

Form and function of the *fibularis brevis* muscle in some passerine birds

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The morphology of the *fibularis brevis* muscle was analysed in 29 passerine species. As expected, most of them showed only one point of origin, the head arising cranially from the fibula and the adjacent tibiotarsus. However, *Panurus biarmicus*, *Regulus regulus*, *Parus ater*, *P. caeruleus*, *Certhia familiaris* and *C. brachydactyla* showed an extra point of origin, with fleshy fibres arising from the outer cnemial crest of the tibiotarsus. The occurrence of such a tibial head was compared with the foraging postures of the species and a correlation was found between the presence of two fully developed heads in *fibularis brevis* and a greater propensity in the species for hanging and/or creeping. The muscular requirement important to these actions is for flexing of the leg joints. Hence, the results seem to indicate that the presence of a tibial head in *fibularis brevis* might be related to tarsometatarsal flexion. The mechanics of the situation seems to support this interpretation, as the torque of the muscular force is increased, which enhances the effectiveness of the flexing action of the muscle. This adaptive hypothesis is tested by the outgroup comparison method.

1. Introduction

Bock's (1974) statement that "a thorough knowledge of functional morphology is essential for all types of morphological studies, including those done as a basis for systematic investigations" is frequently ignored.

Being the largest order of living birds and devoid of clear phylogenetic relationships within the lower level taxa, the Passeriformes have engendered numerous enquiries into the subject of the morphological variation (e.g. Stallcup 1954, Berger 1968, Bock & Morony 1971, Raikow

1976, 1977a, 1977b, 1978, 1985a, 1987, Bentz 1979, Raikow et al. 1980, Zusi & Bentz 1982, 1984, McKittrick 1985, 1986, Moreno 1988, 1990), yet a functional explanation has been found for only a few (e.g. Bock & Morony 1971, Raikow 1977a, 1985a, Zusi & Bentz 1982, McKittrick 1986, Moreno 1988, 1990).

Many opinions have been expressed on the function of the *fibularis brevis* muscle. Abduction (Hudson 1937, Fisher 1946, Owre 1967) and active rotation (Stolpe 1932, Rüggeberg 1960, Raikow 1985b) of the tarsometatarsus are frequently proposed as its main roles, and extension

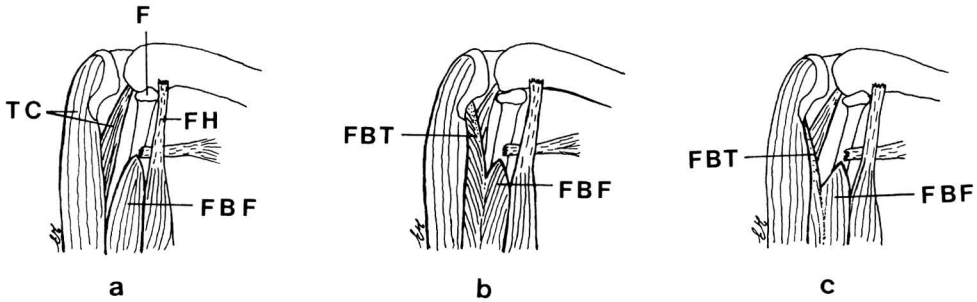


Fig. 1. Variation in the origin of the *fibularis brevis* muscle. — a. *Phylloscopus collybita*, only a fibular head. — b. *Parus caeruleus*, both a fibular and a tibial head. — c. *Parus major*, tibial head only a narrow tendinous branch. F = fibula, FBF = *fibularis brevis*, fibular head, FBT = *fibularis brevis*, tibial head, FH = *flexor hallucis longus*, lateral head, TC = *tibialis cranialis*. (×20)

is sometimes suggested (Miller 1937), although Cracraft (1971) pointed out that in most birds the muscle flexes rather than extends the tarsometatarsus and “possibly operates to counteract the forces of tarsometatarsal extension created by the toe flexors and thereby aid the latter muscle in toe flexion” (Cracraft 1971:239).

In this study,

- 1) new information is provided concerning the morphology of the *fibularis brevis* muscle in some passerinè species,
- 2) using ecological data it is proposed that modifications in this muscle are an adaptation helping tarsometatarsal flexion in species with an increased hanging and/or creeping behaviour, and
- 3) the adaptive hypothesis is tested on the basis of the available phylogeny (Sibley et al. 1988).

