INTRODUCTION

Woodcreepers (family Dendrocolaptidae) comprise a diverse group of mainly humid and montane forest species endemic to Central and South America. They typically forage vertically on tree trunks well above ground level (Ridgely and Tudor 1994). Vertical movement on tree trunks is achieved using the tail as a support for body weight. This rather unusual means of body support (hereafter described as scansorial) is found in other avian families including the woodpeckers (Picidae), the creepers (Certhiidae), and the swifts (Apodidae). The scansorial condition correlates with several putative morphological adaptations (Burt 1930, Stolpe 1932, Richardson 1942, Bock and Miller 1959, Spring 1965, Fe-

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duccia 1972). However, a rigorous test of the adaptive value of these characters is still lacking because of the absence of three things: (1) a comparative analysis based on a cladistic phylogenetic hypothesis, (2) an appropriate control for confounding factors such as body mass differences, and (3) distinctive and clear-cut predictions about morphological patterns expected for scansorial birds.

Tail feathers of scansorial birds are normally fixed at both ends (i.e., to the pygostyle and the tree trunk), and to function as an effective support of the body, compressive axial forces acting along the feather rachis should be resisted. Thus, feather rachises are analogous to a slender column which might collapse by crushing or buckling. Principles of basic physics indicate that the greater the compressive axial force the higher the cross-sectional area of a column required to avoid crushing failure (Alexander 1968, Wainwright et al. 1976, McGowan 1999). Feather shafts are tubes made of a compact keratin cortex enclosing medullary foam (Rutschke 1976). The Young's modulus (a measure of stress to strain) of feather cortical keratin is highly conserved among and within species (Bonser and Purslow 1995, Bonser 1996). This implies that most differences in feather strength across species can be attributed to differences in cross-sectional distribution of the cortex keratin rather than to differences in composition (Bonser and Purslow 1995). These observations considered together suggest that scansorial species with large body masses should have a reinforced rachis with a wider cortical section in order to resist crushing by axial compressive forces.

A column also may fail by buckling along its longitudinal axis long before compressive collapse of its material (Wainwright et al. 1976). Long, thin columns tend to fail by buckling, either because they arch along their length or because a local section of the column ripples. These phenomena are termed Euler buckling and local buckling, respectively (Vogel 1988). The loads that produce both Euler and local buckling are directly related to cross-sectional distribution of material along the column length. In addition, Euler buckling shows a positive relationship with column length (Alexander 1968, Wainwright et al. 1976, Vogel 1988). This means that a longer tail is more prone to failure through Euler buckling than a short tail. To compensate for this, longer-tailed species should have proportionately wider rachises. This should be evident even after one has controlled for the effect of differences in axial forces.

A typical tail feather not involved in body support is attached at its proximal end to the pygostyle and is free to bend at its distal end. Therefore, these feathers experience loading regimes analogous to cantilever beam structures (Worcester 1996). In particular, tail feathers should be of sufficient strength to resist the bending moments of its own weight and the lift forces generated during flight (Thomas and Balmford 1995). The resistance to dorsoventral deflection of the tail is directly related to the cross-sectional distribution of the keratin and inversely related to the moment arm of force acting on the tail. Thus, because of the contribution of the feather's own weight on its bending moment and the increasing moment of lift forces at the tail's base, an optimally designed rachis that is not directly involved in body support should be widest at the base and tapered distally (Wainwright et al. 1976).

Based on such theoretical considerations, one would predict that, after controlling for phylogeny, nonscansorial birds should show the following patterns: First, we expect a significant positive correlation between rachis basal diameter and tail length, in order to avoid the bending of the tail at its base where the maximum moment of the forces occurs. Second, there should be no such relationship between rachis tip diameter and tail length, because the moments of the forces are at minimum at the distal end. Third, we would expect no relationship between body size and rachis diameter at the base, unless tail length is positively associated with body size.

In contrast, in scansorial species one would predict that the rachis width at both the base and tip of the tail should be positively correlated with body mass and tail length. This is because a tail acting as a slender column should be strong enough to avoid crushing and buckling along its entire length.

In other words, in a linear regression, there should be a positive relationship between the rachis basal width and tail length for birds generally because the tail acts either as a cantilever beam or as a slender column. Instead, a positive relationship between the rachis tip width and both body mass and tail length should exist only for scansorial birds, in order to avoid crushing and buckling.

We tested these ideas using a comparative analysis of the tail structure in woodcreepers (Dendrocolaptidae) and Neotropical ovenbirds (Furnariidae). We chose these families because they are sister groups but only the former has a generalized scansorial habit. With the exception of the genera *Pygarrhichas*, *Margarornis*, and *Pseudocolaptes*, all furnariid species are non-scansorial (Vaurie 1980, Ridgely and Tudor 1994). Thus, the furnariids provide an ideal group to control for the effects on tail structure of factors other than physical support on vertical surfaces. Moreover, there are cladistically based phylogenies for both families (dendrocolaptids: Raikow 1994; furnariids: Zyskowski and Prum 1999) that allow us to control for phylogenetic effects on tail structure as well.

In the present study, we explored the relationship between tail function, body mass, and tail structure of woodcreepers and ovenbirds using a comparative method of independent contrasts. Specifically, we examined the relationship between rachis width and rachis length controlling for the possible confounding effects of body size and phylogeny in these two families of Neotropical passerines.

METHODS

The present analyses were based on study skins deposited at the Museo Argentino de Ciencias Naturales ‘‘Bernardino Rivadavia’’ (Buenos Aires, Argentina) and the American Museum of Natural History (New York). For each species (39 woodcreepers and 72 Neotropical ovenbirds), we measured from one to five adult males depending on availability. We were careful to avoid the inclusion of individuals with significant feather wear. The hypertrophy of the medial rectrices of scansorial birds is correlated with the predominant role that these feathers play in body support (Richardson 1942). For this reason, we based our study on the two medial rectrices, although only the one with less wear was measured in each individual. We measured the following variables: (1) tail length (TLENGTH, the length of the shaft of the feather from the tip to the attachment to the body); (2) rachis width at the tip (TIPWIDTH, dorsoventral width of the rachis measured 0.5 cm from the tip of the feather); and (3) rachis width at the base (BASEWIDTH, dorsoventral width of the rachis at a point as close as possible to the calamus). Tail length was measured using a compass and a flat metal ruler to the nearest mm. Rachis widths were measured with a dial caliper to the nearest 0.01 mm. Body mass data were obtained from Dunning (1993). All mensural data, together with common and scientific names of species, are provided in the Appendices.

