



*The Condor* 95:497-506  
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## INTRASPECIFIC VARIATION IN THE HINDLIMB MUSCLES OF THE IVORY-BILLED WOODCREEPER AND THE BLUE JAY, WITH A REVIEW OF OTHER SPECIES<sup>1</sup>

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**Abstract.** Systematists have long used myology in phylogenetic studies of birds, but have only recently begun to assess the extent of intraspecific variation in muscles and the potentially disruptive effect of such variation on investigations of phylogeny. We provide information on the Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*) and the Blue Jay (*Cyanocitta cristata*), and integrate these results with those of previous studies.

Bilateral dissection of 19 specimens of *X. flavigaster* revealed seven major variants in six different muscles. Ten of the 19 specimens (52.6%) possessed variant muscles; of these, four were unilateral and seven bilateral. Overall, 1.6% of the individual muscles varied from their species-typical states. Six of the 11 variants were found in *M. flexor cruris lateralis*, suggesting an association with that muscle.

The 26 specimens of *C. cristata* exhibited a different pattern. Major variations occurred in only three muscles, but for each of these a typical condition could not be ascribed because variation was extensive and polymorphic.

Analysis of similar information for a total of 14 species of passerine birds indicated that variation is common enough that many individuals in a sample can be expected to possess at least one variant muscle. However, the probabilities of error in designating species-typical conditions from bilateral dissection of single specimens were low (0.00–0.06), suggesting that intraspecific variation does not significantly compromise phylogenetic analyses of myological data. Simulation experiments are needed to test this hypothesis.

**Key words:** *Cyanocitta cristata*; *Xiphorhynchus flavigaster*; myology; variation; phylogeny; passerines.

### INTRODUCTION

Although systematists have long used the muscular system in taxonomic and phylogenetic studies of birds, they have only recently begun to assess the nature and extent of intraspecific (individual) variation in muscles. Such information permits the evaluation of procedures for obtaining species-typical myological data from the dissection of small numbers of specimens. This is important because undetected intraspecific variation can have disruptive effects on

studies of phylogeny (McKittrick 1986; Raikow et al. 1990). In addition, documenting the extent and nature of species-level myological variation provides baseline information for discussions of the origin and biological meaning of such variation (e.g., McKittrick 1986; Raikow, in press), and hence of the origin of myological evolutionary novelties.

Recent studies (McKittrick 1985, 1986; Berman et al. 1990; Raikow et al. 1990; Rudge and Raikow 1992; Raikow, in press) suggest that intraspecific myological variation in birds is usually infrequent but is occasionally common in specific muscles (e.g., McKittrick 1986), and that the muscular system, studied with care, is a source

<sup>1</sup> Received 11 January 1993. Accepted 23 March 1993.

of accurate phylogenetic information. However, these generalizations are based on relatively few studies, and the information that is available has not been integrated to provide a general assessment of intraspecific myological variation. In this paper, we provide new information on intraspecific myological variation for two passerine species, the Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*; Furnariidae: Dendrocolaptinae), and the Blue Jay (*Cyanocitta cristata*; Corvidae). In addition, we integrate these results with those of earlier studies to provide an overview of the current status of the problem of intraspecific myological variation in birds.

Our study is modeled on the work of Raikow et al. (1990) and uses the following classification of intraspecific variation. As a first approximation, a *typical* condition is defined as one that occurs in a majority of the specimens of a given species, and a *variant* as one that occurs in a minority of specimens (Raikow et al. 1990:368). *Minor variants* are slight differences in size or shape that are either nonbiological in origin or too indistinct to assess objectively. *Major variations* include the following. *Incongruous variants* are distinctive, functionally compromised aberrancies. *Mimicking variants* are conditions atypical in one species that closely resemble conditions typical in other species. *Singular variants* are distinctive and functional, but are unknown in other species. *Explosive variation* is a special case with a high frequency of multiple variations in a muscle. This classification has its limitations because, in principle, variation akin to polymorphism in the population genetical sense defies simple categorization. In addition, in practice a *typical* state cannot be assigned when only two variants are observed and are of equal frequency. We treat such cases separately from those for which our classification is appropriate.

