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Title: Functional morphology and behavioral correlates to postcranial musculature

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Abstract

In this the second issue of a two-volume set of the *Anatomical Record* on the relationship between muscle functional morphology and behavior, the focus is on the postcranial musculature.

Traditionally, when talking of the postcranium we think of the skeletal parts that primarily provide the lever system necessary for body movements. However, without the force produced by muscle, the postcranial skeleton could not perform these or most other tasks. In this special issue, our colleagues present ten papers that focus on postcranial muscle morphology and function from different perspectives. They include papers on forelimb and hindlimb muscle functional morphology of vertebrates, including lizards, bats, primates, a carnivoran and a rodent, and involved in different substrate use (arboreal, terrestrial and flying) and locomotion behavior (quadrupedal, leaper, and suspensory) along with a historical overview to help bookend the contextualization of the issues. The picture that these papers provides is one of great liveliness in the field of muscle functional morphology where both young students and affirmed professors continue to contribute with both traditional approaches and new techniques to further our knowledge of muscle morphology and its relationship with animal behavior.

Key Words: Forearm muscles; Hindlimb muscles; Muscle fiber architecture; Arboreal; Terrestrial.

This special issue of the *Anatomical Record*, the second of a two-volume set focused on muscle functional morphology, focuses on the functional morphology of postcranial muscles and their correlates with behavior. Unlike in the cranium (the musculature of which was the subject of the first issue in the pair), the anatomy of the postcranium induces us to think primarily of "long bones," the arrangement of the beams that form the scaffolding that provides the lever system necessary for body movements. A lever system is, however, of no use in the absence of the forces that move the levers. And the forces that move the bones through space and against gravity are provided by muscles.

The muscular system is composed of muscle fibers whose main function is contractibility. Muscles attach to bones and are responsible for movement. Given that the movement of animals is primarily a consequence of the limb action on the substrate (with the notable exceptions of limbless species and taxa that move by other means like gliding), and given that limb movement is primarily the result of muscle contraction, it is easy to understand the great interest of functional morphologists in studying postcranial muscular architecture. The papers included in this second special issue on muscle functional morphology are mainly focusing on the relationship between muscle functional morphology and animal behaviors with special reference to locomotion. The study of animal locomotion has been one of the main focuses of the students of functional morphology since the beginning of the discipline, whose focus was mainly bone mechanics (Gregory, 1912). The importance of muscle action in producing movement has always been acknowledged, but muscles – whose knowledge was the results of classical comparative anatomy studies between animals involved in different behaviors – were often factored in as if they were simple vectors operating on the bone (Mosauer, 1932; Hartstone-Rose and Santana, 2018). Starting in the 1950s the application of electromyography led to investigating the electrical activity of muscles during various actions (Basmajian, 1957, 1972). Starting in the 1960s cineradiographic studies on the primate masticatory apparatus (Crompton and Hiiemae, 1967; Hiiemae and Adran, 1968; Hylander, 1977; Hylander et al., 1987) and locomotion (Stern et al., 1977; Susman and

Stern, 1979; Jungers and Stern, 1980) allowed researchers to formulate hypotheses concerning which muscle (or muscle group) was used in biologically important activities (Schmitt, 2003).

Traditional approaches to muscle functional morphology research focus mainly on the gross anatomy of muscles and their attachment to bones, while recently researchers are exploring muscle functional morphology using new approaches, in particular, analyses of fiber architecture – more elaborate analyses of the arrangements and dimensions of the fascicles and fibers present in a muscle. A growing body of studies is coupling traditional gross anatomical dissections with chemical dissection (Perry et al., 2011; Hartstone-Rose et al., 2012; 2018), Diffusible Iodine-based Contrast-Enhanced Computed Tomography (diceCT) and virtual dissection (Gignac et al., 2016; Dickinson et al., 2018; Santana, 2018) providing deeper information on muscle fiber architecture.