2. Material and methods

Spirit specimens of the following species were available for dissection (number of specimens dissected in parentheses): *Melanocorypha calandra* (1), *Alauda arvensis* (1), *Hirundo rustica* (1), *Delichon urbica* (1), *Motacilla flava* (1), *Cinclus cinclus* (1), *Turdus merula* (1), *Oenanthe leucura* (1), *O. hispanica* (1), *O. oenanthe* (2), *Locustella naevia* (2), *Acrocephalus scirpaceus* (1), *A.*

arundinaceus (1), *Hippolais pallida* (1), *Regulus regulus* (1), *Phylloscopus collybita* (1), *Muscicapa striata* (2), *Ficedula hypoleuca* (2), *Panurus biarmicus* (1), *Aegithalos caudatus* (1), *Parus ater* (1), *P. caeruleus* (2), *P. major* (2), *Certhia familiaris* (2), *C. brachydactyla* (2), *Sturnus vulgaris* (1), *Passer domesticus* (1), *Carduelis chloris* (1) and *Emberiza citrinella* (2).

The gross morphology of the muscles was studied with the aid of a stereomicroscope (5–20×), using an iodine stain (Bock & Shear 1972) to enhance visibility of the fibre arrangements. Drawings were made with the aid of a camera lucida microscope attachment. The anatomical nomenclature follows Baumel et al. (1979).

3. Results

In most of the species dissected, the *fibularis brevis* muscle has a fleshy head arising from the fibula below the tendon of insertion of the *iliofibularis* muscle and from the adjacent surface of the tibiotarsus, the muscle lying caudal to the *tibialis cranialis* muscle on the lateral surface of the crus. Fibres converge onto a stout tendon that descends along the tibiotarsus and passes beneath a fibrous loop proximal to the tibiotarsal lateral condyle, being inserted laterally on the proximal end of the cranial half of the tarsometatarsus (Fig. 1a). This arrangement has been considered typical of the

muscle in passerine birds (Mitchell 1913, Hudson 1937, Stallcup 1954, Berger 1956, 1968, 1969, George & Berger 1966, Gaunt 1969, Raikow et al. 1980, Zusi & Bentz 1984, McKittrick 1985, Raikow 1987).

However, in *Panurus biarmicus*, *Regulus regulus*, *Parus ater*, *P. caeruleus*, *Certhia familiaris* and *C. brachydactyla*, two sites of origin are present. A fleshy tibial head arises from the caudal margin of the outer cnemial crest (Fig. 1b). Caudally, the origin is aponeurotic, the aponeurosis covering the surface of the belly caudo-laterally. This tibial head joins a fleshy fibular head arising from the craniolateral surface of the fibula and fibres converging from the two heads give rise to a tendon that is held firmly against the bone by a fibrous loop cranioproximal to the lateral condyle of the tibiotarsus. The tendon crosses the intratarsal joint and is inserted on the lateral margin of the proximal end of the tarsometatarsus on its cranial half. The tibial head has a unipennate arrangement, the fibres running caudally from the cnemial crest to the aponeurosis, but the whole muscle is bipennate.

A tendinous tibial head is present in *P. major* and *A. scirpaceus* (Fig. 1c). A slim tendon arises from the distal tip of the outer cnemial crest and joins the fibular head distally. In *Serinus* (Raikow 1977b), some muscle fibres arise from this tendon, distally joining the fibular head.

4. Discussion

The comparative study of the hindlimb musculature of the present passerines shows that the *fibu-*

laris brevis muscle is modified in *Panurus biarmicus*, *Regulus regulus*, *Parus ater*, *P. caeruleus*, *Certhia familiaris*, and *C. brachydactyla* towards an increase in the number of fibres as there exist two points of origin instead of one. In attempting to find an explanation for the variability and probable function of the muscle, two aspects have been considered: the foraging behaviour of the species, and the mechanical action of the muscle.