## MATERIALS AND METHODS

We dissected 19 specimens of *X. flavigaster* bilaterally. (Specimen numbers are as follows. Carnegie Museum of Natural History: 1123, 1615, 3780, 3781, 3908, 3912, 3915, 4081, 4082, 4189, 4249, 4335; University of Kansas Museum of Natural History: 040077, 051232, 056838; Yale Peabody Museum: 4812, 4813, 4814, 4858.) We also dissected both hindlimbs of 26 specimens of *C. cristata* (Carnegie Museum: 858, 2379, 2497, 5123, 5146, 5203, 5338, 5971, 6038, 6075, 6076, 6127, 6192, 6210, 6302; Kansas: 038805,

038806, 045195, 045196, 067423; Yale: 7061, 8778, 8779, 10226, 12935, 12936). Dissection was performed under a stereomicroscope at magnifications of 6X–25X. Specimens were stained with iodine to enhance contrast (Bock and Shear 1972). 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; FCRLA, M. flexor cruris lateralis pars accessoria; FCRM, M. flexor cruris medialis; FDL, M. flexor digitorum longus; FHB, M. flexor hallucis brevis (absent in *X. flavigaster*); 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. iliotrochantericus caudalis; ITCRM, M. iliotrochantericus cranialis et medius (in *C. cristata*, M. iliotrochantericus cranialis [ITCR] and, as a separate muscle, M. iliotrochantericus medius [ITM]); L, M. lumbricalis; OL, M. obturatorius lateralis; OM, M. obturatorius medialis; PIFCA, M. puboischio-femoralis pars caudalis; PIFCR, M. puboischio-femoralis pars cranialis; PL, M. plantaris; TCR, M. tibialis cranialis. Minor variants, as they are described in the introduction and by Raikow et al. (1990), were not included in our analyses. We dissected 1,140 muscles in *X. flavigaster* and 1,612 in *C. cristata*, for a total of 2,752 muscles.

To test for an association between frequency of variation and muscle or individual specimen, we followed the procedure described by Raikow et al. (1990), which employs an  $R \times C$  test of independence ( $G$ -statistic) and Williams' (1976) adjustment for small sample size. For these tests, the columns ( $C$ ) of the contingency table were "variant" and "not variant." A specimen was coded as variant if it showed either unilateral or bilateral variation. Association with the frequency of such variation was tested with the rows ( $R$ ) of the contingency table being muscle names (30 muscles for *X. flavigaster*, with M. gastrocne-

mius divided into lateral, medial, and intermediate bellies for the analysis) or individual specimen number. For the variable muscles in *C. cristata*, no typical condition could be designated; therefore we did not perform the  $R \times C$  tests for this species.

For each species we calculated the frequency of error in the assessment of species-typical conditions under the assumption that one specimen per species is dissected bilaterally. We used the procedure described by Raikow et al. (1990), in which each cell of a matrix of muscle names by specimen numbers is scored either "T" (typical condition present on both sides of a specimen; "T" entries are designated by blanks in Table 1), "B" (a single variant condition present on both sides of a specimen), "U" (right and left sides differed), or "d" (damage to one or both sides precluded determination). From the matrices, we calculated the frequency of error as the number of "B" entries (excluding incongruous variants, which are easily recognized and would not be used in phylogenetic analysis) divided by the number of non-"d" cells. For several species, information on the number of damaged or unassessed muscles was not available; for these species, frequency of error was calculated under the assumption that damaged muscles and undamaged muscles had equal frequencies of variation.

## RESULTS

### IVORY-BILLED WOODCREEPER

*M. ilioprochantericus cranialis et medius*. Mm. ilioprochantericus cranialis and ilioprochantericus medius are small muscles that arise on the ventral margin of the ilium and insert side-by-side on the femur in most birds. In 18 specimens only a single muscle occurred, which was termed cranialis et medius because it is thought to be the product of fusion between the two muscles (Raikow, in press; Rowe 1986). However, in specimen CM 3780 medialis occurred in the right leg only (Table 1), occupying a space between cranialis and *M. iliofemoralis internus* that usually lacks a muscle. Inasmuch as the presence of a separate *M. ilioprochantericus medius* is the ancestral condition in passerines (Raikow, in press), this variant appears to be an atavistic reappearance, and a mimicking variation. A comparable variation in another species is illustrated elsewhere (Raikow, in press, Fig. 4B).

*M. flexor cruris lateralis*. In most specimens

pars accessoria was a strap-shaped muscle whose insertion onto the femur was adjacent to and continuous with the origin of *M. gastrocnemius pars intermedia* (Fig. 1A). However, in eight of thirty-eight limbs a variation occurred in which the muscle was slightly reduced, and its insertion was separated by a gap from pars intermedia (Fig. 1B). This occurred bilaterally in three specimens and unilaterally in two (Table 1). It may be considered a mimicking variant, as the size of this muscle varies widely among passerine groups.

A different variant was observed bilaterally in specimen YPM 4858 (Table 1), where pars accessoria possessed two distinct bellies (Fig. 1C), a singular variant.