It is important to note that among the 72 Neotropical ovenbird species included in the study, only *Pygarrhichas albogularis* is scansorial. We decided not to exclude this species from the data set, because it makes the analysis more conservative (i.e., less prone to show differences between woodcreepers and Neotropical ovenbirds).

We based our phylogenetic analysis on published cladistic analyses (Fig. 1 and 2). Raikow’s (1994) phylogenetic hypothesis of Dendrocolaptidae is primarily based on osteological and myological characters for 39 species. Zyskowski and Prum’s (1999) phylogenetic hypothesis of the Furnariidae uses nest architecture characters for 184 species. We estimated the ancestral states of the tail and body-mass characters using two different models of evolution: the random model and the punctuated model (Harvey and Purvis 1991). The random model assumes that changes occurred at each time interval along the branches of the phylogeny and that the direction of the change was random. The ancestral values of the characters may be reconstructed using the values of the derived species adjusted by estimated branch length. Alternatively, the punctuated model assumes that changes occurred only at the nodes of a tree. Details of the general procedure for estimating the ancestral character values are outlined in Felsenstein (1985).

We performed nondirectional comparative tests using the independent contrasts method (Felsenstein 1985) and using the CAIC software v. 2.0 (Purvis and Rambaut 1995). The independent contrasts method is based on the comparison between pairs of sister species. Each comparison produces a new variable (a ‘‘contrast’’) based on the difference between the values of the variable measured on the species within the pair. Contrasts may be standardized if divided by the square root of branch lengths. These contrasts are considered independent among pairs of sister species because they result from the evolutionary divergence that occurred after the origin of each pair. We examined the association between the standardized contrasts of different variables using a standard linear regression mod-

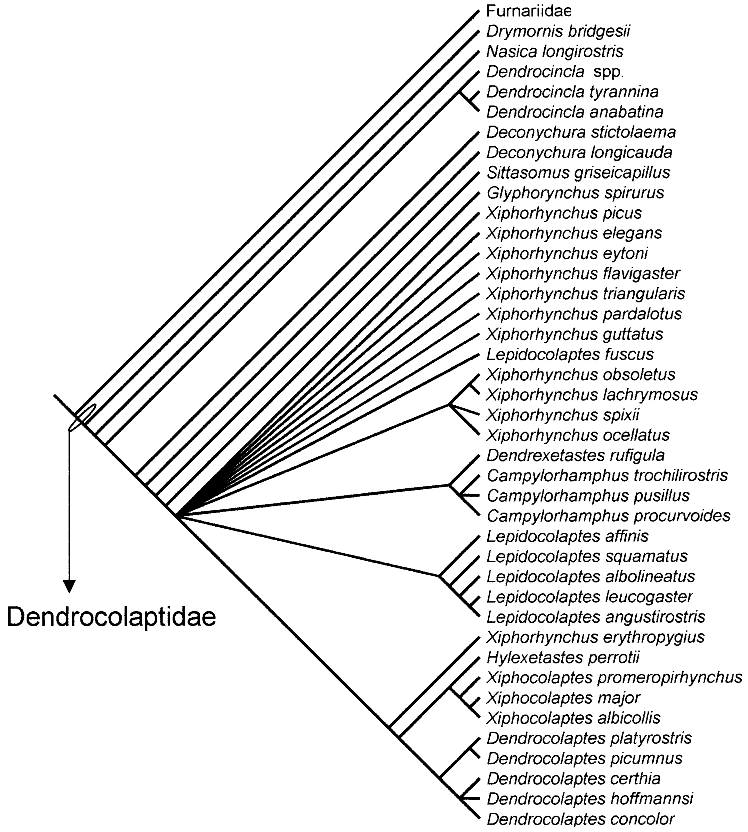

FIGURE 1. Phylogenetic hypothesis about the relationship among woodcreeper species (family Dendrocolaptidae) used in the independent-contrasts analysis. Family Furnariidae, at the top of the tree, is the sister group of woodcreepers. After Raikow (1994).

el adjusted to pass through zero (Grafen 1989, Garland et al. 1992). The latter condition was appropriate because the expected value of the dependent variable contrast must be zero when the independent variable contrast is zero. For our comparative analyses, polytomies were resolved using the method of Pagel (1992).

Because the morphological and body mass data did not belong to the same individuals, and even the number of individuals weighed varied among species (range = 1–113 subjects), we assessed the robustness of our analyses by increasing or decreasing by 10% the body mass and tail measures assigned to each species. Because we have a complete set of data for 39 species of woodcreepers and 54 species of furnariids, the theoretical number of possible matrices is about 3×10^{23} and 3.3×10^{32}, respectively. Therefore, we only made a random subset of 10 additional data matrices for each group like the ones depicted in the Appendices, and repeated the comparative analyses. All statistical tests were performed on the log-transformed values of the original variables.

RESULTS

Scatterplots of tail variables versus body mass showed that woodcreepers have relatively longer tails with wider rachises than Neotropical ovenbirds of comparable size (Fig. 3). Tail length increased with body mass in woodcreepers (least-squares linear regression, $\beta = 0.25$, $F_{1,37} = 56.5$, $P < 0.001$), but not in Neotropical ovenbirds ($\beta < 0.01$, $F_{1,52} = 0.01$, $P > 0.9$, Table 1). In addition, rachis width at the tip increased markedly with body mass in woodcreepers ($\beta = 0.37$, $F_{1,37} = 40.5$, $P < 0.001$), but only slightly in Neotropical ovenbirds ($\beta = 0.14$, $F_{1,52} = 4.9$, $P < 0.05$). Rachis width at the base varied positively with body mass in both groups ($\beta = 0.37$,