The occurrence of a tibial point of origin in this muscle in the species studied here can be compared with observations made by Carrascal & Tellería (1985) on the foraging methods of a group of wintering forest passerines. Among the species that I dissected and that were also represented in their study, *Regulus regulus*, *Parus ater*, *P. caeruleus*, and *Certhia brachydactyla* reveal a greater propensity for hanging and/or creeping than do *Phylloscopus collybita*, *Aegithalos caudatus*, and *Parus major* (Table 1, Fig. 2). In these postures flexion of the leg joints is required (Norberg 1979, Berman & Raikow 1982) and muscles effecting such flexion can be expected to develop greater force in the species concerned. *R. regulus*, *P. ater*, *P. caeruleus*, and *C. brachydactyla* all show an extra point of origin of *fibularis brevis* and the muscular force developed is thereby increased with the increase in the number of fibres and the physiological cross-section (Bock 1974). In the other three species in this comparison, *Phylloscopus collybita*, *Aegithalos caudatus*, and *Parus major*, which are all less given to hanging and/or creeping, a tibial head is absent in *fibularis brevis* (the two former) or not fully developed (the latter). This coincidence seems to indicate that the

Table 1. Percentages of total foraging time devoted to various foraging methods in some of the dissected species. *n*, sample size; GL, gleaning (horizontal); HG, hanging; CR, creeping; HV, hovering; SE, standard error for CR+HG calculated as $\sqrt{p(1-p)/n}$. Taken from Carrascal & Tellería (1985).

	<i>n</i>	GL	HG	CR	HV	CR+HG	SE
<i>Phylloscopus collybita</i>	37	93.1	3.5	0	3.4	3.5	3.0
<i>Regulus regulus</i>	282	63.6	26.2	0	10.2	26.2	2.6
<i>Aegithalos caudatus</i>	88	82.4	8.2	5.9	3.5	14.1	3.7
<i>Parus ater</i>	211	53.5	33.4	13.1	0	46.5	3.4
<i>Parus caeruleus</i>	86	66.7	23.6	9.7	0	33.3	5.1
<i>Parus major</i>	121	90.1	4.4	5.5	0	9.9	2.7
<i>Certhia brachydactyla</i>	121	0	10.1	89.9	0	100.0	0

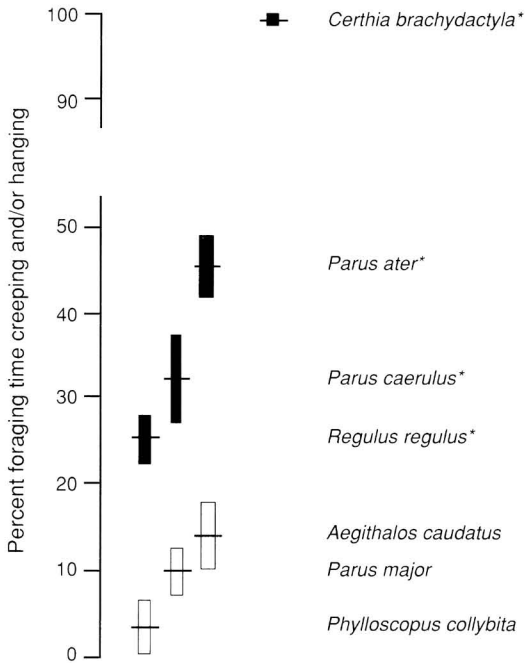


Fig. 2. Percentages of foraging time spent hanging and creeping in some of the dissected species. Filled bars and asterisk, species with extra point of origin in the *fibularis brevis* muscle; open bars, species without extra point. For details see Table 1.

presence of such a tibial head might be related to tarsometatarsal flexion, corroborating Cracraft's (1971) suggestion.

Data from Alatalo (1982) on the winter foraging behaviour of *Parus montanus* and *Certhia familiaris* show that they also have a greater propensity for hanging and/or creeping (*P. montanus* 24%; *C. familiaris* 100%) than the other species he studied, and this is associated with the presence of two points of origin in the *fibularis brevis* muscle (Palmgren 1932, Moreno pers. obs). Unfortunately, I am unable to check whether the same association exists in *Panurus biarmicus*, as no ecological data are available.

