

INTRASPECIFIC VARIATION AND EVOLUTIONARY REDUCTION OF TENDON OSSIFICATION IN *DENDROCINCLA* WOODCREEPERS¹

ANTHONY H. BLEDSOE AND ROBERT J. RAIKOW

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, and Section of Birds, The Carnegie Museum of Natural History, Pittsburgh, PA 15213.
e-mail: bledsoe+@pitt.edu, ror6+@pitt.edu

LORETTA S. CROWELL

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260,
e-mail: lcrowell+@pitt.edu

Abstract. We compared levels of intraspecific variation in hindlimb tendon ossification and other hindlimb myological traits in the Tawny-winged Woodcreeper (*Dendrocincla anabatina*) with our previous data on the Barred Woodcreeper (*Dendrocolaptes certhia*) and the Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*). In *D. anabatina*, a member of a clade characterized by reduced tendon ossification, variation in tendon ossification was markedly greater than in other aspects of the hindlimb muscles, as were occurrences of bilateral variation and the number of individuals exhibiting atypical conditions. Variation in tendon ossification in *D. anabatina* is 5–10 times more frequent than in the other species, which have not experienced reduction in ossification. Tendon ossification in *D. anabatina*, and possibly in other *Dendrocincla* species, provides a rare example of extensive intraspecific variation in the hindlimb myology of passerines. The variant conditions in *D. anabatina* evolved within the *Dendrocincla* clade, either since *D. anabatina* and its sister group split, or as ancestral polymorphisms retained through speciation events. In either case, the available evidence does not support a role for directional selection in the process of evolutionary reduction in tendon ossification in *Dendrocincla*.

Key words: intraspecific variation, evolutionary reduction, tendon ossification, *Dendrocolapinae*, myology, phylogenetic analysis, directional selection.

INTRODUCTION

Comparative studies of avian hindlimb myology consistently have revealed low levels of intraspecific variation. Atypical conditions within species are rare, usually occurring in but a few percent of the total number of muscles represented in series of specimens (Raikow et al. 1993). For example, in passerines, extensive polymorphism has been reported only in three muscles in the Blue Jay (*Cyanocitta cristata*) and in one muscle (*M. flexor cruris lateralis*) in several species of tyrannid flycatchers (McKittrick 1986). Herein, we report an additional example of extensive intraspecific variation in passerine musculature, specifically in tendon ossification in the hindlimb of a series of the Tawny-winged Woodcreeper (*Dendrocincla anabatina*).

Woodcreepers (*Dendrocolapinae*) are unique among passerine birds in possessing extensive

ossification of the tendons of the hindlimb (Bledsoe et al. 1993, Raikow 1993). Among birds, only certain galliforms, gruids, and strigids are known to exhibit such extensive tendon ossification in the hindlimb (Vanden Berge and Storer 1995). Tendon ossification in woodcreeper hindlimbs appears to constitute an adaptation to resist the unusual forces placed on the toe and ankle flexors during prolonged, tail-braced scansorial postures (Bledsoe et al. 1993). Consistent with this interpretation are results for species in the woodcreeper genus *Dendrocincla*, which less frequently adopt scansorial postures. They have lost ossification in six of 19 tendon segments ossified in other woodcreepers (Bledsoe et al. 1993). The data of Bledsoe et al. (1993) also raise the possibility that *Dendrocincla* woodcreepers are unusually variable intraspecifically in tendon ossification. However, the number of specimens dissected in that study was too small to establish such a conclusion firmly.

Below, we present results for the Tawny-winged Woodcreeper (*Dendrocincla anabatina*) that indicate that this species is in fact highly

¹Received 1 May 1996. Accepted 13 November 1996.

variable in hindlimb tendon ossification. In addition, we place our results within the context of the growing body of information on the implications of intraspecific variation for phylogenetic studies of birds (Raikow et al. 1990, 1993, Rudge and Raikow 1992, Raikow 1993) and discuss the meaning of our results for understanding the evolutionary mechanisms involved in reduction and loss of hindlimb muscular traits in birds.

To provide a frame of reference for analyzing levels of variation, we compared levels of intraspecific variation in *D. anabatina* with those obtained previously for two non-*Dendrocincla* woodcreepers (Raikow 1993, Raikow et al. 1993). The basic design of the study contrasts levels of intraspecific variation between tendon ossification traits and other myological attributes within and between species of woodcreepers. We also compared the levels of variation observed within these species with those of other passerine species that do not show extensive tendon ossification. This approach makes it possible to specify whether an observed increase in intraspecific variation is restricted to the tendon ossification system. In addition, in association with previous phylogenetic work on the woodcreeper group as a whole (Raikow 1994), the study permits an analysis of the possible evolutionary origins of within-species variation in *D. anabatina*.

