THE MUSCULI FLEXOR PERFORATUS DIGITI II AND FLEXOR DIGITORUM LONGUS IN PARIDAE[1]

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Abstract. The hindlimb muscles were studied in 17 passerine species. In comparison, *Parus* spp. showed several myological modifications involving muscles flexor perforatus digiti II and flexor digitorum longus. Considering changes in functional muscular properties these modifications are explained as adaptations of the leg apparatus for an increase in grasping strength in species with a high propensity for hanging upside down under branches. The adaptive hypothesis is tested on the basis of the outgroup comparison method.

Key words: Toe flexor muscles; morphology; Paridae.

INTRODUCTION

Studies recently undertaken on the morphology of the skeleto-muscular system of some European oscines have revealed the existence of some important modifications in the "normal" muscular pattern (George and Berger 1966, Berger 1969, Raikow 1985). Relative to the species examined to date parids have shown some myological modifications involving several toe flexors, in particular M. flexor perforatus digiti II. This muscle is situated on the caudolateral side of the crus and runs in a more superficial position in passerine birds than in other species (George and Berger 1966). It originates from the lateral femoral condyle either from a tendon shared with the lateral head of M. flexor hallucis longus (George and Berger 1966; Raikow 1976, 1978, 1987; Bentz 1979) or from a tendon shared with Mm. flexor perforans et perforatus digiti II and flexor perforans et perforatus digiti III (Hudson 1937, Stallcup 1954, George and Berger 1966).

In Trochilidae (Zusi and Bentz 1984) the tendon arises from the cranial edge of the common tendon of origin of Mm. flexor perforatus digiti III, flexor perforans et perforatus digiti II, and flexor perforatus digiti IV. The same occurs in Tyrannidae (McKitrick 1985) in which the tendon is also shared with M. flexor hallucis longus. Stallcup (1954) and Raikow (1987) described a tendinous connection between the fibula and the tendon from which M. flexor perforatus digiti II originates. Raikow (1978) showed *Rodinocichla rosea* as having a secondary head arising

from the surface of M. flexor hallucis longus. Palmgren (1932) has been the only one to point out this muscle as having some fibers arising from the tibia in *Parus atricapillus (montanus)*. However, his data have been overlooked by later authors.

Although it is not as highly modified as M. flexor perforatus digiti II, M. flexor digitorum longus also bears morphological modifications in Paridae. It is typically a two-headed muscle in passerines, one head arising from the fibula and another from the tibiotarsus (George and Berger 1966). A third, femoral head has been described in *Corvus* (Hudson 1937), *Paradisea rubra* (Berger 1956), Hirundinidae (Gaunt 1969), *Sericossypha albocristata* (Raikow 1978), *Lanius, Corvinella, Eurocephalus* (Raikow et al. 1980), most of the Tyrannidae studied by McKitrick (1985), and *Philepitta* (Raikow 1987).

The present study (1) provides new data on the morphology of Mm. flexor perforatus digiti II and flexor digitorum longus in some parid species, (2) proposes that modifications of those two muscles are adaptations favoring a grasping trend in species with an increased occurrence of hanging upside down in relation to other passerines, and (3) tests the adaptive hypothesis using an available phylogeny (Sibley et al. 1988) as a framework.

MATERIAL AND METHODS

The hindlimb muscles of preserved specimens of the following species were studied by dissection (number of specimens dissected follows in parentheses): *Alauda arvensis* (1), *Melanocorypha calandra* (1), *Motacilla flava* (1), *Locustella*

naevia (2), *Acrocephalus scirpaceus* (1), *A. arundinaceus* (1), *Muscicapa striata* (2), *Ficedula hypoleuca* (2), *Parus ater* (1), *P. caeruleus* (2), *P. major* (2), *Certhia familiaris* (2), *C. brachydactyla* (1), *Sturnus vulgaris* (1), *Passer domesticus* (1), *Carduelis chloris* (1), and *Emberiza citrinella* (2). Mm. flexor perforatus digiti II and flexor digitorum longus were also examined in *Sitta europaea* (1) and *Remiz pendulinus* (1).

The gross morphology of muscles was studied using an iodine staining technique (Bock and Shear 1972) to enhance visibility of fiber arrangements. Drawings were made with the aid of a camera lucida microscope. Anatomical nomenclature follows the Nomina Anatomica Avium (Baumel et al. 1979).

RESULTS

With the exception of *Parus* spp., the birds presently studied do not show significant differences in the arrangement of Mm. flexor perforatus digiti II and flexor digitorum longus from that of *Loxops virens* as described by Raikow (1976). However, in *Parus* those muscles are modified.