From the mechanical viewpoint, *fibularis brevis*, lying on the lateral surface of the crus, does not seem to be a flexor muscle. However, upon contraction it exerts a torque on the tarsometatarsus with respect to the intratarsal joint. This torque is equal to the product of the force and its moment

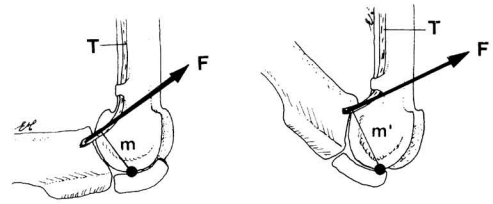


Fig. 3. Elongation of the moment arm of the force developed by the *fibularis brevis* muscle as the tarsometatarsus is flexed from 90° (left) to 45° (right). T = tendon of the muscle. ($\times 20$)

arm. Fig. 3 shows how the moment arm lengthens as the tarsometatarsus is flexed from 90° to 45°. Hence, the torque on the tarsometatarsus is increased, which increases the mechanical advantage (effectiveness of action) of the muscle (Bock 1974).

The increase of the muscular force developed by *fibularis brevis* by the addition of an extra point of origin in *P. biarmicus*, *R. regulus*, *P. ater*, *P. caeruleus*, *C. familiaris* and *C. brachydactyla* also increases the torque. In these species, therefore, the muscle flexes the tarsometatarsus more effectively.

Having very short fibres, *fibularis brevis* will contribute very little to tarsometatarsal flexion (Cracraft 1971), and so is probably not one of the main flexor muscles of the tarsometatarsus, but serves mainly to maintain the position of the bone once it is flexed.

In summary, the results of this study seem to indicate that the modification of the *fibularis brevis* muscle is an adaptation favouring tarsometatarsal flexion in species with increased hanging and/or creeping behaviour, and that it represents the derived state of the character. This adaptive hypothesis can be tested by the outgroup comparison method on the basis of the phylogenetic hypothesis presented by Sibley et al. (1988).

According to the data now to hand, the *fibularis brevis* muscle with a fully developed tibial head exists in species of the families Certhiidae (Moreno pers. obs), Paridae (Palmgren 1932, Moreno pers. obs), Regulidae (Palmgren 1932, Raikow 1978, Moreno pers. obs), and Fringillidae