*M. pubo-ischio-femoralis pars caudalis* (Fig. 2). In woodcreepers this muscle typically arises by a tendon from the ischium, and becomes fleshy at about the level of the pubis or distad to the latter (Raikow, in press). The narrow, strap-shaped belly inserts on the distal end of the femoral shaft. In the right leg of specimen KU 040077, however, the muscle had an anomalous extra head that arose from the mid-region of the medial side of *M. flexor cruris medialis* (Table 1). The belly of this anomalous portion extended distad to join the distal one-third of the normal belly. In addition, the fascicles of *M. flexor cruris medialis* were distinctly skewed toward the fleshy attachments of the anomalous portion. If the anomalous fibers contracted they would contribute to the normal action of the muscle. Because we know of no other occurrence of this condition, it is best considered a singular variation. In most passerines this muscle is much wider than in the woodcreepers (Raikow, in press), and so this aberrant form may represent a deformed atavism.

*M. gastrocnemius pars lateralis*. In specimen CM 3915 this muscle exhibited bilaterally a second, medial head of origin in addition to the usual origin on the lateral side of the crus (Table 1). This head arose fleshy from the medial surface of the common origin of *M. flexor perforatus digiti III* and *M. flexor perforatus digiti IV*, lateral to *M. gastrocnemius pars intermedia*. It passed distad to join the normal part of the belly a short distance beyond the level of the iliofibularis tendon. This extra mass of muscle tissue was structurally integrated with the normal part of the muscle and presumably contributed to its function. To our knowledge it does not mimic any condition normal in other species, and thus is a singular variant.

TABLE 1. Major variations in the hindlimb muscles of *Xiphorhynchus flavigaster*. Symbols: B, bilateral; d, muscle damaged; M, mimicking; S, singular; U, unilateral. Abbreviations of muscle names are under Materials and Methods.

Muscles	Specimen numbers															Vari- ant	Type					
	CM 3908	CM 3912	CM 3781	CM 4189	YPM 4813	CM 4249	CM 3915	CM 1615	YPM 4812	YPM 4814	KU 040077	KU 051232	CM 4081	CM 4082	CM 4335			KU 056838	CM 1123	CM 3780	YPM 4858	
ICR								d	d		d										0	
IL									d												0	
IF																					0	
ITCA																					0	
ITCRM						d												U			1	M
IFI																					0	
FTEM						d															0	
FTI																					0	
FCRL		B <sup>1</sup>		B <sup>1</sup>					B <sup>1</sup>	U <sup>1</sup>							U <sup>1</sup>		B <sup>2</sup>	6	M <sup>1</sup> S <sup>2</sup>	
FCRM																					0	
CF																					0	
ISF																					0	
OL																					0	
OM																					0	
PIF											U										1	S
TCR																					0	
EDL																					0	
FL																					0	
FB																					0	
GM																					0	
GL							B				d										1	S
GI																					0	
PL																					0	
FPPD2				B							d										1	M
FPPD3											d										0	
FPD2											d										0	
FPD3																					0	
FPD4											d										0	
FHL																		B			1	S
FDL																					0	
EHL																					0	
L																					0	

<sup>1</sup> Variant with gap at insertion.  
<sup>2</sup> Variant with two bellies.

*M. flexor perforans et perforatus digiti II.* In specimen CM 3781 this muscle was atypically wide bilaterally as it arose from the femur and adjacent lateral collateral ligament (Table 1). This is similar to a variation shown elsewhere (Raikow, in press, Fig. 17D) except that it did not extend far enough to reach the head of the fibula. It is considered to be a mimicking variation because it closely resembles the typical condition in treerunners (Rudge and Raikow 1992).

*M. flexor hallucis longus.* In specimen CM 3780 an anomalous fusion was observed between *M. flexor hallucis longus* and *M. flexor perforatus digiti IV* (Table 1). A group of fibers about 4.5 mm wide passed from the distolateral surface of *M. flexor hallucis longus* to insert on the lateral margin of the tendon of the proximal belly of *M.*

*flexor perforatus digiti IV*, just distal to that belly. This anomaly occurred bilaterally, and is a simple example of two adjacent muscles gaining an atypical interconnection. It is best considered as a singular variant (Raikow et al. 1990).

*Tendon ossification.* Woodcreepers differ from other passerines in possessing extensive tendon ossification in the limb muscles. Variation in *X. flavigaster* is discussed elsewhere (Bledsoe et al. 1993) as part of a study of ossification.

