



Muscular anatomy of the legs of the forward walking crab, *Libinia emarginata* (Decapoda, Brachyura, Majoidea)

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ABSTRACT

Decapod crustaceans have been the focus of neuroethological studies for decades. With few exceptions, however, their musculature remains scarcely described. We study the neuroethology of legged locomotion in the portly spider crab, *Libinia emarginata* (Brachyura, Majoidea), which preferentially walks forward. Majoid crabs are thought to be among the first to have adopted the crab form (carcinification) from lobster-like ancestors, making them interesting subjects for comparative and phylogenetic studies. The radial arrangement of the legs around the thorax, coupled with its unidirectional walking modality makes *L. emarginata* a good candidate for the presence of anterior and posterior limb specializations. Here we describe the complete muscular anatomy of all the pereopods of *L. emarginata* and compare our findings with other decapods described in the literature. The number of proximal muscle bundles differs between the anterior and posterior pereopods of *L. emarginata*. We describe an intersegmental bundle of the flexor muscle similar to the one present in distantly related, forward walking macruran species. The behavioral repertoire, amenability to experimental investigations, and phylogenetic position make spider crabs useful species for the study of the neural control of legged locomotion. To our knowledge, this is the first instance of a complete description and comparison of the musculature in all the locomotor appendages of one species.

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1. Introduction

Decapod crustaceans have been used successfully in the study of behavior and neuroscience for many decades (Atwood, 1977; Clarac et al., 1987; Hoyle, 1975; Huxley, 1880; Macmillan, 1975; Paul, 2006; Rathmayer and Bévangut, 1986). They perform interesting and diverse behaviors (Faulkes and Paul, 1997, 1998; Hoyle and Burrows, 1973; Hoyle, 1973) with relatively simple and accessible nervous systems. Because of the diversity of research approaches that these organisms accommodate, they have contributed much to neuroethology (Atwood, 1977; Clarac, 1977; Macmillan, 1975; Sattelle and Buckingham, 2006). Despite the important progress achieved in diverse fields dealing with the study of animal behavior, however, our knowledge of the muscular anatomy of these organisms has not kept up with advances in other aspects of neuroethology (examples of work in the field are Antonsen and Paul, 2000; Bévangut et al., 1983; Boxshall, 2004; Cochran, 1935; Hessler, 1982; Huxley, 1880; Pilgrim, 1964; Pilgrim and Wiersma, 1963), and remains patchy at best.

Research on the walking machinery of crustaceans is usually carried out on individual legs chosen for their accessibility and often under the assumption that different legs behave similarly. This assumption was supported in sideways walking brachyurans by the finding that different legs are used in similar fashion (with the exception of the specialized terminal pereopods) (Barnes, 1975; Burrows and Hoyle, 1973; Clarac et al., 1987). Sideways walking is bidirectional in nature (the same leg can be leading or trailing on different occasions); however, the same adaptations that allow animals to walk in opposite directions might also prevent the specialization of limbs for walking in a particular direction, as is often the case for animals that walk forward (Ritzmann et al., 2004). For example, animals that walk unidirectionally have limbs anterior to the center of mass that always pull, and limbs behind it that always push. This division in labor can lead to the specialization into hind and fore limbs observed in diverse taxa. In crustaceans, forward walking crayfish (Jamon and Clarac, 1994, 1997) and lobsters (Macmillan, 1975; Ritzmann et al., 2004) have different legs that assume different roles in forward walking behavior.

Although capable of walking sideways, the portly spider crab (*L. emarginata*) is a brachyuran that walks preferentially forward

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(Schreiner, 2004; Vidal-Gadea et al., 2008). Spider crabs are majoids and as such are thought (Rice, 1983; Morrison et al., 2002) to be basal to the brachyurans. Because they are not laterally compressed (as is the case for many decapods), the thoracic nervous system of spider crabs is ventrally accessible without disruption of the walking musculature. The behavioral repertoire, accessible nervous system, and phylogenetic position of *L. emarginata* make an excellent model for the study of the neural control of legged locomotion. The present study is the second of a series looking at the anatomy and physiology of *L. emarginata*, and how they relate to its locomotor behavior. We have previously shown (Vidal-Gadea et al., 2008) that *L. emarginata* has skeletal adaptations that reflect its walking preference. We hypothesized that the forward walking spider crabs possess differences in musculature between anterior and posterior pereopods that reflect their specialization into fore limbs and hind limbs. As part of our ongoing neuroethological studies of walking behavior, we describe the complete muscular anatomy of the legs of *L. emarginata* in order to gain understanding of the adaptations that are concomitant with forward walking.