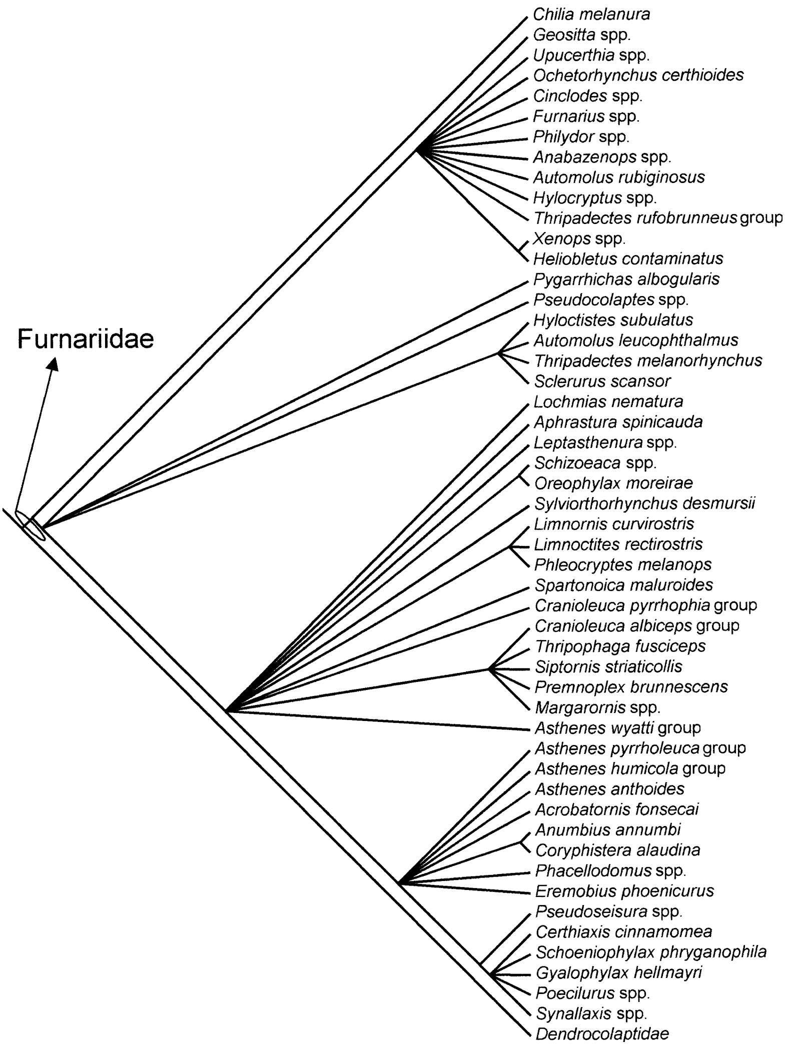

FIGURE 2. Phylogenetic hypothesis about the relationship among Neotropical ovenbirds (family Furnariidae) used in the independent-contrasts analysis. *Heliobletus contaminatus* is considered related to the genus *Xenops* (Ridgely and Tudor 1994). After Zyskowski and Prum (1999). Family Dendrocolaptidae, at the bottom of the tree, is the sister group of Neotropical ovenbirds.

$F_{1,37} = 124.5$, $P < 0.001$, and $\beta = 0.19$, $F_{1,52} = 28.1$, $P < 0.001$, for woodcreepers and Neotropical ovenbirds, respectively), but the slopes of the regressions differed significantly (their 95% CI did not overlap). It is interesting to note that in woodcreepers the slopes of the regressions between tail variables and body mass did not differ from the relationships required to maintain geometric similarity (i.e., showed isometry). In contrast, Neotropical ovenbirds showed a negative allometry for rachis width at the tip and at the base (Table 1). Rachis width at the base and at the tip varied isometrically with tail length in woodcreepers ($\beta = 0.87$, $F_{1,37} = 42.1$, $P < 0.001$; $\beta = 1.12$, $F_{1,37} = 37.3$, $P < 0.001$, respectively), but only rachis width at the base showed a significant negative allometry with tail length in Neotropical ovenbirds ($\beta = 0.57$, $F_{1,52} = 48.6$, $P < 0.001$, Table 2). However, this description should be taken with caution because it assumes that species are independent points of comparison.

Because the results of the comparative analyses of independent contrasts were similar for both models of character evolution, we present those obtained under the punctuated model (with comments on results from the random model analyses when appropriate). We found that tail length contrasts were positively related to body mass contrasts in woodcreepers ($\beta = 0.31$, $F_{1,24} = 23.9$, $P < 0.001$). In Neotropical ovenbirds this was evident under the random model ($\beta = 0.19$, $F_{1,21} = 8.3$, $P < 0.01$), but not under the punctuated model ($\beta = 0.05$, $F_{1,21} = 0.6$, $P > 0.4$). Contrasts of the rachis width at the tip and at the base of the rectrix also showed significant regressions with body mass contrasts in woodcreepers ($\beta = 0.33$, $F_{1,24} = 14.7$, $P < 0.001$; $\beta = 0.35$, $F_{1,24} = 25.3$, $P < 0.001$, respectively). Rachis width at the base and at the tip varied with body mass in Neotropical ovenbirds ($\beta = 0.21$, $F_{1,21} = 20.6$, $P < 0.001$; $\beta = 0.24$, $F_{1,21} = 5{,}9$, $P < 0.03$, respectively). We assessed the robustness of these results by running the independent contrast tests using 10 replicates of the data matrix for both woodcreepers and Neotropical ovenbirds. All 120 regressions (2 families × 3 variables × 10 replicates × 2 modes of character evolution) were positive, and in 50 and 33 out of 60 tests the slope was significant for woodcreepers and Neotropical ovenbirds, respectively. Independent-contrasts analyses also showed that tail variables in woodcreepers change isometrically and with higher scaling factors than in Neotropical ovenbirds (Table 1).

Rachis width at the tip and at the base also showed significant relationships with tail length in woodcreepers ($\beta = 0.76$, $F_{1,24} = 14.7$, $P < 0.001$; $\beta = 0.57$, $F_{1,24} = 17.4$, $P < 0.001$, respectively). In contrast, Neotropical ovenbirds showed a positive relationship between rachis width at the base and tail length ($\beta = 0.59$, $F_{1,23} = 41.9$, $P < 0.001$), but not between rachis width at the tip and tail length ($\beta = 0.01$, $F_{1,23} < 1$, $P > 0.9$, Table 2).

Robustness analysis indicated that all the replicates of the independent-contrasts analysis showed a significant excess of positive contrasts of rachis width at the base and at the tip associated to positive contrast of tail length in woodcreepers. When Neotropical ovenbirds' contrasts of rachis width at the base and at the tip were considered, 20 and 8 out of 20 replicates showed a positive and significant relationship to contrasts of tail length, respectively. These results confirm our previous findings that the structure