*Analysis of patterns of variation.* Seven major variations occurred in 6 different muscles, or 20% of the 30 muscles recognized in this species (Tables 1, 5). All of these had a single variant state except *M. flexor cruris lateralis*, which had two. Three variations were of the mimicking type, and 4 were singular. Ten of the 19 specimens (52.6%)

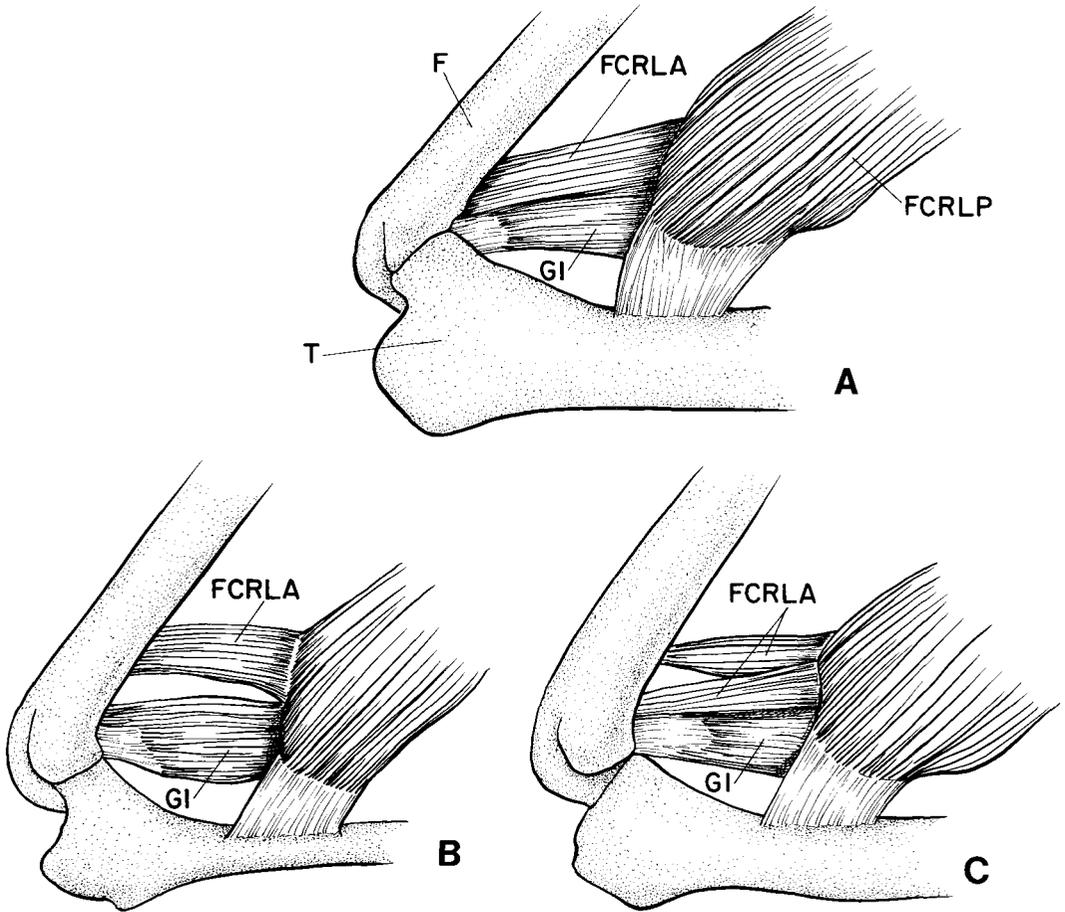


FIGURE 1. Deep muscles on the lateral surface of the knee region in *Xiphorhynchus flavigaster*, showing variation in *M. flexor cruris lateralis* pars accessoria. (A) Typical condition, in which pars accessoria inserts adjacent to *M. gastrocnemius* pars intermedia. (B) Variant in which pars accessoria is separated from pars intermedia by a gap. (C) Variant in which pars accessoria is divided into two separate bellies. See text for discussion. Abbreviations: F, femur; FCRLA, *M. flexor cruris lateralis* pars accessoria; FCRLP, *M. flexor cruris lateralis* pars pelvica; GI, *M. gastrocnemius* pars intermedia; T, tibiotarsus.

possessed variant muscles; four of these variants were unilateral and seven were bilateral. Nine specimens had only one variant muscle, whereas one specimen had two. A total of 1,140 muscles were examined, of which 11 were damaged. Of the remaining 1,129, eighteen individual muscles had variant conditions; thus 1.6% of the individual muscles varied from their species-typical states, and excluding the unilateral variants, 1.2% of the muscles were bilateral variants. The latter are the most likely to be misinterpreted, even with bilateral dissection.