The appreciation of the crucial link present between postcranial muscle morphology and bone mechanics in association with the new techniques that have been developed in recent years is producing invaluable contributions to our understanding of animal behavior, and to the creation of models that can be applied in paleontology to infer extinct species behavior. Like the first volume in the series, this second issue on postcranial muscle functional morphology includes authors that participated in the symposium that we held at the 2016 International Congress of Vertebrate Morphology (Hartstone-Rose, Marchi, 2016), whose contributions focused on muscle functional morphology. In an attempt to provide a more comprehensive overview of the many new exciting results that students of muscle functional morphology and architecture are providing, we extended our invitation to several other colleagues so that we were able to include here contributions written by a vast array of researchers spanning from undergraduates to named professors and, as with the first issue, the contributions hail from colleagues representing many nationalities who focus on a wide range of anatomical regions and taxonomic groups. Below, we summarize the contributions in this issue in the order they appear.

The first contribution of this special issue is an anatomical investigation of the shoulder musculature by Michael Wade and colleagues from the Ziermann lab (Howard University College

of Medicine) which provides a fresh look at our understanding of the innervation of the three heads of the triceps brachii in humans (Wade et al., 2018, this issue). It is generally assumed that the motor innervation of the triceps brachii muscle originates from the radial nerve – indeed the standard teaching in gross anatomy is that the radial nerve innervates all of the muscles of the posterior compartment of the arm and forearm, though some studies contradict this assumption finding that the innervation of long head of the triceps (LHT) arises from the axillary nerve or directly from the posterior cord (De Sèze et al., 2004). By dissecting 27 human triceps, Wade and colleagues (Wade et al., 2018) found that the LHT is always innervated by the radial nerve. The authors also conducted a literature review where they found that in some cases the innervation of LHT is by the axillary nerve and suggested that the different methodologies used may create confusion in the results. The axillary nerve is often involved in shoulder injuries and knowing the precise prevalence of its innervation is therefore clinically relevant. The authors conclude with the suggestion that in the case of an axillary nerve trauma, the LHT should be examined and evaluated for any sign of paralysis and consequently treated, and that the standardization of the dissection of this region and presentation of data should be developed.

The next seven papers provide functional investigation of muscle morphology with special reference to the relationship between animal muscle architecture and habitat use. The first four of them focus on forelimb musculature. Aurélien Lowie (Muséum National d'Histoire Naturelle, France) and colleagues analyze the morphology of the forelimb flexor muscles in lizards and its correlation with the different habitats were they live (Lowie et al., 2018). This is an excellent example of how the study of muscle architecture can be useful to test hypotheses concerning animal behavior. Lowie and colleagues predicted that arboreal lizards have greater physiological cross-sectional area (PCSA) of the flexor muscles than do terrestrial lizards which would allow them to grip more firmly the substrate, and longer muscle fibers on the long digital flexors for enhanced reach and grasping ability in the arboreal environment. The authors found that only the PCSA of the flexor carpi radialis is different among arboreal and terrestrial lizards and explained this as the need

for arboreal species to have forceful flexion of the wrist to climb and gain better hold on branches. The absence of significant differences in the other muscles led the authors to suggest focusing future studies on other anatomical features, including other muscles and bone shape, and on *in vivo* measures of gripping performance to better understand how the arboreal locomotion of lizards may constrain forelimb morphology.

Arboreal animals are subject to different loading patterns, compared to terrestrial animals, which impose selective pressures affecting the evolution of their locomotor apparatus. Understanding how muscle architecture changes according to different substrate use can help understanding adaptation in living animals useful to identify osteological indicators that can be studied in fossils. In the next contribution, Christine Böhmer (Muséum National d'Histoire Naturelle, France) and colleagues compare the muscle architecture in two sympatric congeneric carnivorans, one more arboreal (pine marten, *Martes martes*) and one more terrestrial (stone marten, *Martes foina*) providing important architectural information on the muscles that are more involved in arboreal locomotion. In particular they find that force-generating capacity of the forelimb flexor and retractor muscles and the excursion capability of the adductor muscles are greater in the more arboreal marten compared to the more terrestrial one. Böhmer and colleagues (2018) interpret these results as reflecting the greater climbing abilities of pine marten by facilitating their locomotion in an arboreal environment.