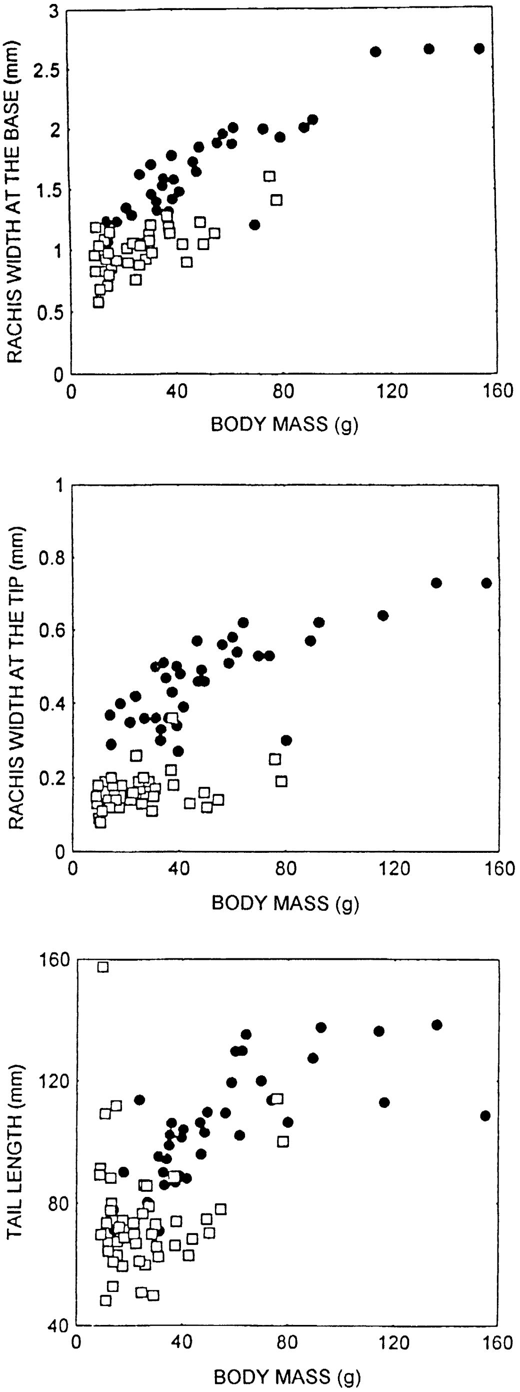

FIGURE 3. Scatterplots of tail variables versus body mass. Filled circles correspond to woodcreeper species, and unfilled squares correspond to Neotropical ovenbirds.

TABLE 1. Least-squares linear regressions for the scaling relationships between tail variables and body mass (both log-transformed). All-species analysis was conducted for 39 dendrocolaptid and 54 furnariid species for which all data were available. Independent-contrasts analysis compared only sister species pairs, assuming a punctuated model of character evolution, and included all species in the Appendices for which all data were available. For comparison, the slope of the predicted relationship among tail variables and body mass, based on geometric similarity (isometry), is given in the last column.

Family	Comparison	All-species analysis		Independent-contrasts analysis[a]	Prediction according to geometric similarity β
		Intercept	β ± 95% CI	β ± 95% CI	
Dendrocolaptidae	TLENGTH[b] vs. body mass	1.59	0.25 ± 0.08	0.31 ± 0.13	0.33
	BASEWIDTH[c] vs. body mass	–0.38	0.37 ± 0.04	0.35 ± 0.09	0.33
	TIPWIDTH[d] vs. body mass	–0.96	0.37 ± 0.12	0.33 ± 0.18	0.33
Furnariidae	TLENGTH[b] vs. body mass	1.86	0.01 ± 0.11	0.05 ± 0.15	0.33
	BASEWIDTH[c] vs. body mass	–0.27	0.19 ± 0.07	0.21 ± 0.10	0.33
	TIPWIDTH[d] vs. body mass	–1.00	0.14 ± 0.13	0.24 ± 0.21	0.33

[a] Regression calculated on standardized contrasts of the corresponding variables, with the regression line forced to pass through the origin.

[b] Tail length.

[c] The width of the rachis at the base of the medial rectrix.

[d] The width of the rachis at the tip of the medial rectrix.

of the rachis tip is related to the tail length in scansorial birds, but not in nonscansorial ones.

DISCUSSION

Most of the recent work on feather structure and flexural stiffness has focused on primary flight feathers (Ennos et al. 1995, Worcester 1996, Corning and Biewener 1998) rather than on feathers modified for body support. Primary feathers are attached to bones of the manus, but their distal ends remain free to bend. Thus, they are analyzed as cantilever beams subjected to normal bending forces. In contrast, tail feathers of scansorial birds are fixed at both ends and subjected to axial loads. In other words, in contrast to primaries and tail feathers of nonscansorial birds, the rectrix rachises in scansorial species should be equivalent to a column designed to avoid compressive collapse and buckling failure. Our study represents the first comparative investigation of the adaptive relationship between structure of the medial rectrix rachis and scansorial habit of a diverse assemblage of Neotropical passerines.

It is important to note that adaptive modifications of woodcreeper rachises for climbing cannot be demonstrated by simple comparisons with members of their nonscansorial sister group, furnariids, because species are not independent points of comparison (Felsenstein

TABLE 2. Least-squares linear regressions for the scaling relationships between rachis widths and tail length (both log-transformed). Details of the analyses as in Table 1, except that independent-contrasts analysis included all the species in the Appendices regardless of availability of body mass data.

Family	Comparison	All-species analysis		Independent-contrasts analysis[a]	Prediction according to geometric similarity β
		Intercept	β ± 95% CI	β ± 95% CI	
Dendrocolaptidae	BASEWIDTH[b] vs. TLENGTH[c]	–1.52	0.87 ± 0.28	0.57 ± 0.29	1.00
	TIPWIDTH[d] vs. TLENGTH[c]	–2.59	1.12 ± 0.37	0.76 ± 0.41	1.00
Furnariidae	BASEWIDTH[b] vs. TLENGTH[c]	–1.07	0.57 ± 0.16	0.59 ± 0.19	1.00
	TIPWIDTH[d] vs. TLENGTH[c]	–0.97	0.08 ± 0.34	0.01 ± 0.50	1.00

[a] Regression calculated on standardized contrasts of the corresponding variables, with the regression line forced to pass through the origin.

[b] The width of the rachis at the base of the medial rectrix.

[c] Tail length.

[d] The width of the rachis at the tip of the medial rectrix.

1985). Higher-node comparison between common ancestors of both families cannot solve the problem because our analyses suggest (under both random and punctuated models of character evolution) that the common ancestor of all woodcreepers probably had a higher body mass and longer and wider tail rachises compared to that of the furnariids. Therefore, we cannot definitively conclude that wider tail rachises of woodcreepers are associated with improved body support and are not a byproduct of the evolution of body size differences. In order to overcome this problem, a crucial point of our demonstration about the adaptive modification of the woodcreeper's tail is the inclusion of within-group morphometric variation in the analyses: we looked at the slopes of the regressions between tail variables and body size among woodcreeper species. These scaling factors are independent of body size and can be compared with those of the furnariids, in order to control for alternative causes.