There was no statistically significant association between the occurrence of variants and in-

dividual muscle ( $G_{adj} = 30.00$ ,  $P > 0.05$ ,  $df = 29$ ) or individual specimen ( $G_{adj} = 2.5$ ,  $P > 0.05$ ,  $df = 29$ ). However, six of the 11 variant entries in Table 1 are found in *M. flexor cruris lateralis*, suggesting an association with that muscle; the lack of statistical significance may reflect the small overall frequency of variation in the matrix. With regard to sex, five of the 10 specimens that possessed a variant muscle were male, and five were female.

#### BLUE JAY

*M. gastrocnemius* pars medialis (Table 2). This muscle arises from the head of the tibiotarsus

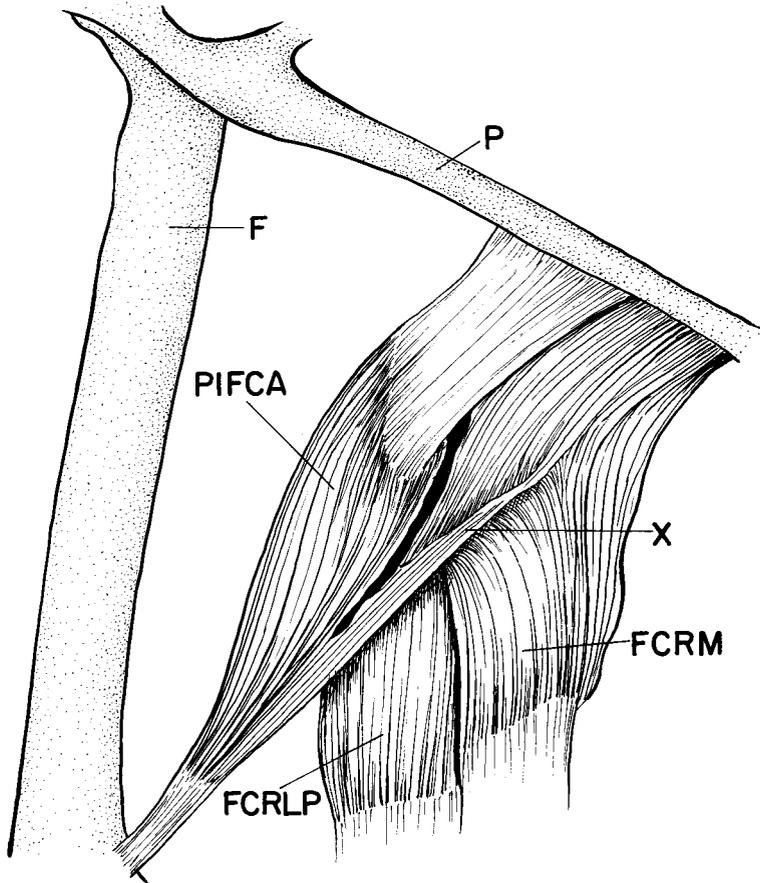


FIGURE 2. Medial surface of thigh in *Xiphorhynchus flavigaster*, showing anomalous extra head arising from the surface of *M. flexor cruris medialis*. See text for discussion. Abbreviations: F, femur; P, pubis; PIFCA, *M. pubo-ischio-femoralis pars caudalis*; FCRLP, *M. flexor cruris lateralis pars pelvica*; FCRM, *M. flexor cruris medialis*; X, anomalous head of PIFCA.

and adjacent structures. Raikow (1978) described and illustrated variations in the origin. In all specimens of the Blue Jay that we examined the muscle has a deep head and a superficial head, both arising from the tibiotarsus, plus a patellar band that arises from the patellar ligament. Differences in the size of the patellar band are characterized by its width relative to the patellar ligament. Variations among Blue Jay specimens require the definition of different types. In Type I the patellar band was narrower than the patellar ligament, ranging from 0.70 to 0.90 of its width. In Type II the patellar band was the full width of the patellar ligament (1.00). In Type III, a new arrangement, the patellar band extended its area of origin onto the patella itself, its relative width varying from 0.10 to 1.00, a

complete overlap. Seven specimens (27%) were Type I bilaterally, seven (27%) were Type II bilaterally, and five (19%) were Type III bilaterally. There was unilateral variation as well. Five specimens (19%) were Type I in one leg and Type II in the other, and two specimens (8%) were Type II in one leg and Type III in the other. Nineteen specimens (73%) had the same size patellar band in both legs, whereas seven (27%) had a different size in each leg.

This is a mimicking variation. The muscle is considered polymorphic because its high frequency of variability did not permit designation of a typical condition.