MATERIALS AND METHODS

SPECIMENS AND DISSECTION

We dissected bilaterally the hindlimb muscles of 10 specimens of *D. anabatina* from The Carnegie Museum of Natural History (specimen catalogue number and gender; m, male; f, female) collected from: Mexico, Quintana Roo (A904, m); Belize, Toledo (A3888, f; A4095, m; A4097, m; A4098, m); Belize, Cayo (A4359, m; A4361, m; A4380, f; A4381, m); Belize, Belize (A3813, m). Mean body masses (g) based on field measurements were: eight males, 36.6 (range, 32.8–41.5); two females, 32.1 (range, 30.0–34.2). Paynter (1955) listed a mean body mass for six females of 31.3 g. Locality of collection and other data important in assessing our results (see Discussion) are given below for previously dissected series of the Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*; Bledsoe et al. 1993, Raikow et al. 1993) and the

Barred Woodcreeper (*Dendrocolaptes certhia*; Raikow 1993). *X. flavigaster* (number of specimens and gender; m, male; f, female; na, not available), collected from: Belize, Toledo (five m, two f); Belize, Belize (one m, one f); Belize, Cayo (one f); Mexico, Veracruz (one f); Mexico, Oaxaca (one m); Mexico, Sinaloa (one m); Costa Rica (one m); Nicaragua (one f); site na (one m, three f). Mean body masses (g) based on field measurements were: six males, 47.1 (range, 43.8–51.5); four females, 42.0 (range, 38.4–46.0). Paynter (1955) listed a mean body mass for 12 females of 40.0 g (range, 35.0–44.1). *D. certhia* (number of specimens and gender; m, male; f, female; na, not available), collected from: Panama, Davian (two f); Peru (two m); Ecuador (one f); British Guiana (one f); site na (one f, one na). We did not obtain body masses for any of the *D. certhia* series. Dunning (1993) listed a mean body mass of 62.4 g (range, 52.7–73.9 g) for a series of 20 individuals (gender not determined).

The specimens were stained with an iodine solution (Bock and Shear 1972) and dissected under a dissecting stereomicroscope at magnifications of 6× to 25×. Drawings were made using a drawing tube attached to the microscope. A total of 620 individual muscles (31 muscles on each side of each of the 10 specimens) was assessed for ossification and variation. The muscles dissected and their abbreviations are: CF, M. caudofemoralis; EDL, M. extensor digitorum longus; EHL, M. extensor hallucis longus; FB, M. fibularis brevis; FCRL, M. flexor cruris lateralis; FCRM, M. flexor cruris medialis; FDL, M. flexor digitorum longus; FHL, M. flexor hallucis longus; FL, M. fibularis longus; FPD2, M. flexor perforatus digiti II; FPD3, M. flexor perforatus digiti III; FPD4, M. flexor perforatus digiti IV; FPPD2, M. flexor perforans et perforatus digiti II; FPPD3, M. flexor perforans et perforatus digiti III; FTEM, M. femorotibialis externus et medius; FTI, M. femorotibialis internus; GI, M. gastrocnemius pars intermedia; GL, M. gastrocnemius pars lateralis; GM, M. gastrocnemius pars medialis; ICR, M. iliotibialis cranialis; IF, M. iliofibularis; IFI, M. iliofemoralis internus; IL, M. iliotibialis lateralis; ISF, M. ischiofemoralis; ITCA, M. ilirotrochantericus caudalis; ITCRM, M. ilirotrochantericus cranialis et medius; OL, M. obturatorius lateralis; OM, M. obturatorius medialis; PIF, M. pubo-ischiofemoralis; PL, M. plantaris; TCR, M. tibialis cran-

ialis. One hindlimb muscle, *M. lumbricalis*, was not assessed because its minute size and tendency to consist of poorly-staining elastic fibers prevented consistent and confident anatomical assessment in *D. anabatina*. We used the anatomical nomenclature of Baumel et al. (1993).