Carissa Leischner (University of South Carolina School of Medicine) and colleagues (including both of us, DM and AHR) contributes a paper on the relationship between forearm muscle architecture and locomotion and substrate use in a sample of 44 primate species (Leischner et al., 2018, this issue). This is a notable study (see also Marchi et al., 2018) because it includes all major locomotor (quadrupedal, leapers and suspensory) and substrate uses (arboreal and terrestrial) in primates, and presents a sample spanning the entire body size and taxonomic breadth of the order. The authors find that larger primates have relatively stronger forearm muscles, but neither faster nor more flexible than smaller primates, similar to what has been found in previous studies on

the masticatory muscles (Hartstone-Rose and Perry, 2011; Perry et al., 2011; Hartstone-Rose et al., 2012). As previously noted, however, this observed functional trade-off between strength and stretch is accompanied by behavioral correlates. Leischner and colleagues (2018) find that terrestrial primates have shorter muscle fiber lengths than do arboreal primates and explain the results on the basis of the adaptation for greater speed and flexibility of the latter group in the trees. The authors suggest that these results can be used to refine biomechanical models that are usually referred to (i.e., in Jenkins, 1973) concerning joint stress and movement at the elbow joint. The last paper dealing mainly (but not only) with forelimb musculature is contributed by Scott Simpson (Case Western Reserve University School of Medicine) and colleagues. The authors investigate antebrachial muscle architecture in *Pan* and *Gorilla* to test the hypothesis that knuckle-walking in apes is an adaptation to recruiting the wrist and long digital flexor muscles as shock absorbers to mitigate the deleterious effects of the repetitive impulse loading on the forelimb (Simpson et al., 2018). Through a thorough review of the literature, the authors provide evidence for their hypothesis from forearm muscular architecture and torso shape in knuckle-walking apes compared to apes that do not knuckle-walk. They also suggest that some features of the carpo-metacarpal articulation, such as the dorsal shelf on lateral metacarpals, are not traits limiting motion in the hand and wrist during knuckle-walking but rather an alteration due to cartilaginous remodeling during ontogeny. The authors conclude their analysis by suggesting that all the evidence fits well with the proposed parallel evolution of knuckle-walking in *Pan* and *Gorilla* (Kivell et al., 2013).

The next three contributions address the problem of the relationship between muscle anatomy and habitat use investigating hindlimb muscular structure. The contribution by Kathryn Stanchak and Sharlene Santana (University of Washington) is the only paper in this second special issue dealing with flying animals (Stanchak and Santana, 2018). The authors focus on the membrane and limb muscles associated with the calcar, a structure found in the hindlimb of most bats which extends in the posterior margin of the uropatagium, and its relationship with flight

maneuverability. This paper is an excellent example of the application of new leading-edge technologies in muscle functional morphological studies, i.e. diceCT and virtual dissection. Bats are a very diverse clade with many dietary adaptations associated with different flight abilities. Stanchack and Santana (2018) include three species of bats, *Myotis californicus*, an aerial insectivore with relatively slow flight, *Molossus molossus*, an aerial insectivore with fast flight, and *Artibeus jamaicensis* a frugivore that forages within the cluttered forest. The authors find that calcar dimensions and the morphology of muscles that insert on it are consistent with the difference in flight performance documented in the three species and prove the importance of studying hindlimb musculature and uropatagium morphology to better understand bat flight. This paper clearly shows the potentiality of application of diceCT and virtual dissection in muscle functional morphological studies – especially important when very small musculature is present, as in the case of bats.

In the next paper, Joseph Rupert and colleagues from the Organ Lab (Indiana University School of Medicine), approach the investigation of arboreal morphological determinants examining the muscular plasticity in functional and structural properties of mice hindlimb (Rupert et al., 2018). The authors use as a model mouse known to have high developmental plasticity of the postcranial skeleton and raise a group of them in a climbing enclosure and a second group in a flat control enclosure with no climbing possibilities. In partial agreement with Lowie et al., (2018), Rupert and colleagues (2018) found that the mass and architecture of the muscles they analyzed (i.e. the soleus and the extensor digitorum longus) were not different between the mice raised in the climbing and non-climbing environments. Interestingly, however, examining the *ex vivo* contractility of the muscles, they found that the extensor digitorum longus of climbing mice contracted at higher rate compared to control. The authors explain this result as evidence that functional adaptation in muscles does not necessarily requires an architectural adaptation to achieve greater force contractility, an important finding to consider in future research dealing with the functional morphology of muscles.