In particular, we found that the woodcreepers have wider rachises than Neotropical ovenbirds of comparable size. In addition, the slopes of the regressions between tail variables and body size were higher in woodcreepers than in Neotropical ovenbirds. These patterns were present even after controlling for interspecific differences in body mass and phylogeny, and show the existence of important differences in tail design between the two groups. Such differences are consistent with the idea that the structure of the rachis in woodcreepers is adapted to support body weight (i.e., it has been adaptively modified for climbing), because wider rachises can support higher axial loads before crushing and buckling. Moreover, in woodcreepers rachis widths at the tip and at the base were positively related to tail length, as we expected for an axial-loaded structure designed to avoid buckling. In contrast, Neotropical ovenbirds showed that only rachis width at the base was positively associated with tail length, as predicted for a feather experiencing loading regimes analogous to cantilever beam structures.

Ideally, our study should have been carried out using body mass and tail data from the same birds. Unfortunately, due to the fact that most (old) skin specimens were not weighed, this goal is beyond the limit of our data. Additionally, interindividual and geographic variation in body size and tail variables would be needed. We made an effort to include these mostly unknown factors by independently varying the body mass and tail characteristics by ±10%. This procedure did not lead to changes in the results, even though we made 10 replicates of our original matrix for both woodcreepers and Neotropical ovenbirds.

In woodcreepers, the finding of an isometric relationship between TIPWIDTH and BASEWIDTH with body mass is quite unexpected because a positive allometry may be necessary to maintain a functional (mechanical) equivalence in a structure subjected to the loading regime of a column. Assuming isometry, the cross-sectional area of the feather rachis will increase in relation to the square of the radius, but body mass scales with the cube of the radius making the rachis more susceptible to a crushing failure. In addition, the flexural stiffness of the rachis scales in proportion to the fourth power of the radius, thus growing faster than body mass (Vogel 1988). In spite of this, bigger rachises are weaker because they have to support an increased body mass, and the threshold of forces that the rachis can tolerate before failing by Euler buckling decrease in relation to the square of tail length. An interesting question is if longer tails are more susceptible to buckling failure, why do not woodcreepers shorten their tails, instead of reinforcing their rachis? A possible response is that long tails are advantageous for scansorial birds. It has been proposed that increased tail length lessens the impact of gravity in pulling the bird outward from a vertical surface (Stolpe 1932), reducing energy expenditure (Jackson 1971). This is a consequence of an inverse relationship between tail length (all else being equal) and the subtended angle between the tail and the vertical. This means that a greater proportion of body weight is transmitted to the tail, leaving a small component of force pulling the bird away from the trunk (but see Richardson 1942, Winkler and Bock 1976). Perhaps this can account for the finding that tail length scaled isometrically in woodcreepers, but did not vary at all with body mass in Neotropical ovenbirds.

Finally, some woodcreeper species such as *Sittasomus griseicapillus*, *Lepidocolaptes squamatus*, and *L. fuscus* show strongly curved tips of the rachises of rectrices. The White-throated Treerunner (*Pygarrhichas albogularis*), one of the few scansorial furnariids, has the same kind of modification. This trait decreases the angle between the base of the tail and the vertical. In other words, distally curved rectrices may be able to bear loads commensurate with species with much longer tails (Richardson 1942). We suspect that rachis curvature has an important adaptive consequence for these birds ensuring that tails buckle dorsally when loaded axially. In turn, this would tend to maximize its body support function by bringing the weight of the body directly over the tail, but requires a specially modified rachis at the point of curvature where most of the stress is concentrated.

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APPENDIX 1. Database used in the comparative analysis of the relationship between body mass and the structure of the medial rectrix rachis of the family Dendrocolaptidae. Values of medial rectrix variables are means ± SD. Only one rectrix rachis per individual was measured.

Species (number of individuals)	TLENGTH[a] (mm)	TIPWIDTH[a] (mm)	BASEWIDTH[a] (mm)	Body mass[b] (g)	Phylogenetic position[c]
Curve-billed Scythebill (5) *Campylorhamphus procurvoides*	90.0 ± 5.3	0.30 ± 0.05	1.40 ± 0.01	33.0	BBBBBBBBJBC
Brown-billed Scythebill (5) *Campylorhamphus pusillus*	101.4 ± 5.9	0.27 ± 0.08	1.58 ± 0.05	39.6	BBBBBBBBJBB
Red-billed Scythebill (3) *Campylorhamphus trochilirostris*	89.7 ± 4.2	0.34 ± 0.08	1.78 ± 0.12	39.1	BBBBBBBBJBA
Long-tailed Woodcreeper (5) *Deconychura longicauda*	113.8 ± 2.6	0.42 ± 0.02	1.29 ± 0.20	23.8	BBBBBA
Spot-throated Woodcreeper (5) *Deconychura stictolaema*	90.2 ± 5.6	0.40 ± 0.01	1.24 ± 0.05	18.1	BBBBA
Cinnamon-throated Woodcreeper (5) *Dendrexetastes rufigula*	120.0 ± 4.6	0.53 ± 0.05	1.89 ± 0.16	70.0	BBBBBBBBJA
Tawny-winged Woodcreeper (5) *Dendrocincla anabatina*	86.8 ± 5.4	0.43 ± 0.03	1.32 ± 0.11	37.4	BBBABB
Tyrannine Woodcreeper (5) *Dendrocincla tyrannina*	129.6 ± 2.3	0.58 ± 0.01	1.87 ± 0.03	60.2	BBBABA
Barred Woodcreeper (5) *Dendrocolaptes certhia*	135.2 ± 6.8	0.62 ± 0.01	2.00 ± 0.08	64.2	BBBBBBBBLBBBA
Concolor Woodcreeper (5) *Dendrocolaptes concolor*	129.8 ± 3.0	0.53 ± 0.03	2.01 ± 0.09	62.7	BBBBBBBBLBBBC
Hoffmanns' Woodcreeper (4) *Dendrocolaptes hoffmannsi*	127.3 ± 3.4	0.57 ± 0.03	2.01 ± 0.09	89.0	BBBBBBBBLBBBB
Black-banded Woodcreeper (3) *Dendrocolaptes picumnus*	113.6 ± 0.6	0.53 ± 0.03	2.00 ± 0.06	73.8	BBBBBBBBLBBAB
Planalto Woodcreeper (3) *Dendrocolaptes platyrostris*	102.0 ± 7.8	0.54 ± 0.04	1.88 ± 0.25	61.9	BBBBBBBBLBBAA
Scimitar-billed Woodcreeper (3) *Drymornis bridgesii*	106.3 ± 10.5	0.30 ± 0.07	1.93 ± 0.07	80.0	BA
Wedge-billed Woodcreeper (5) *Glyphorhynchus spirurus*	71.4 ± 2.2	0.29 ± 0.01	1.07 ± 0.10	14.6	BBBBBBBA
Red-billed Woodcreeper (3) *Hylexetastes perrotii*	136.3 ± 2.1	1.11 ± 0.41	2.66 ± 0.09	114.0	BBBBBBBBLBAA

APPENDIX 1. Continued.