Each muscle or muscle component was examined in all specimens at one time before proceeding to the next muscle or muscle component, so that direct comparisons could be made between specimens. We assessed variation both in tendon ossification (Table 1) and in myological traits other than tendon ossification. Tendons were classified into three groups. (1) "Fully ossified" tendons appeared extremely rigid, gray, and opaque, with a gritty surface texture and a clearly visible region of bony material. The "fully ossified" category is equivalent to the "ossified" category of Bledsoe et al. (1993). (2) "Slightly ossified" tendons appeared somewhat rigid, less gray and opaque, and have a smoother surface; no region of bony material is visible. In addition, manipulation of the tendon by moving forceps along its length and applying force perpendicular to its long axis revealed stiffness. (3) "Unossified" tendons appeared silvery and smooth, and were fully flexible under manipulation with forceps. The second author, in consultation with the other authors, scored tendons for ossification.

TERMS AND DATA ANALYSIS

For purposes of analysis, we termed the *typical condition* of a species as that which occurs in the majority of specimens, whereas a *variant* was defined as a condition that occurs in a minority of specimens. As noted by Raikow et al. (1993), this approach is inappropriate when variation is such that no typical state can be defined. We observed only one such instance. For the crural segment of the tendon of *M. flexor perforatus digiti II*, five specimens bilaterally had the proximal part of the segment fully ossified and the distal part unossified. Because other specimens possessed this configuration unilaterally, we chose to treat the condition observed bilaterally in the five specimens as the typical condition. As in previous work on myological variation (Raikow et al. 1990, 1993, Raikow 1993, 1994), minor differences of the sort that may constitute artifacts of preservation or dissection were not considered in assessing variation.

To tabulate variation, we used the approach described by Raikow et al. (1990), in which each cell of a matrix of specimen numbers by tendon-segment names (for tendon ossification) or muscle names (for variation other than in tendon ossification) is scored for the occurrence of a variant condition (see Table 2). In woodcreeper hindlimbs, including those of the *D. anabatina* series we dissected, tendon ossification is restricted to the tendons of insertion of crural muscles (see Bledsoe et al. 1993). Thus, to tabulate variation in tendon ossification, we used the tendon categories established by Bledsoe et al. (1993, Tables 1a and 1b) and, in addition, established two new categories to reflect proximo-distal variation within the crural segments of *Mm. flexor perforans et perforatus digiti III* (see Fig. 1) and *flexor perforatus digiti II* in *D. anabatina*. To tabulate variation in myological traits other than tendon ossification, we used muscle names as the categories for the matrix.

For tendon ossification and for other myological characters, a separate matrix of specimen numbers by tendon segments or muscle names was constructed. Each cell for which a typical condition was observed bilaterally was scored "T." "T" entries are designated by blanks in Table 2. When a single variant condition was present on both sides of a specimen, the cell was scored "B." When the right and left sides differed, the cell was scored "U." When damage precluded assessment, the cell was scored "d." Matrices also were constructed for variation in nonossification traits in the *D. anabatina* series and for the tendon-ossification variation described by Raikow (1993) in *D. certhia* and by Raikow et al. (1993) in *X. flavigaster*. These matrices are not presented here because so little variation was discovered. For nonossification variation in *D. certhia* and *X. flavigaster*, we based our calculations on the matrices published by Raikow (1993) and Raikow et al. (1993), respectively.

We calculated from the matrices the "percent variant" by adding the number of "U" entries to twice the number of "B" entries, dividing the resulting sum by twice the number of non-"d" cells, and multiplying the resulting quotient by 100. The "percent variant" therefore is the percentage of legs (among undamaged birds) exhibiting a variant condition; it is equivalent to what Raikow et al. (1993, Table 5) called the percentage of all individual muscles that are

TABLE 1. Hindlimb tendon ossification in *Dendrocincla anabatina*.^a [Table 1 continued on next page.]

Specimen	TCR	EDLC	EDLT	FL	FB	GL	PL	FPPD2C	FPPD2T	FPPD3C	FPPD3T	FPD2C
R A4380	+	±	±	+	+	-	-	-	±	± -	±	+ -
L	+	±	±	-	+	-	-	-	-	± -	±	± -
R A4098	+	±	+	-	+	-	-	-	±	± -	±	+ -
L	+	±	+	-	+	-	-	-	±	± -	±	+ -
R A3813	+	±	±	-	+	-	-	-	±	- -	±	± -
L	+	±	±	-	+	-	-	-	±	± -	±	± -
R A4381	+	+	±	+	+	+	-	-	±	± -	±	+ -
L	+	+	±	+	+	+	-	-	±	± -	±	+ -
R A3888	+	+	+	-	+	-	-	-	±	± -	±	+ -
L	+	+	+	-	+	-	-	-	±	± -	±	+ -
R A4359	+	±	±	-	+	-	-	-	±	± -	±	± -
L	+	+	±	-	+	-	-	-	±	± -	±	± -
R A904	+	+	+	-	+	-	-	-	±	- -	±	- -
L	+	?	+	-	+	-	-	-	±	- -	±	- -
R A4097	+	+	+	+	+	-	-	-	±	± -	±	+ -
L	+	+	+	-	+	-	-	-	±	± -	±	+ -
R A4095	+	+	+	±	+	-	-	-	±	+	±	+
L	+	+	+	+	+	-	-	-	±	+	±	+
R A4361	+	+	+	-	+	-	-	-	±	± -	±	+ -
L	+	+	+	-	+	-	-	-	±	± -	±	+ -