M. flexor perforatus digiti II lies on the lateral surface of the crus deep to M. flexor perforans et perforatus digiti III and cranial to the lateral head of M. flexor hallucis longus (Fig. 1). The belly is formed by fibers converging from two different heads. The tibial (cranial) head arises fleshy from the caudal edge of the outer cnemial crest on its distal half, deep to the cranial head of M. flexor perforans et perforatus digiti III. The fibular (caudal) head arises fleshy from the fibula cranio-laterally, just distal to its head, the origin extending about half the length of the fibular shaft, and some fibers arise from the tendon of origin of the lateral head of M. flexor hallucis longus. Fibers from the two heads converge on a central tendon to form a common, bipennate belly. The belly extends about half-way down the crus in *P. ater* and about two-fifths in *P. major* and *P. caeruleus*. The tendon of insertion passes distally along the tibiotarsus caudo-laterally and in close relation to the tendon of M. flexor perforans et perforatus digiti III, through the tibial cartilage and then through the centromedial canal of the hypotarsus. It runs down the plantar surface of the tarso-metatarsus to digit II, where it inserts medially on the base of the first phalanx. It is not perforated by the tendons of Mm. flexor perforans et perforatus digiti II or flexor digitorum longus (cf. Raikow 1978 for discussion of this
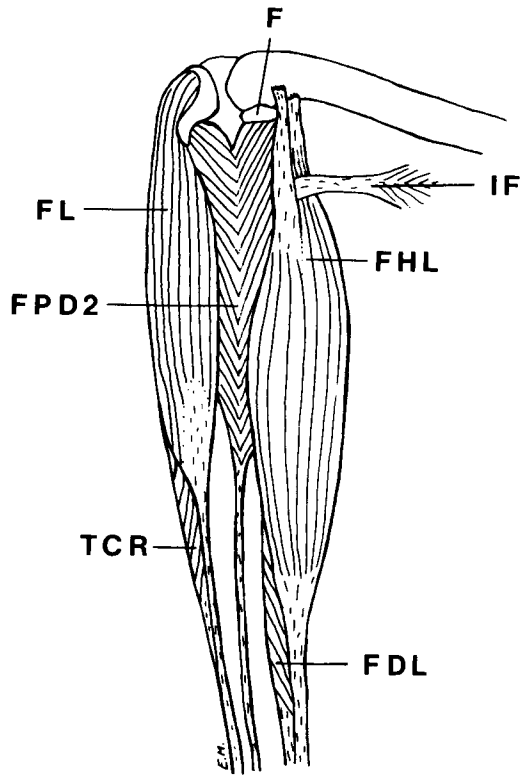

FIGURE 1. Lateral view of the crus of *Parus caeruleus*. The following muscles have been removed: M. gastrocnemius, pars lateralis; M. flexor perforans et perforatus digiti III. Abbreviations: F—fibula; FDL—M. flexor digitorum longus; FHL—M. flexor hallucis longus; FL—M. fibularis longus; FPD2—M. flexor perforatus digiti II; IF—M. iliofibularis; TCR—M. tibialis cranialis.

character in other species). Palmgren (1932) and Raikow (pers. comm.) found the same morphology of M. flexor perforatus digiti II in *P. atricapillus* (*montanus*).

M. flexor digitorum longus lies deep to M. flexor hallucis longus. In *Parus* spp. it is composed of two heads. However, it does not show the typical V-shaped origin (George and Berger 1966). A bigger medial (tibial) fan-shaped head (Fig. 2) originates by fleshy fibers in the whole caudal surface of the tibiotarsal head, some fibers also arising from nearly two-thirds of the caudal surface of the bone. A thin aponeurosis covers the outer surface of the muscle distally and contributes to the tendon of insertion. The lateral (fibular) head develops fleshy from the caudal side of the fibula, some fibers also arising from
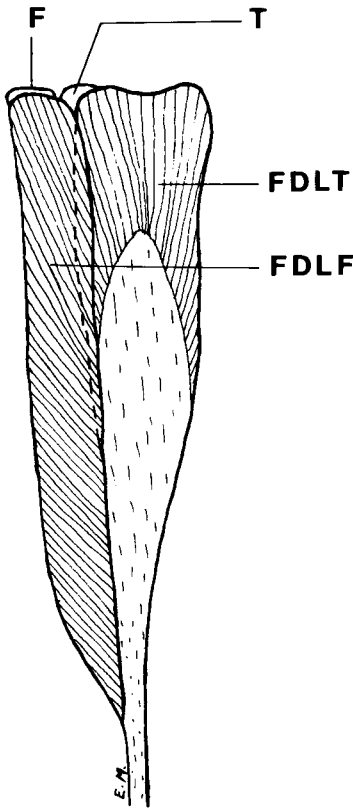
FIGURE 2. Caudal view of the crus of *Parus ater* showing the two heads of the origin of M. flexor digitorum longus. Abbreviations: F—fibula; FDLF—M. flexor digitorum longus, fibular head; FDLT—M. flexor digitorum longus, tibial head; T—tibiotarsus.

the adjacent tibio-tarsal head. Medially, it overlaps with the lateral border of the tibial head. The fibers have a unipennate arrangement running from the fibula to the aponeurosis covering the tibial head. The whole belly extends more than two-thirds the length of the crus. The tendon proceeds distally through the inner medial canal of the hypotarsus. It passes along the plantar surface of the tarsometatarsus and is divided at the level of metatarsal I into three branches, each of them passing along the plantar surface of digits II, III, and IV respectively. Each branch inserts into the base of the ungual phalanx and by an elastic band onto the distal end of the preungual phalanx (insertion pattern: AAA; Raikow 1978).