*M. fibularis longus* (Table 3). This muscle originates on the head of the tibiotarsus, where a range of variation was observed. In Type I the

TABLE 2. Variation in *M. gastrocnemius pars medialis* in *Cyanocitta cristata*. Type I: Patellar band ranged from 70% to 90% of the width of the patellar ligament. Type II: Patellar band 100% width of patellar ligament. Type III: Patellar band extended onto the patella.

Specimen number	Right leg	Left leg
CM 6076	I	I
CM 5338	I	II
YPM 7061	III	III
YPM 12935	III	III
YPM 8778	I	I
CM 5203	II	II
CM 5123	II	II
KU 038805	II	III
CM 6127	II	II
YPM 12936	I	I
CM 6192	I	II
CM 6038	II	II
KU 038806	I	I
CM 6302	III	III
CM 2379	II	I
CM 5971	II	II
CM 2497	III	III
CM 6075	I	I
KU 045195	III	III
CM 858	II	II
CM 5146	II	I
KU 45196	III	II
YPM 8779	II	II
CM 6210	I	I
KU 067423	I	I
YPM 10226	I	II

TABLE 3. Variation in *M. fibularis longus* in *Cyanocitta cristata*. Type I: Origin completely fleshy. Type II: Origin slightly tendinous. Type III: Origin extensively tendinous.

Specimen number	Right leg	Left leg
CM 6076	I	I
CM 5338	II	III
YPM 7061	III	III
YPM 12935	III	III
YPM 8778	II	II
CM 5203	III	II
CM 5123	I	I
KU 038805	II	I
CM 6127	I	I
YPM 12936	II	II
CM 6192	II	I
CM 6038	II	II
KU 038806	III	III
CM 6302	I	I
CM 2379	II	II
CM 5971	III	II
CM 2497	I	I
CM 6075	III	III
KU 045195	II	III
CM 858	II	II
CM 5146	I	I
KU 45196	I	I
YPM 8779	I	I
CM 6210	II	II
KU 067423	I	I
YPM 10226	II	II

origin is completely fleshy, Type II has a slightly tendinous origin, and Type III has an extensive tendinous origin. Nine specimens (35%) were Type I bilaterally, seven (27%) were Type II bilaterally, and four (15%) were Type III bilaterally. In addition, two specimens (8%) were Type I in one leg and Type II in the other, and four specimens (15%) were Type II in one leg and Type III in the other.

These are mimicking variations. Because no variant occurred in a majority of specimens, there is no typical state as defined above. Instead, the condition is best described as polymorphic.

*M. extensor digitorum longus* (Fig. 3; Table 4). This is the deepest muscle on the cranial surface of the tibiotarsus. It arises fleshy from the cnemial and patellar crests and the cranial face of the tibial shaft. In *C. cristata* variations were found in the presence, position, and number of extra heads arising on the tibiotarsus. Variations ranged from two heads, one head, and scattered fascicles, to the absence of any heads or fascicles.

Type I has a single extra head (Fig. 3A), Type II has two extra heads (Fig. 3B), Type III has scattered fascicles, and Type IV has no distinct extra parts (Fig. 3C).

Six specimens (24%) were Type I bilaterally, one (4%) was Type II bilaterally, three (12%) were Type III bilaterally, and two (8%) were Type IV bilaterally. Unilateral variation also occurred. Three specimens (12%) were Types I and III, five (20%) were Types I and II, three (12%) were Types III and IV, and two (8%) were Types I and IV. One leg of specimen YPM 10226 was damaged and could not be recorded; the undamaged leg was Type I.

Because no typical condition could be determined in *C. cristata*, this is another case of polymorphism. This condition in *Cardinalis cardinalis* (Raikow et al. 1990) was classified as a singular variation, but now that the variant is known from more than one species it is better considered as mimicking.

*Analysis of patterns of variation.* The pattern in *C. cristata* was distinctly different from that