Species (number of individuals)	TLENGTH[a] (mm)	TIPWIDTH[a] (mm)	BASEWIDTH[a] (mm)	Body mass[b] (g)	Phylogenetic position[c]
Spot-crowned Woodcreeper (5) *Lepidocolaptes affinis*	102.2 ± 1.9	0.37 ± 0.03	1.53 ± 0.08	35.4	BBBBBBBBKA
Lineated Woodcreeper (5) *Lepidocolaptes albolineatus*	86.0 ± 2.9	0.33 ± 0.01	1.33 ± 0.09	33.3	BBBBBBBBKBBA
Narrow-billed Woodcreeper (3) *Lepidocolaptes angustirostris*	71.0 ± 1.7	0.36 ± 0.20	1.71 ± 0.20	31.3	BBBBBBBBKBBBB
Lesser Woodcreeper (3) *Lepidocolaptes fuscus*	70.3 ± 2.5	0.35 ± 0.03	1.35 ± 0.02	21.8	BBBBBBBBH
White-striped Woodcreeper (5) *Lepidocolaptes leucogaster*	106.0 ± 3.7	0.36 ± 0.01	1.59 ± 0.08	36.0	BBBBBBBBKBBBA
Scaled Woodcreeper (3) *Lepidocolaptes squamatus*	80.3 ± 1.5	0.36 ± 0.04	1.63 ± 0.10	27.0	BBBBBBBBKBA
Long-billed Woodcreeper (5) *Nasica longirostris*	137.4 ± 6.5	0.62 ± 0.05	2.07 ± 0.07	92.0	BBA
Olivaceous Woodcreeper (3) *Sittasomus griseicapillus*	78.0 ± 6.9	0.37 ± 0.08	1.24 ± 0.15	14.3	BBBBBBA
White-throated Woodcreeper (3) *Xiphocolaptes albicollis*	113.0 ± 1.7	0.64 ± 0.07	2.63 ± 0.14	116.0	BBBBBBBBLBABBB
Great Rufous Woodcreeper (3) *Xiphocolaptes major*	108.7 ± 9.5	0.73 ± 0.06	2.65 ± 0.15	155.0	BBBBBBBBLBABBA
Strong-billed Woodcreeper (5) *Xiphocolaptes promeropirhynchus*	138.4 ± 6.5	0.73 ± 0.02	2.65 ± 0.04	136.0	BBBBBBBBLBABA
Elegant Woodcreeper (5) *Xiphorhynchus elegans*	94.4 ± 3.2	0.51 ± 0.02	1.57 ± 0.03	34.1	BBBBBBBBB
Spotted Woodcreeper (5) *Xiphorhynchus erythropygius*	106.2 ± 6.2	0.57 ± 0.11	1.72 ± 0.03	46.8	BBBBBBBBLA
Dusky-billed Woodcreeper (5) *Xiphorhynchus eytoni*	119.4 ± 9.6	0.51 ± 0.06	1.96 ± 0.08	58.8	BBBBBBBBC
Ivory-billed Woodcreeper (5) *Xiphorhynchus flavigaster*	95.8 ± 5.1	0.46 ± 0.06	1.73 ± 0.04	47.2	BBBBBBBBD
Buff-throated Woodcreeper (5) *Xiphorhynchus guttatus*	109.6 ± 5.3	1.46 ± 0.02	1.85 ± 0.10	49.5	BBBBBBBBG

APPENDIX 1. Continued.

Species (number of individuals)	TLENGTH[a] (mm)	TIPWIDTH[a] (mm)	BASEWIDTH[a] (mm)	Body mass[b] (g)	Phylogenetic position[c]
Black-striped Woodcreeper (5) *Xiphorhynchus lachrymosus*	109.4 ± 10.0	0.56 ± 0.03	1.89 ± 0.18	56.4	BBBBBBBBIAB
Striped Woodcreeper (5) *Xiphorhynchus obsoletus*	88.8 ± 4.7	0.50 ± 0.08	1.42 ± 0.05	39.0	BBBBBBBBIAA
Ocellated Woodcreeper (5) *Xiphorhynchus ocellatus*	98.8 ± 5.4	0.47 ± 0.03	1.43 ± 0.10	35.1	BBBBBBBBIC
Chestnut-rumped Woodcreeper (5) *Xiphorhynchus pardalotus*	104.0 ± 2.5	0.48 ± 0.05	1.61 ± 0.06	40.4	BBBBBBBBF
Straight-billed Woodcreeper (5) *Xiphorhynchus picus*	88.0 ± 2.3	0.39 ± 0.03	1.48 ± 0.07	41.6	BBBBBBBBA
Spix's Woodcreeper (5) *Xiphorhynchus spixii*	95.2 ± 4.0	0.50 ± 0.02	1.46 ± 0.05	31.2	BBBBBBBBIB
Olive-backed Woodcreeper (5) *Xiphorhynchus triangularis*	103.0 ± 2.6	0.49 ± 0.01	1.65 ± 0.01	48.4	BBBBBBBBE

[a] Tail variables are the length of the tail (TLENGTH) and the width of the rachis at the base (BASEWIDTH) and the tip (TIPWIDTH) of the medial rectrix.

[b] Dunning 1993.

[c] After Raikow 1994, and according to the convention of Purvis and Rambaut 1995. Starting from the root, at each node of the phylogeny a letter is assigned to each daughter branch, creating a unique code for each species.

APPENDIX 2. Database used in the comparative analysis of the relationship between body mass and the structure of the medial rectrix rachis of the family Furnariidae. Values of medial rectrix variables are means ± SD of up to three males. Only one medial rectrix rachis was measured per individual.