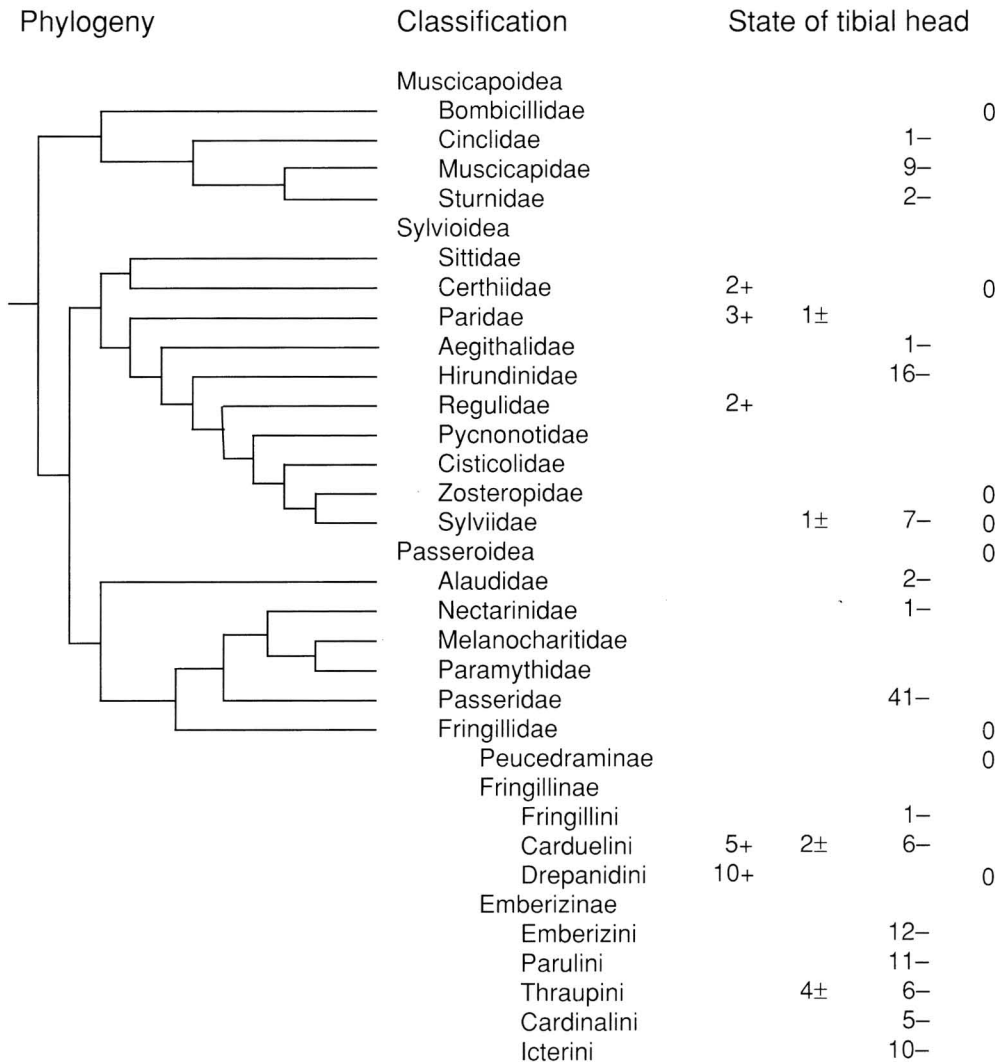


Fig. 4. Distribution of the state of the tibial head of the *fibularis brevis* muscle in the Passerida. +, fully developed; ±, partially developed; -, absent; 0, no available data. Number of species showing each state preceding the sign. Phylogeny from Sibley et al. (1988).

(Raikow 1978). Within the Fringillidae a two-headed *fibularis brevis* is present in the Drepanidini (creeping species) and some Carduelini (Fig. 4).

Among the carduelines dissected by Raikow (1978), the species with two fully developed points of origin in *fibularis brevis* have a greater propensity for clinging and/or hanging while feeding (more than 70% of their foraging time, Newton

1967), with the exception of *Chloris chloris*. Clinging to vertical surfaces requires a capacity for flexing the legs to keep the centre of gravity as close as possible to the vertical axis (Winkler & Bock 1976). Hence, modification of *fibularis brevis* seems likely to be related to tarsometatarsal flexion in some carduelines as well. Thus, within the superfamilies Sylvioidea and Passeroidea, species lacking the tibial head of *fibularis brevis*

also lack the habit of hanging, clinging and/or creeping. This supports the adaptive hypothesis.

The superfamily Muscicapoidea, the hypothesized sister group of the clade that includes the superfamilies Sylvioidea and Passeroidea (Fig. 4), has been chosen as the appropriate outgroup for testing the adaptive hypothesis. None of the Muscicapoidea species dissected to date show two points of origin in *fibularis brevis*. Nor are these species with a high propensity for hanging, clinging and/or creeping. This also provides support for the adaptive hypothesis.

On the basis of these results, it seems admissible to assume that species in which *fibularis brevis* has two points of origin are able to forage easily in a greater range of comfortable postures than species in which it has only the fibular head. McKittrick (1986) also found a correlation between the morphological variation in the *flexor cruris lateralis* muscle and the foraging behaviour (terrestrial vs. aerial) of the Tyrannidae. The present observations seem to agree with hers in indicating that morphology determines not only the technique that species are able to use to capture prey, but also the techniques which they cannot use.

Raikow (1977b, 1978) concluded that the presence of a tibial head in *fibularis brevis* is a derived condition in passerines. My results agree with his and seem to indicate that the modification of that muscle occurs as an adaptation in species with a high tendency to flex their legs.

The occurrence of a partially developed tibial head in some Sylvioidea and Passeroidea species (Fig. 4) might represent the intermediate state of the character between the primitive and the derived condition (Raikow 1977b), probably being a transient stage in the active process of evolution of the character. Such a transformation hypothesis is supported by the individual variation within *Chloris chloris* (presence vs. absence of a tibial head; Raikow 1978, Moreno pers. obs).

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