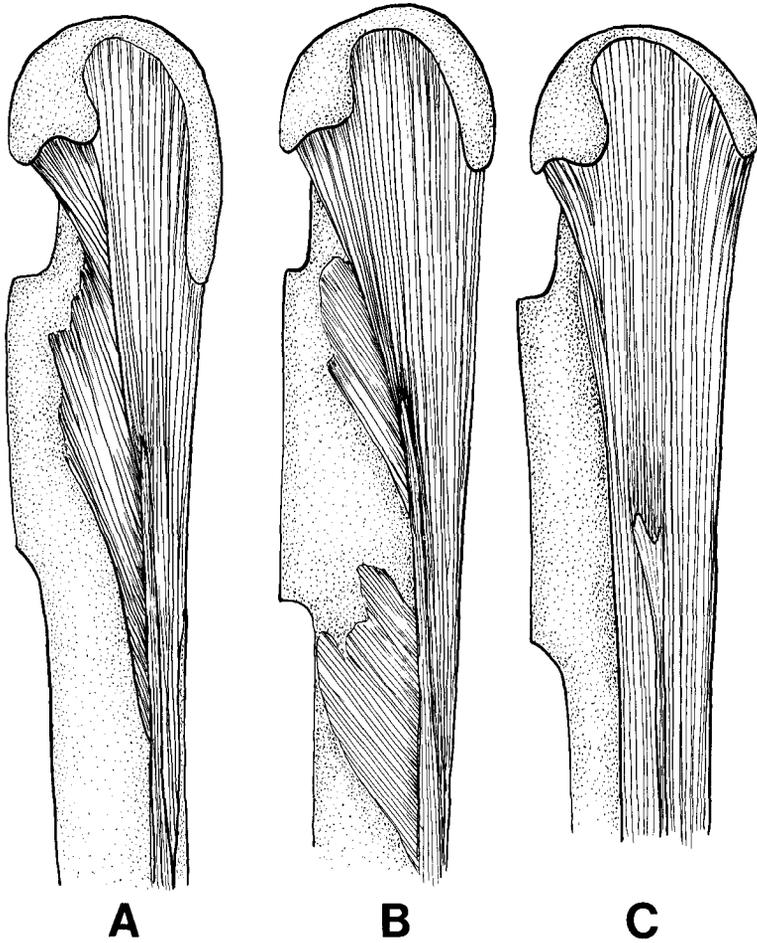


FIGURE 3. Variation in the origin of *M. extensor digitorum longus* from the tibiotarsus in *Cyanocitta cristata*. (A) Type I, with a single extra head. (B) Type II, with two extra heads. (C) Type IV, with no extra parts.

in *X. flavigaster* (Table 5). Major variations occurred in three of 31 muscles (9.7%). For each of the three variable muscles, no typical condition could be designated because variation was extensive and polymorphic. This indicates an association between individual muscle and the occurrence of variation, although it precludes use of our statistical tests; in any event, the tests are unnecessary to document such an association in this clear-cut instance. There is no evidence of association between individual specimen or sex and the occurrence of variation, because each individual is equivalent in possessing one of the several possible states for each of the three variable muscles.

#### DISCUSSION

The levels of variation that we observed in *X. flavigaster* and *C. cristata* are generally similar to those reported for other species of passerine birds (Table 5). The levels are similar in the overall frequency of atypical muscles among each series, expressed as the percentage of atypical muscles among all individual muscles, in the percentage of different muscles that have at least one atypical example, and in the percentage of specimens having at least one atypical muscle. For the latter measure, the value of 0% for *C. cristata* does not reflect the absence of variation. Rather, each of the three variable muscles had

several conditions, none being present in over 50% of the sample. This situation is similar to the explosive variation reported by McKittrick (1986) for *M. flexor cruris lateralis* in tyrannid flycatchers.

Comparative studies of myology often rely upon dissection of one specimen per species, under the assumption that the musculature of the dissected specimen is typical for the species as a whole. This procedure usually cannot be expanded to include extensive series because dissection is so labor-intensive and the number of available specimens is often limited. The use of single specimens nonetheless introduces the potential for error in assessments of species-typical conditions.

The frequencies of errors in assessing species-typical conditions are estimated in the last column of Table 5 (see Materials and Methods for explanation) and range from 0% to 6.3%, with an average of 1.9%. These values are low, suggesting that the bilateral dissection of single specimens provides accurate myological information. An estimate of the improvement in accuracy provided by bilateral (as opposed to unilateral) dissection can be obtained from Table 5. The percentage of atypical muscles among all individual muscles is equivalent to the frequency of error in assessing species-typical conditions under unilateral dissection of a single specimen per species. This averages 2.6%, an increase in error of 0.7% over bilateral dissection.

Although intraspecific variation in passerine hindlimb muscles is comparatively rare when the full set of muscles is considered, a fairly substantial proportion of the individuals of most of the species in Table 5 possesses at least one atypical muscle. The percentage of individual specimens having atypical muscles (Table 5) is as high as 65% for large series ( $n > 10$ ) and 80% for certain small series ( $n = 5$ ), averaging 47.8% for the 14 species as a whole. The overall level of variation is actually somewhat higher, because explosive variation is excluded from the figures in Table 5. The number of different muscles that include atypical examples is smaller, however, and the number of atypical individual muscles among the total dissected is smaller still.

These considerations support the contention of Raikow et al. (1990) that the best approach is bilateral dissection of single specimens, augmented by a series of specimens of one species

TABLE 4. Variation in *M. extensor digitorum longus* in *Cyanocitta cristata*. Type I: One anomalous head in origin. Type II: Two anomalous heads in origin. Type III: Anomalous fascicles in origin. Type IV: No anomalous heads or fascicles in origin.