2. Material and methods

2.1. Animals used

L. emarginata ($n = 10$) were obtained from the Marine Resources Center of the Marine Biological Laboratories in Woods Hole, Massachusetts, and kept at 20 °C in artificial seawater.

2.2. Muscular anatomy

We used male and female crabs that ranged 7–10 cm in carapace length. Animals were euthanized by cooling and dissected dorsally. The carapace was removed and the animals were immersed in crab saline. Methylene blue enhanced contrast between the muscles. Photographs were obtained by mounting a digital camera on a dissecting microscope and used to generate musculature drawings in Corel Photo-Paint.

3. Results

3.1. Pereopod architecture

As with other brachyurans, the five pereopods of spider crabs consist of six segments (Fig. 1) that articulate with each other via bicondylar joints. This restricts the range of motion of each segment to a single plane. Most of these planes are positioned so that they are perpendicular to that of their neighbor. The sole exception to this is the basis–ischiopodite joint which pitches the axis of the leg forward and thus allows crustaceans to articulate their legs in a wide range of directions.

3.2. Distal musculature

The distal musculature of decapod crustaceans is highly conserved and has been described in a number of diverse taxa (Atwood, 1977; Clarac and Vedel, 1971; Hessler, 1982; Wiersma and Ripley, 1952). The distal musculature of spider crabs resembles that described for related species. All but two distal muscles have common features between the different pereopods. For this reason, the description of the distal musculature (unless stated) applies to all the pereopods of this animal.

3.2.1. Opener muscle

The opener muscle (Fig. 2), responsible for abduction of the dactyl, originates on the dorsal half of the propodite segment and

inserts on a single apodeme that is connected to the dorsal projection of the dactyl. In the first pereopod, this muscle is much reduced to accommodate the larger closer muscle.

3.2.2. Closer muscle

The closer muscle, which closes (adducts) the dactyl, originates on the ventral half of the propodite and inserts onto a single apodeme attached to the ventral projection of the dactyl. The enlarged first propodite of *L. emarginata* possesses a larger closer muscle that occupies much of the volume of this segment. This particular muscle is further differentiated from other closers in that the muscle fibers are more oblique (and correspondingly shorter) than in other legs. The fiber arrangements in the first pereopod allow this muscle to accommodate a larger number of (shorter) fibers than homologs in posterior legs (Fig. 2).

3.2.3. Stretcher muscle

The stretcher muscle is similar in each of the pereopods. It originates on the posteroproximal half of the carpopodite and inserts onto a single, wide apodeme connected by arthrodistal membrane to an invagination on the posterior edge of the propodite (Fig. 2). This muscle is responsible for adduction of the propodite and moves this segment in the posterior direction.

3.2.4. Bender muscles

The bender muscles, responsible for flexing the propodite in the anterior direction (forwards) originate on the proximal and anterior edge of the carpopodite, and insert onto a broad apodeme connected by arthrodistal membrane to an invagination on the anterior edge of the propodite (Fig. 2). Although this muscle is practically identical in pereopods 2–5, it is different in pereopod 1. Pereopod 1 has two bender muscles with distinct origins and apodemes (Fig. 2). The largest bender in leg 1 is similar to the bender in the rest of the legs in origin, attachment and size. There is a smaller bender muscle that inserts on a smaller apodeme just dorsal to the main bender muscle (Fig. 2). We also found this pair of muscles in the first pereopods of the green shore crab *Carcinus maenas*, and the crayfish *Procambarus clarkii* (data not shown).

3.2.5. Extensor muscle

The extensor muscle shares many features with the opener. It consists of a single muscle of dorsal (and proximal) origin in the meropodite segment, which inserts onto a single apodeme that is connected to the dorsal edge of the carpopodite by arthrodistal membrane (Fig. 2). The fibers of this muscle are long and run less perpendicularly to the axis of the apodeme than flexor fibers.

3.2.6. Flexor muscles

The flexor muscle is anatomically the most complex of the distal muscles. It consists of two apodemes and five muscle heads.

3.2.6.1. Main flexors. The main flexor muscle, together with the closer in leg 1, is one of the two largest distal muscles. It originates on the ventral half of the meropodite segment and inserts onto a long apodeme. The anterior half of this apodeme connects, via the arthrodistal membrane, directly to the carpopodite. The posterior half of the main flexor apodeme inserts via a flexible ligament onto an anterior lip of the apodeme of the accessory flexor apodeme (see insert “a” in Fig. 2). The flexor of *L. emarginata* differs from related species (Parsons and Mosse, 1982) in having two additional muscle bundles that insert onto the narrow proximal lip of the main flexor apodeme. A small muscle bundle originating proximally on the postero-ventral edge of meropodite (Flexor_p, see Table 1 for

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