atypical. One "U" entry in Table 2 (FL in specimen A4095) actually represents the occurrence of different variant states on the right and left sides of the specimen; this was treated as a "B" entry in the "percent variant" calculation.

RESULTS

DESCRIPTIONS OF VARIATIONS IN TENDON OSSIFICATION IN *DENDROCINCLA ANABATINA*

The tendon of insertion of *M. extensor digitorum longus* crosses the intertarsal joint and thus has crural and tarsal components. Both parts varied between slightly and fully ossified, but neither was ever unossified. The typical condition for both components was full ossification, which occurred in the crural segment of 12 limbs in seven specimens and in the tarsal segment of 12 limbs in six specimens (Table 1).

In *M. fibularis longus*, the species-typical state was the absence of ossification, whereas variant states were the presence of a small bony splint, either slightly or fully ossified, in the tendon of insertion as the latter arose from the belly. The typical state occurred bilaterally in six specimens. In two specimens, one side lacked ossification and the other side was fully ossified. One specimen had full ossification bilaterally, and one specimen had one side fully ossified and the other slightly ossified (Table 1).

The tendon of insertion of *M. gastrocnemius pars lateralis* was unossified bilaterally in nine

of the 10 specimens; one specimen had atypical, full ossification on both sides (Table 1).

In *M. flexor perforans et perforatus digiti II*, the typical state was slight ossification of the tarsal component of the tendon of insertion. It occurred bilaterally in nine specimens and unilaterally in one; the other side of which was unossified (Table 1).

M. flexor perforans et perforatus digiti III showed variation in ossification of the crural part of the tendon of insertion (Fig. 1). The tendon may be unossified (- -); there may be a short (4-5 mm) slight ossification of the proximal part of the tendon (± -); or the tendon may be fully ossified for its entire length (++), becoming soft just before entering the tibial cartilage (Table 1). Seven specimens had the typical, slightly ossified/unossified combination (± -) bilaterally. One specimen each lacked ossification bilaterally or was fully ossified throughout. A single specimen lacked ossification in the right leg and had the typical condition on the left (Table 1).

M. flexor perforatus digiti II showed a complex pattern of variation along the length of the crural part of the tendon of insertion. Five specimens had, bilaterally, full ossification proximally and no ossification distally (+ -). One specimen lacked ossification bilaterally (- -), and one specimen was fully ossified bilaterally both proximally and distally (++). Bilaterally, two specimens were slightly ossified proximally

TABLE 1. Continued.

Specimen	FPD2T	FPD3C	FPD3T	FPD3B	FPD4P	FPD4D	FPD4T	FHLC	FHLT	FDLC	FDLT
R A4380	±	-	±	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A4098	±	-	+	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A3813	±	-	+	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A4381	±	+	+	+	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A3888	±	-	+	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A4359	±	-	+	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A904	±	-	+	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A4097	±	-	+	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A4095	±	-	+	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+
R A4361	±	-	+	-	-	-	±	+	-	+	+
L	±	-	+	-	-	-	±	+	-	+	+

* Character symbols: +, tendon fully ossified; -, not ossified; ±, slightly ossified; + +, fully ossified proximally and distally; + -, fully ossified proximally, unossified distally; ± -, slightly ossified proximally, unossified distally; - -, unossified proximally and distally; ?, missing data. First column lists specimen catalog numbers from the Section of Birds, The Carnegie Museum of Natural History. R, right limb; L, left limb. Muscle and tendon-segment abbreviations are: TCR, M. tibialis cranialis; EDLC, M. extensor digitorum longus, crural part of tendon; EDLT, M. extensor digitorum longus, tarsal part of tendon; FL, M. fibularis longus; FB, M. fibularis brevis; GL, M. gastrocnemius pars lateralis; PL, M. plantaris; FPPD2C, M. flexor perforans et perforatus digiti II, crural part of tendon; FPPD2T, M. flexor perforans et perforatus digiti II, tarsal part of tendon; FPPD3C, M. flexor perforans et perforatus digiti III, crural part of tendon; FPPD3T, M. flexor perforans et perforatus digiti III, tarsal part of tendon; FPD2C, M. flexor perforatus digiti II, crural part of tendon; FPD2T, M. flexor perforatus digiti II, tarsal part of tendon; FPD3C, M. flexor perforatus digiti III, crural part of tendon; FPD3T, M. flexor perforatus digiti III, tarsal part of tendon; FPD3B, M. flexor perforatus digiti III, bony plate; FPD4P, M. flexor perforatus digiti IV pars proximalis; FPD4D, M. flexor perforatus digiti IV pars distalis; FPD4T, M. flexor perforatus digiti IV, tarsal part of tendon; FHLC, M. flexor hallucis longus, crural part of tendon; FHLT, M. flexor hallucis longus, tarsal part of tendon; FDLC, M. flexor digitorum longus, crural part of tendon; FDLT, M. flexor digitorum longus, tarsal part of tendon.