Next, our own team has contributed an investigation of the correlation of leg muscle architecture and locomotion patterns and substrate use in extant primates (Marchi et al., 2018). We carried out this study to test if leg muscle architecture correlated with primate behavior following what has been observed for leg bone structure (Marchi, 2007; 2015). We provide data from a vast array of primates species involved in both arboreal and terrestrial substrate use, in quadrupedal, leaper and suspensory locomotor behavior for both strepsirrhines and haplorrhines. As for forelimb muscles (Leischner et al., 2018; many derived from the same individuals as those used in this paper), we find that larger primates are relatively stronger than smaller ones, but they have relatively shorter leg muscle fibers than do smaller primates. Results also show that leapers possess larger plantarflexor belly vs. muscle tendon unit ratio and surprisingly nonsignificant results are found concerning the correlation between muscle architecture and substrate use and locomotor groups. However, we highlight a series of trends and suggest that a larger sample (perhaps as large as the one we were able to present in the forearm study) and a more fine-grained definition of the categories included in the study may provide significant results. These results show the complexity of the relationship between muscle architecture and bone biomechanics and call for future research on this topic.

The main topic treated in the above summarizes contributions to this special issue – muscle architecture and its relationship with different locomotor behaviors – has traditionally been the main focus of students involved in muscular structure analyses (Tuttle, 1972; Langdon, 1990; Payne et al., 2006; Michilsens et al., 2009; Tulli et al., 2011; Carrizzo et al., 2014). The next contribution by Magdalena Muchlinski (University of North Texas) and colleagues provides a different perspective in the study of muscle architecture by addressing evolutionary questions about energetics, in particular to challenge the “expensive tissue hypothesis” (Aiello and Wheeler, 1995) which proposes that energetic demands imposed on the body by the brain result in a reduction in other expensive tissue such as the gastrointestinal tract (Muchlinski et al., 2018). The authors hypothesize instead that primates with larger brains will have less muscle mass and muscle fibers that convert

glucose to ATP using oxygen (type I fibers). To test their hypothesis they collect body mass, muscle mass and histological information from biopsied muscles from 11 species of primates and compare their results with endocranial volume collected from the literature. The authors use an innovative approach to muscle fiber composition study: instead of examining fiber composition of a single muscles across several species, they studied four muscles for each species in order to approximating total muscle fiber composition. Results show an inverse correlation between brain size and muscle size and type I fibers. Moreover, the authors find that primates have more type II than type I muscle fibers. Muchlinski and colleagues (2018) suggest that these findings are indicative of a possible energetic trade-off between relative brain size and relative muscle size. The authors suggest expanding, in future studies, the number of muscles analyzed for each species and to use more refined histological techniques to identify fiber type to further test their hypothesis.

The final contribution, by Jonathan Perry and Kristen Prufrock's (The Johns Hopkins University School of Medicine), is a literature review of muscle functional morphology studies (Perry and Prufrock, 2018). After providing a description of what muscle functional morphology consists of, the authors guide us through the main achievements of the discipline since the beginning of the twentieth century. They introduce the reader to the importance of experimental studies on muscle activity (i.e. electromyography) as well as of "traditional" comparative anatomy studies to understand muscle functional morphology. Then, the authors talk about the importance of muscle fiber architecture study in advancing the fields of locomotor and feeding biomechanics (two themes strictly correlated with this issue and the previous one on muscle functional morphology). Perry and Prufrock (2018) also talk in detail about the main changes that happen to muscles during ontogeny and as consequence of exercise. Finally, they outline the important inferences about behavior that the study of muscle functional morphology allows as to make on fossil species.

The papers in this special issue provide a good example of the many different points of view through which we can approach the study of muscle functional morphology and to the many questions that such studies can address. Using different methodologies and approaches and studying

different species, the contributions of this volume give a view of the new tendencies in muscle functional anatomy studies. We hope they will stimulate and inspire other students, especially young ones, to collect new data and to test new methods to increase our knowledge of muscle morphology and its relationship with animal behavior.

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