Species (number of individuals)	TLENGTH[a] (mm)	TIPWIDTH[a] (mm)	BASEWIDTH[a] (mm)	Body mass[b] (g)	Phylogenetic position[c]
Firewood-Gatherer (3) *Anumbius annumbi*	74.0 ± 4.6	0.18 ± 0.01	1.14 ± 0.02	37.8	AFKEA
Thorn-tailed Rayadito (3) *Aphrastura spinicauda*	73.7 ± 3.5	0.15 ± 0.01	0.97 ± 0.04	11.6	AFB
Austral Canastero (3) *Asthenes anthoides*	68.7 ± 2.1	0.13 ± 0.01	0.91 ± 0.03	—	AFKC
Short-billed Canastero (3) *Asthenes baeri*	67.6 ± 5.1	0.12 ± 0.02	0.86 ± 0.07	15.9	AFKBA
Rusty-vented Canastero (3) *Asthenes dorbignyi*	73.0 ± 3.6	0.13 ± 0.03	0.90 ± 0.09	—	AFKBB
Hudson's Canastero (3) *Asthenes hudsoni*	81.0 ± 6.1	0.18 ± 0.04	1.11 ± 0.08	—	AFJA
Dusky-tailed Canastero (3) *Asthenes humicola*	73.7 ± 1.5	0.15 ± 0.02	1.02 ± 0.03	21.8	AFKBC
Cordilleran Canastero (3) *Asthenes modesta*	72.3 ± 4.7	0.14 ± 0.01	0.89 ± 0.04	16.6	AFKAA
Patagonian Canastero (3) *Asthenes patagonica*	68.3 ± 4.2	0.12 ± 0.03	0.90 ± 0.01	—	AFKBD
Sharp-billed Canastero (3) *Asthenes pyrrholeuca*	80.0 ± 1.7	0.14 ± 0.02	0.93 ± 0.04	13.6	AFKAB
Puna Canastero (3) *Asthenes sclateri*	94.3 ± 1.5	0.13 ± 0.03	1.12 ± 0.05	—	AFJB
Steinbach's Canastero (2) *Asthenes steinbachi*	74.5 ± 2.1	0.12 ± 0.02	0.87 ± 0.04	17.8	AFKBE
White-eyed Foliage-Gleaner (1) *Automolus leucophthalmus*	79.0	0.15	1.06	27.5	AEB
Yellow-chinned Spinetail (3) *Certhiaxis cinnamomea*	63.3 ± 1.2	0.16 ± 0.03	0.86 ± 0.08	15.8	AFKHBA
Blackish Cinclodes (1) *Cinclodes antarcticus*	80.0	0.21	1.22	—	ABDA
White-winged Cinclodes (3) *Cinclodes atacamensis*	78.0 ± 1.7	0.14 ± 0.02	1.14 ± 0.06	54.7	ABDB
Cordoba Cinclodes (1) *Cinclodes comechingonus*	71.0	0.12	0.73	—	ABDC
Bar-winged Cinclodes (3) *Cinclodes fuscus*	68.3 ± 2.3	0.13 ± 0.02	0.90 ± 0.06	44.0	ABDD
Gray-flanked Cinclodes (3) *Cinclodes oustaleti*	66.0 ± 3.0	0.15 ± 0.05	0.95 ± 0.08	30.5	ABDE
Dark-bellied Cinclodes (3) *Cinclodes patagonicus*	73.3 ± 2.5	0.12 ± 0.06	1.21 ± 0.02	30.7	ABDF
Lark-like Brushrunner (3) *Coryphistera alaudina*	62.7 ± 1.5	0.17 ± 0.02	0.98 ± 0.08	31.1	AFKEB

APPENDIX 2. Continued.

Species (number of individuals)	TLENGTH[a] (mm)	TIPWIDTH[a] (mm)	BASEWIDTH[a] (mm)	Body mass[b] (g)	Phylogenetic position[c]
Olive Spinetail (2) *Cranioleuca obsoleta*	64.5 ± 3.5	0.15 ± 0.05	0.75 ± 0.08	12.3	AFHB
Stripe-crowned Spinetail (3) *Cranioleuca pyrrhophia*	72.0 ± 5.2	0.11 ± 0.01	0.80 ± 0.04	14.9	AFHAA
Sulphur-bearded Spinetail (3) *Cranioleuca sulphurifera*	80.7 ± 3.1	0.17 ± 0.02	0.89 ± 0.07	—	AFHAB
Band-tailed Earthcreeper (3) *Eremobius phoenicurus*	73.3 ± 1.2	0.11 ± 0.01	1.13 ± 0.03	30.0	AFKG
Crested Hornero (3) *Furnarius cristatus*	60.0 ± 1.0	0.13 ± 0.03	0.88 ± 0.03	26.2	ABEA
Rufous Hornero (3) *Furnarius rufus*	70.3 ± 3.2	0.12 ± 0.02	1.05 ± 0.05	50.4	ABEB
Short-billed Miner (3) *Geositta antarctica*	54.7 ± 3.2	0.17 ± 0.02	0.98 ± 0.10	—	ABAA
Common Miner (3) *Geositta cunicularia*	50.0 ± 1.0	0.15 ± 0.03	0.89 ± 0.11	29.3	ABAB
Creamy-rumped Miner (1) *Geositta isabellina*	63.0	0.19	1.10	—	ABAC
Puna Miner (3) *Geositta punensis*	48.7 ± 4.5	0.17 ± 0.04	0.83 ± 0.01	—	ABAD
Rufous-banded Miner (3) *Geositta rufipennis*	63.0 ± 5.0	0.14 ± 0.02	1.05 ± 0.05	42.5	ABAE
Slender-billed Miner (3) *Geositta tenuirostris*	57.0 ± 1.7	0.14 ± 0.01	1.03 ± 0.03	—	ABAF
Sharp-billed Treehunter (2) *Heliobletus contaminatus*	53.0 ± 1.4	0.12 ± 0.01	0.71 ± 0.01	14.2	ABKC
Plain-mantled Tit-Spinetail (3) *Leptasthenura aegithaloides*	91.3 ± 4.7	0.13 ± 0.05	0.96 ± 0.04	9.3	AFCA
Brown-capped Tit-Spinetail (3) *Leptasthenura fuliginiceps*	92.0 ± 3.5	0.13 ± 0.07	0.98 ± 0.06	9.8	AFCB
Tufted Tit-Spinetail (3) *Leptasthenura platensis*	89.3 ± 6.5	0.15 ± 0.06	0.97 ± 0.03	8.9	AFCC
Araucaria Tit-Spinetail (3) *Leptasthenura setaria*	109.3 ± 6.4	0.12 ± 0.02	1.04 ± 0.05	11.0	AFCD
Straight-billed Reedhaunter (2) *Limnoctites rectirostris*	69.0 ± 0.0	0.18 ± 0.01	0.95 ± 0.07	18.5	AFFB
Curve-billed Reedhaunter (3) *Limnornis curvirostris*	70.0 ± 2.7	0.19 ± 0.04	0.93 ± 0.04	28.6	AFFA
Sharp-tailed Streamcreeper (2) *Lochmias nematura*	51.0 ± 2.8	0.19 ± 0.01	0.76 ± 0.00	24.8	AFA
Chaco Earthcreeper (3) *Ochetorhynchus certhioides*	66.0 ± 3.6	0.12 ± 0.02	0.99 ± 0.05	—	ABC
Canebrake Groundcreeper (2) *Phacellodomus dendrocolaptoides*	97.0 ± 4.2	0.33 ± 0.05	1.48 ± 0.03	—	AFKFA

APPENDIX 2. Continued.