and unossified distally (± -). One specimen had the most common state (+ -) on one side and the slightly ossified/unossified (± -) condition on the other (Table 1).

In M. flexor perforatus digiti III, both the surface of the belly and the crural segment of the tendon of insertion were unossified bilaterally in nine specimens and unilaterally in one; the other side of which had both a fully ossified tendon and a bony plate on the belly's surface (Table 1).

The tarsal part of the tendon of M. flexor perforatus digiti IV was slightly ossified bilaterally in nine specimens and unilaterally in one, the other side of the latter was fully ossified (Table 1).

DESCRIPTION OF OTHER MYOLOGICAL VARIATIONS IN *D. ANABATINA*

Bilaterally in nine of 10 specimens, pars preacetabularis and pars postacetabularis of M. iliotibialis lateralis were continuous. In one specimen, a narrow gap between the pre- and postacetabular portions was present bilaterally. The presence of the gap is therefore variant.

Seven of 10 specimens exhibited bilaterally the typical condition of M. extensor digitorum longus, in which the belly did not extend laterally on the tibial shaft to reach M. fibularis brevis. Thus, a gap along the tibial shaft was present between the two muscles. Bilaterally in one specimen, the belly of M. extensor digitorum longus was expanded laterally, such that it reached M. fibularis longus and closed the gap between the two muscles. This variant was observed unilaterally in two other specimens, the other legs of which had the typical condition.

LEVELS OF OSSIFICATION VARIATION IN *D. ANABATINA*

Twelve of the 23 tendon segments (52.2%) showed no variation in ossification, whereas 11 (47.8%) showed variation (Table 1). Of these 11 segments, 4 (36.4%) showed variation only in presence of ossification, 4 (36.4%) showed variation only in degree of ossification, and 3 (27.2%) showed variation in both degree and presence (Table 1). Of 458 undamaged tendon segments, 42 were variant; these values yielded a "percent variant" of 9.2%. Among the occur-

TABLE 2. Variations in hindlimb tendon ossification in *Dendrocincla anabatina*.^a

Muscles	Specimens										Variants per structure
	A4380	A4098	A3813	A4381	A3888	A4359	A904	A4097	A4095	A4361	
TCR											0
EDLC	B	B	B			U	d				4
EDLT	B		B	B		B					4
FL	U			B				U	U ^b		4
FB											0
GL				B							1
PL											0
FPPD2C											0
FPPD2T	U										1
FPPD3C			U				B		B		3
FPPD3T											0
FPD2C	U		B			B	B		B		5
FPD2T											0
FPD3C				U							1
FPD3T	U										1
FPD3B				U							1
FPD4P											0
FPD4D											0
FPD4T					U						1
FHLC											0
FHLT											0
FDLC											0
FDLT											0
Variants/specimen	6	1	4	5	1	3	2	1	3	0	

^a B, bilateral variant; U, unilateral variant; d, specimen typical on right side, damaged on left side. Muscle abbreviations are in the footnote to Table 1. All blank cells denote the typical condition bilaterally.

^b Specimen had one variant on left side and a different variant on right side.

rences of variant conditions, 11 of 26 (42.3%) were unilateral (Table 2). Of the 10 specimens in the series, nine had at least one variant tendon-segment. The number of structures that deviated from the species-typical state in an individual specimen ranged from zero to six, with a

mean (\pm SD) of 2.50 ± 1.90 variants per specimen ($n = 10$). The number of times a given structure varied either unilaterally or bilaterally ranged from zero to five, with a mean of 1.09 ± 1.56 variants per segment ($n = 23$).