DISCUSSION

The comparative study of the hindlimb musculature of passerines presently studied has shown

that some toe flexor muscles are modified in *Parus* spp. towards an increase in their number of fibers, modifications involving Mm. flexor perforatus digiti II (presence of an extra head of origin and its more lateral location) and flexor digitorum longus (multipennate rather than bipennate in fiber arrangement). Considering both changes in functional muscular properties related to morphological modifications and foraging postures of the species concerned, the assumption that myological modifications found in Paridae are related to their increased hanging behavior relative to the rest of the forms studied, will be tested.

In *Parus* spp. the occurrence of two heads of origin on M. flexor perforatus digiti II gives rise to a shorter-fibered bipennate muscle, opposite to the longer-fibered unipennate muscle of the other species presently studied. As the number of fibers is increased the physiological cross section is also increased and thus the maximal force developed by the muscle (Bock 1974) and thereby the strength of flexion of digit II.

Modifications of M. flexor digitorum longus also increase its maximal force as the muscle is multipennate rather than bipennate in fiber arrangement. That is, the ability for toe flexion strengthens in *Parus* spp. It is assumed, therefore, that such modifications of some species of Paridae favor grasping.

Parid species have a high propensity for hanging under branches. Flexion of leg joints is needed to achieve this position, and the basic muscular requirements are directed towards an increase in force development, as muscles must counteract the effect of gravity. Modifications on Mm. flexor perforatus digiti II and flexor digitorum longus consisting of increased maximal force favor those requirements. This coincidence seems to indicate that toe flexor muscles under study are modified for helping toe joints to close in species which usually hang under branches while foraging, in the same way as Mm. iliotibialis cranialis and tibialis cranialis are modified for favoring to close the hip and intertarsal joints (Palmgren 1932) in such species.

It is proposed, therefore, that modifications on Mm. flexor perforatus digiti II and flexor digitorum longus are adaptations favoring a grasping trend in species with an increased hanging behavior and they would represent the derived states of the characters in *Parus*. This adaptive hypothesis assumes that the closest relatives of parids lack the morphological modifications and the

habit of hanging upside down. To test this hypothesis (1) close relatives of *Parus* that do hang upside down and (2) an appropriate outgroup that lacks the hanging behavior were examined.

Remiz pendulinus has been chosen as the closest relative of *Parus* that do hang. It does not show differences in the arrangement of those muscles analyzed herein from that of parids. This supports the adaptive hypothesis.

The outgroup needed for the second test has been chosen on the basis of the phylogenetic hypothesis available from Sibley et al. (1988). This includes certhiids and sittids, the hypothesized sister group to the clade that includes parids and remizids. *Certhia familiaris, C. brachydactyla,* and *Sitta europaea* have been examined and found to lack the morphological modifications and the hanging behavior. This provides support for the adaptive hypothesis as well.

Muscle flexor perforatus digiti II has two heads (the proposed derived state of the character) in some owls (Hudson 1937, George and Berger 1966), in *Fulica americana* (Rosser et al. 1982) and in some cranes (George and Berger 1966) among others. However, these birds do not hang. On the other hand, M. flexor digitorum longus shows an increased number of fibers (three heads of origin) in several nonhanging birds (Hudson 1937; Berger 1956; Gaunt 1969; Raikow 1978, 1987; Raikow et al. 1980; McKitrick 1985). However, no birds studied to date, beside *Parus* and *Remiz,* show both modifications. That is, there exist some nonhanging birds in which one or the other of the proposed adaptations does occur. However, the hanging behavior and the two anatomical modifications are correlated only in parids and remizids.

The second modification observed on M. flexor perforatus digiti II is location. It is lateral in Paridae instead of caudolateral. Lack of space (Raikow et al. 1980) is assumed to be the reason for this modification. The addition of a new mass of fibers to this muscle as well as the increased number of fibers of M. flexor digitorum longus makes space unavailable on the caudolateral side of the crus.

M. plantaris is absent in the species of Paridae studied. Although for a long time it was considered present in all passerines its absence has been reported in some Hirundinidae (Gaunt 1969), several New World nine-primaried oscines (Raikow 1976, 1978) and some estrildids (Bentz 1979). The role of this muscle has not been agreed upon by authors. However, the most widespread opinion is that it extends the tarsometatarsus either directly (Hudson 1937, Miller 1937) or through the proximal movement of the tibial cartilage (Gadow 1891, Owre 1967, Cracraft 1971). Absence of M. plantaris in those Paridae studied seems to corroborate such a role as it is absent in species with a high tendency for maintaining their leg joints closed.

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