Specimen number	Right leg	Left leg
CM 6076	I	I
CM 5338	I	IV
YPM 7061	I	I
YPM 12935	I	I
YPM 8778	IV	III
CM 5203	IV	I
CM 5123	II	I
KU 038805	I	III
CM 6127	II	II
YPM 12936	III	III
CM 6192	IV	IV
CM 6038	I	II
KU 038806	I	III
CM 6302	I	II
CM 2379	III	IV
CM 5971	III	III
CM 2497	I	I
CM 6075	I	I
KU 045195	I	I
CM 858	IV	III
CM 5146	I	I
KU 45196	III	III
YPM 8779	II	I
CM 6210	IV	IV
KU 067423	III	I
YPM 10226	I	—

for use in developing reference descriptions. Additional dissections may be performed when unilateral variation is detected, or when between-species variation is observed in muscles known to be highly variable in other species. Our understanding of the frequency of error in assessing species-typical conditions is, nonetheless, based upon comparatively few species. In addition, although the levels of error in Table 5 are low, they may have the potential to induce errors in phylogenetic reconstructions. Hence, dissections of additional species and simulation studies of the effects that the levels of error in Table 5 might have on phylogenetic reconstructions are needed.

ACKNOWLEDGMENTS

For the loan of specimens we are grateful to K. C. Parkes and J. Loughlin, The Carnegie Museum of Natural History; R. F. Johnston and T. J. Davis, The University of Kansas Museum of Natural History; and F. C. Sibley, Peabody Museum of Natural History, Yale University. We also thank S. L. Berman, M. C. McKittrick, and D. W. Rudge for providing informa-

TABLE 5. Intraspecific variation in the hind limb muscles of passerine birds.<sup>1</sup>

Species	No. of specimens	Reference	No. of muscles typically present	% of specimens having atypical muscles	% of different muscles having atypical examples or polymorphism	% of all individual muscles that are atypical <sup>2</sup>	Frequency of error (%)
<i>Xiphorhynchus flavigaster</i>	19	This study	30	52.6	20.0	1.6	1.2
<i>Cyanocitta cristata</i>	26	This study	31	0 <sup>2</sup>	9.7	9.7	6.3
<i>Dendrocolaptes certhia</i>	8	Raikow, in press	30	62.5	10.0	2.3	2.1
<i>Margarornis squamiger</i>	5	Rudge and Raikow 1992	31	80.0	12.9	1.9	0.6
<i>Premnoplex brunescens</i>	7	Rudge and Raikow 1992	31	57.1 <sup>2</sup>	9.7	1.8	1.4
<i>Premnornis guttiligera</i>	5	Rudge and Raikow 1992	31	0	0	0	0
<i>Cardinalis cardinalis</i>	23	Raikow et al. 1990	32	61.0	9.8	2.0	1.5
<i>Hylocichla mustelina</i>	25	Raikow et al. 1990	31	36.0	12.9	1.4	1.0
<i>Passer domesticus</i>	40	Berman et al. 1990	32	65.0	12.5	2.4	2.4
<i>Myiozetetes similis</i>	12	McKittrick 1985, 1986	32	0 <sup>2</sup>	3.1	3.6	2.3
<i>Tyrannus verticalis</i>	14	McKittrick 1985, 1986	32	12.5 <sup>2</sup>	6.2	4.0	2.2
<i>Tyrannus melancholicus</i>	7	McKittrick 1985, 1986	32	42.9	6.2	1.3	1.3
<i>Pitangus sulphuratus</i>	5	McKittrick 1985, 1986	32	40.0	12.5	2.2	1.9
<i>Myiodynastes maculatus</i>	5	McKittrick 1985, 1986	32	80.0	9.4	2.8	1.9

<sup>1</sup> Excluding minor variations. See text for discussion.

<sup>2</sup> Excluding cases in which a muscle is so variable that no typical condition can be defined (see p. 504). These include the following: *Cyanocitta cristata*: M. gastrocnemius pars medialis, M. fibularis longus, and M. extensor digitorum longus; *Premnoplex brunescens*: M. gastrocnemius pars medialis; *Myiozetetes similis*: M. flexor cruris lateralis; *Tyrannus verticalis*: M. flexor cruris lateralis.

<sup>3</sup> Including both unilateral and bilateral variants.

tion about their published studies. The illustrations were drawn by W. R. Filer. This material is based upon work supported by the National Science Foundation under Grant No. BSR-8617896 to R. J. Raikow.

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