INTERSPECIFIC COMPARISON OF LEVELS OF VARIATION

Table 3 presents measures of variation for ossification and nonossification traits in *Dendrocincla anabatina*, *X. flavigaster*, and *Dendrocolaptes certhia*. In tendon-ossification traits, *D. anabatina* shows higher levels of variation than the other species for each measure, with the exception of the percentage of variant occurrences that are unilateral, which is higher in *D. certhia*. However, a very small number of variants (two) occurred in that species. In traits not involved in ossification, the levels of variation are comparable between the three species and substantially lower than the levels shown by tendon-ossification traits in *D. anabatina*. The only exception to this statement is the percentage of variant occurrences that are unilateral, which in *D. anabatina* is higher in nonossification traits, but

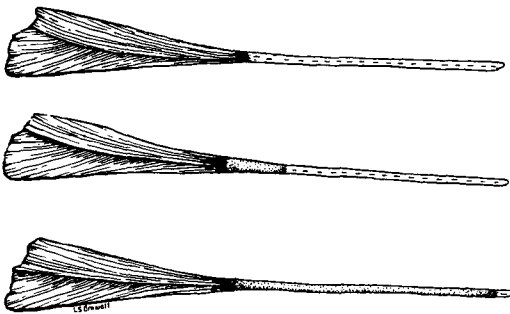


FIGURE 1. Variations in ossification of the crural part of the tendon in *M. flexor perforans et perforatus digiti III* in *D. anabatina*. Upper figure, no ossification (coded “- -” in Table 1). Middle figure, ossification of the first 4–5 mm of the tendon only (coded “± -”). Lower figure, ossification of the entire crural segment (coded “+ +”).

TABLE 3. Comparison of intraspecific variation in three species of Dendrocolaptnae.

Type of trait	Measure	<i>Dendrocincla anabatina</i> (n = 10)	<i>Xiphorhynchus flavigaster</i> (n = 19)	<i>Dendrocolaptes certhia</i> (n = 8)
Ossification	% tendon segments showing intraspecific variation	47.8	8.7	4.3
	% variant	9.2	1.8	0.8
	% variant occurrences that are unilateral	42.3 (11/26)	22.2 (2/9)	50.0 (1/2)
	% specimens showing a variant condition	90.0	47.4	25.0
Non-ossification	% muscles showing intraspecific variation	6.5	20.0	10.0
	% variant	1.0	1.6	2.5
	% variant occurrences that are unilateral	50.0 (2/4)	36.4 (4/11)	28.6 (2/7)
	% specimens showing a variant condition	40.0	52.6	62.5

again this value is based on very few variant occurrences (four).

The “percent variant” value for tendon ossification traits in *D. anabatina* is higher than any of the values reported for general myological variation by Raikow et al. (1993), with the exception of the 9.7% value for the Blue Jay (*Cyanocitta cristata*). For 13 other species discussed by Raikow et al. (1993), the mean (\pm SD) “percent variant” is $2.1 \pm 1.0\%$, and the highest value is 4.0%, less than half the value of 9.2% for tendon ossification in *D. anabatina*. The value for variation in tendon ossification in *D. anabatina* is more than six standard deviations higher than the mean for general myological variation in those 13 species. The values for variation in tendon ossification in *D. certhia* and *X. flavigaster*, and for nonossification traits in all three species of woodcreeper considered here are low, never exceeding the mean for the 13 species by more than 0.2 standard deviations, and being lower than the mean by no more than 1.3 standard deviations.

DISCUSSION

LEVELS OF VARIATION

Tendon ossification is substantially more variable in *D. anabatina* than in *Dendrocolaptes certhia* and *Xiphorhynchus flavigaster*. It likewise is much higher than the level of variation in other aspects of musculature of the *D. anabatina* hindlimb, which in turn is very similar to the levels of general myological variation in *D. certhia*, *X. flavigaster*, and other passerine species (see Raikow et al. 1993). These considera-

tions indicate that the higher level of variation in tendon ossification in *D. anabatina* is not a result of a higher level of overall myological variation within that species or of a lower level of myological variation in the other species.