Species (number of individuals)	TLENGTH[a] (mm)	TIPWIDTH[a] (mm)	BASEWIDTH[a] (mm)	Body mass[b] (g)	Phylogenetic position[c]
Greater Thornbird (3)					
Phacellodomus ruber	88.7 ± 7.4	0.22 ± 0.02	1.28 ± 0.06	36.9	AFKFB
Common Thornbird (3)					
Phacellodomus rufifrons	76.7 ± 3.5	0.17 ± 0.03	1.06 ± 0.08	25.2	AFKFC
Little Thornbird (3)					
Phacellodomus sibilatrix	59.7 ± 3.2	0.12 ± 0.02	0.92 ± 0.04	17.8	AFKFD
Streak-fronted Thornbird (3)					
Phacellodomus striaticeps	71.0 ± 3.5	0.16 ± 0.03	0.98 ± 0.10	—	AFKFE
Freckle-breasted Thornbird (3)					
Phacellodomus striaticollis	86.0 ± 2.7	0.16 ± 0.02	1.08 ± 0.10	25.7	AFKFF
Black-capped Foliage-Gleaner (1)					
Philydor atricapillus	67.0	0.16	0.88	22.8	ABFA
Ochre-breasted Foliage-Gleaner (3)					
Philydor lichtensteini	70.0 ± 1.7	0.14 ± 0.02	0.90 ± 0.04	22.1	ABFB
Buff-fronted Foliage-Gleaner (3)					
Philydor rufus	85.7 ± 1.5	0.20 ± 0.05	1.04 ± 0.05	26.7	ABFC
Wren-like Rushbird (3)					
Phleocryptes melanops	54.7 ± 2.5	0.13 ± 0.02	0.72 ± 0.02	15.0	AFFC
White-throated Cacholote (3)					
Pseudoseisura gutturalis	100.0 ± 3.6	0.19 ± 0.05	1.41 ± 0.03	78.2	AFKHAA
Brown Cacholote (3)					
Pseudoseisura lophotes	114.0 ± 7.6	0.25 ± 0.06	1.61 ± 0.07	75.9	AFKHAB
White-throated Treerunner (3)					
Pygarrhichas albogularis	58.0 ± 3.6	0.26 ± 0.04	1.06 ± 0.04	24.0	AC
Chotoy Spinetail (3)					
Schoeniophylax phryganophila	112.0 ± 9.0	0.18 ± 0.03	1.15 ± 0.08	15.2	AFKHBB
Rufous-breasted Leaftosser (3)					
Sclerurus scansor	66.3 ± 2.08	0.36 ± 0.03	1.19 ± 0.03	37.4	AED
Bay-capped Wren-Spinetail (3)					
Spartonoica maluroides	70.0 ± 4.4	0.18 ± 0.02	0.83 ± 0.06	9.5	AFG
Des Murs' Wiretail (3)					
Sylviorthorhynchus desmursii	157.5 ± 6.4	0.09 ± 0.01	1.19 ± 0.05	9.9	AFE
Pale-breasted Spinetail (3)					
Synallaxis albescens	69.0 ± 1.0	0.19 ± 0.01	0.94 ± 0.06	12.1	AFKHBEA
Gray-bellied Spinetail (2)					
Synallaxis cinerascens	61.0 ± 1.4	0.20 ± 0.00	0.84 ± 0.03	14.2	AFKHBEB
Sooty-fronted Spinetail (3)					
Synallaxis frontalis	80.0 ± 1.7	0.20 ± 0.02	0.98 ± 0.06	14.7	AFKHBEC
Rufous-capped Spinetail (3)					
Synallaxis ruficapilla	77.7 ± 4.0	0.18 ± 0.03	1.00 ± 0.08	13.2	AFKHBED
Ochre-cheeked Spinetail (3)					
Synallaxis scutatus	67.3 ± 3.2	0.19 ± 0.02	0.83 ± 0.02	12.3	AFKHBEE
Spix's Spinetail (3)					
Synallaxis spixi	88.3 ± 6.4	0.20 ± 0.02	1.09 ± 0.02	13.2	AFKHBEF

APPENDIX 2. Continued.

Species (number of individuals)	TLENGTH[a] (mm)	TIPWIDTH[a] (mm)	BASEWIDTH[a] (mm)	Body mass[b] (g)	Phylogenetic position[c]
Buff-browed Spinetail (3) *Synallaxis superciliosa*	88.3 ± 4.5	0.20 ± 0.03	0.92 ± 0.05	—	AFKHBEG
Rock Earthcreeper (2) *Upucerthia andeacola*	77.0 ± 8.5	0.18 ± 0.05	1.08 ± 0.25	—	ABBA
Scale-throated Earthcreeper (3) *Upucerthia dumetaria*	74.4 ± 2.1	0.16 ± 0.03	1.23 ± 0.10	49.3	ABBB
Straight-billed Earthcreeper (3) *Upucerthia ruficauda*	73.7 ± 2.1	0.11 ± 0.01	1.08 ± 0.08	30.1	ABBC
Buff-breasted Earthcreeper (3) *Upucerthia validirostris*	83.3 ± 3.1	0.17 ± 0.04	1.07 ± 0.04	—	ABBD
Plain Xenops (3) *Xenops minutus*	49.7 ± 2.5	0.08 ± 0.01	0.58 ± 0.07	10.6	ABKA
Streaked Xenops (3) *Xenops rutilans*	48.3 ± 2.5	0.11 ± 0.03	0.68 ± 0.04	11.3	ABKB

[a] Tail variables are the length of the tail (TLENGTH) and the width of the rachis at the base (BASEWIDTH) and the tip (TIPWIDTH) of the medial rectrix.

[b] Dunning 1993.

[c] After Zyskowski and Prum 1999, and according to the convention of Purvis and Rambaut 1995 (see Appendix 1).