The variability of tendon ossification provides one of the few instances in which levels of myological variation in passerine hindlimbs are high; previous studies (summarized by Raikow et al. 1993) have almost uniformly reported very low levels of variation. The high variation we observed in *D. anabatina* is unlike other instances of high variation (McKittrick 1986, Raikow et al. 1993), however, in pertaining essentially to tendon histology, as opposed to variation in the muscle as a whole. Nonetheless, our findings contrast with our previous results (Raikow et al. 1993), which indicated that the probabilities of error in designating species-typical conditions from bilateral dissection of single specimens are low (0.00–0.006), and hence that intraspecific myological variation is unlikely to compromise phylogenetic analysis of myological data. Instead, the results of this study and those of McKittrick (1986) indicate that, in rare instances, errors in designating species-typical conditions may be frequent. Within *Dendrocincla* at least, study of patterns of tendon ossification thus will require the use of techniques for dealing with polymorphic characters (e.g., frequency coding, Weins 1995) to achieve good character reconstructions based on phylogenetic analysis.

The differences in levels of variation in tendon ossification among the woodcreepers are

large enough to warrant explanation. We cannot ascribe the higher levels of variation in *D. anabatina* to increased sensitivity to variation, because all of the studies summarized by Raikow et al. (1993) were performed in the Raikow laboratory, or by workers trained in that laboratory, where consistent standards for describing variation are applied (see Raikow et al. 1990). The differences in levels of variation do not appear to be artifacts of the nature of our samples. All specimens of the *D. anabatina* series were collected from a restricted region (see Materials and Methods) and represent a single subspecies, *anabatina*, recognized by Peters (1951), yet the series shows higher levels of variation in tendon ossification than does the *X. flavigaster* series, which includes four of the subspecies recognized by Peters (1951). Hence, the higher level of variation in *D. anabatina* is not an artifact of a wider geographic sampling of that species. Body-mass differences are slight between males of *D. anabatina* and females of *X. flavigaster* and large between the latter species and *Dendrocolaptes certhia* (see Materials and Methods), suggesting that size is not a major factor. Observer bias can be excluded because the same worker made all of the assessments of ossification. Likewise, possible differences in female breeding condition and associated calcium metabolism do not explain the different levels of variation because the *D. anabatina* series was predominantly composed of males (see Materials and Methods) and the 10 *X. flavigaster* males available for comparison showed low levels of variation. We have no information on age differences between our series, but tendon ossification in birds generally develops early and is typically present by the subadult stage (Vanden Berge and Storer 1995). If our sample is representative, then taken together these considerations suggest that the higher levels of variation observed in tendon ossification traits in *D. anabatina* represent a real increase in variation over that typical for members of the woodcreeper clade.

EVOLUTIONARY BASIS OF INCREASED VARIATION IN *D. ANABATINA*

There are two general types of phylogenetic explanation for variation within any species. First, variation may occur through the origin of novel conditions within the species under consideration, that is, after it and its sister lineage have

split. Second, an ancestral species that split to yield two descendants may itself have been variable, that variation being retained through the speciation event. Put another way, variation either originated after the last splitting, or before it. Additional data for other *Dendrocincla* woodcreepers are needed to evaluate rigorously these possibilities. However, the available evidence hints at increased levels of variation in other species of *Dendrocincla*. Two specimens of *D. merula* studied by Bledsoe et al. (1993) differed from each other in four of 23 tendon segments, and two specimens of *D. fuliginosa* differed from each other in 11 of 23 segments. Some of these variable segments are the same segments that vary in *D. anabatina*. This indicates that retained ancestral polymorphism is at least a reasonable possibility (the value for *D. fuliginosa* differs from that published by Bledsoe et al. 1993, because one specimen, CM 1883, studied therein as an example of *D. anabatina*, is in fact an example of *D. fuliginosa* that was mislabeled during museum processing). Nevertheless, if one makes the assumption that *D. certhia* and *X. flavigaster* are representative of other non-*Dendrocincla* woodcreepers in their levels of variation in tendon ossification, then the increased variation in *D. anabatina* represents polymorphism evolved somewhere within the *Dendrocincla* clade, although exactly where is unclear.

The finding that increased polymorphism originated within the *Dendrocincla* clade permits a tentative assessment of the role of natural selection in reduction and loss of tendon ossification in *Dendrocincla* woodcreepers. Tendon ossification in woodcreepers is probably an adaptation to resist increased forces that act to extend the limb during vertical climbing (Bledsoe et al. 1993). The species of *Dendrocincla* studied to date have lost or have reduced ossification in many leg-tendon segments (Bledsoe et al. 1993), which correlates with the observation (Feduccia 1973, Willis 1982, 1983, Chapman and Rosenberg 1991) that species of *Dendrocincla* adopt scansorial postures less frequently than do other woodcreepers. It is reasonable to suppose that the function performed by extensive tendon ossification is no longer required in *Dendrocincla* woodcreepers and hence that these ossifications have been released from selection. Yet selection might operate to reduce ossifications, e.g., for energetic savings. If such directional selection were operating, we might predict

that novel states that evolved within *D. anabatina* would consist of reductions or losses. If polymorphism arose before speciation of *D. anabatina* and its sister-group, then within-species variation should be low, having been acted upon by selection over a fairly substantial period of time. Yet levels of variation are high in *D. anabatina*, and preliminary analysis indicates that only some of the states that might have evolved as novelties within *D. anabatina* are most parsimoniously interpreted as reductions or losses; others are best interpreted as *gains* of ossification. Further research on other species of *Dendrocincla* is required to investigate the role, or lack thereof, of natural selection in evolutionary reduction in the *Dendrocincla* clade.

ACKNOWLEDGMENTS

Specimens were kindly provided by B. C. Livezey, K. C. Parkes, and R. Panza of The Carnegie Museum of Natural History. We are grateful to P. C. Chu, B. C. Livezey, M. C. McKittrick, K. C. Parkes, J. C. Vanden Berge, C. J. Welsh, and two anonymous reviewers for their comments on the manuscript, and to D. Johnston for assistance in literature searches. This work was supported by NSF under grant DEB-9207553 to R. J. Raikow.

LITERATURE CITED

- BAUMEL, J. J., A. S. KING, J. E. BREAZILE, H. E. EVANS, AND J. C. VANDEN BERGE [EDS.]. 1993. Handbook of avian anatomy: nomina anatomica avium, 2nd ed. Publ. Nuttall Ornithol. Club 23.
- BLED SOE, A. H., R. J. RAIKOW, AND A. G. GLASGOW. 1993. Evolution and functional significance of tendon ossification in woodcreepers (Dendrocolaptinae). *J. Morphol.* 215:289–300.
- BOCK, W. J., AND C. R. SHEAR. 1972. A staining method for gross dissection of vertebrate muscles. *Anat. Anz.* 130:222–227.
- CHAPMAN, A., AND K. V. ROSENBERG. 1991. Diets of four sympatric Amazonian woodcreepers (Dendrocolaptidae). *Condor* 93:904–915.
- DUNNING, J. B., JR. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, FL.
- FEDUCCIA, A. 1973. Evolutionary trends in the Neotropical ovenbirds and woodhewers. *Ornithol. Monogr.* 13.
- McKITTRICK, M. C. 1986. Individual variation in the flexor cruris lateralis muscle of the Tyrannidae (Aves: Passeriformes) and its possible significance. *J. Zool.* 209:251–270.
- PAYNTER, R. A. 1955. The ornithogeography of the Yucatan Peninsula. *Bull. Peabody Mus. Nat. Hist.* 9:1–347.
- PETERS, J. L. 1951. Check-list of birds of the world. Vol. VII. *Mus. Comp. Zool., Harvard Univ., Cambridge, MA.*
- RAIKOW, R. J. 1993. Structure and variation in the hindlimb musculature of the woodcreepers (Aves: Passeriformes: Dendrocolaptinae). *Zool. J. Linn. Soc.* 107:353–399.
- RAIKOW, R. J. 1994. A phylogeny of the woodcreepers (Dendrocolaptinae). *Auk* 111:104–114.
- RAIKOW, R. J., A. H. BLED SOE, B. A. MYERS, AND C. J. WELSH. 1990. Individual variation in avian muscles and its significance for the reconstruction of phylogeny. *Syst. Zool.* 39:362–370.
- RAIKOW, R. J., A. H. BLED SOE, T. SYED, AND A. G. GLASGOW. 1993. Intraspecific variation in the hindlimb muscles of the Ivory-billed Woodcreeper and the Blue Jay, with a review of other species. *Condor* 95:497–506.
- RUDGE, D. W., AND R. J. RAIKOW. 1992. Structure, function, and variation in the hindlimb muscles of the *Margarornis* assemblage (Aves: Passeriformes: Furnariidae). *Ann. Carnegie Mus.* 61:207–237.
- VANDEN BERGE, J. C., AND R. W. STORER. 1995. Intratendinous ossification in birds: a review. *J. Morphol.* 226:47–77.
- WEINS, J. J. 1995. Polymorphic characters in phylogenetic systematics. *Syst. Biol.* 44:482–500.
- WILLIS, E. O. 1982. The behavior of the Black-banded Woodcreepers (*Dendrocincla picumnus*). *Condor* 84:272–285.
- WILLIS, E. O. 1983. Cis-Andean *Xiphorhynchus* and relatives (Aves, Dendrocolaptidae) as army ant followers. *Rev. Brazil. Biol.* 43:133–142.