

Evolution of Locomotion in Arachnida: The Hydraulic Pressure Pump of the Giant Whipscorpion, *Mastigoproctus giganteus* (Uropygi)

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ABSTRACT Many arachnids lack extensor muscles at the femoropatellar (knee) joint of their legs and extend this joint with hydraulic pressure during locomotion. Pressure is generated through compression of the prosoma, but there is disagreement about which muscles are involved in this process. Many arachnologists consider contraction of the *musculi laterales*, a group of modified extrinsic leg muscles, as the cause of high prosomal pressure and regard hydraulic extension as a derived feature. However, integration of results from phylogenetic and comparative anatomical studies supports the view that hydraulic extension is primitive in Arachnida and that fluid pressure is generated by contraction of endosternal suspensor muscles.

The functional predictions of the *musculi laterales* and endosternite hypotheses were tested by measuring muscle activity and prosomal pressure during unrestrained locomotion in a primitively "extensorless" arachnid, the giant whipscorpion. The results corroborate the endosternite model and refute the *musculi laterales* model. Changes in the prosomal pressure baseline were correlated with changes in endosternal muscle activity, while the *musculi laterales* fired in a step-coupled pattern of discrete bursts that appeared to be incapable of generating the pressure observed during locomotion. Step-coupled fluctuations in prosomal pressure were observed but were apparently caused by rapid flexing of the femoropatellar joints of the fourth leg pair rather than contraction of the *musculi laterales*.

Many arachnids lack extensor muscles at the femoropatellar (knee) joints of their walking legs but extend these joints by increasing the fluid pressure of their bodies. Several studies have shown that spiders (Araneae) extend the femoropatellar joints with pressure generated through compression of the prosoma (Wilson and Bullock, '73; Stewart and Martin, '74; Anderson and Prestwich, '75; Prestwich, '88; Paul et al., '89), but the muscles used in this process have not been identified conclusively. Arachnologists have proposed two hypotheses to explain pressure generation, the *musculi laterales* and endosternite hypotheses. Supporters of the *musculi laterales* hypothesis generally regard the absence of extensor muscles and use of hydraulic extension as derived features (Wilson, 1970; Anderson and Prestwich, '75; Rovner, '80), but the endosternite hypothesis is consistent with the view that hydraulic extension is the primitive method of propul-

sion in Arachnida (Parry, '60; Shultz, '89). The purpose of this study is to test the evolutionary and functional predictions of these two hypotheses.

In his study of the skeletomuscular anatomy of spiders, Wilson ('70) noted an association between levels of locomotor activity and the development of certain prosomal muscles, the *musculi laterales* (Fig. 5AC). These muscles are largest in salticid jumping spiders but are also well developed in "wandering" spiders such as lycosids and pisaurids. The *musculi laterales* are smallest in web-weaving spiders, which presumably do not rely as much on propulsive leg extension as vagrant species. These observations have led many arachnologists to conclude that hydraulic pressure used in joint extension is generated through contraction of the

musculi laterales. Supporters of this view typically regard the absence of extensor muscles and use of hydraulic extension as derived features of spiders that may have evolved to enhance use of the legs in prey capture (Anderson and Prestwich, '75; Rovner, '80).

Alternatively, several workers have suggested that fluid pressure in many arthropods is altered by contraction of segmentally arranged dorsoventral muscles associated with the mesodermally derived internal skeleton, the intersegmental tendon system or endosternite (e.g., Gaubert, 1892; Mitchell, '57; Hessler, '64; Firstman, '73; Cisne, '81). Although uncertain as to the precise mechanism by which arachnids generate hydraulic pressure, Parry ('60) argued that absence of extensors and use of hydraulic extension are primitive features that were maintained or enhanced in certain arthropods, including spiders, a view supported by a recent comparative study of appendicular musculature in Arachnida (Shultz, '89). Thus it is possible that the hydraulic pump of ancestrally "extensorless" arachnids is powered by contraction of endosternal muscles, a hypothesis that Wilson ('70) dismissed in his discussion of hydraulic extension in spiders.

This paper tests the evolutionary and functional predictions of the musculi laterales and endosternite hypotheses. The sequence of character transformations predicted by these hypotheses is compared to that derived from a well-supported cladogram of the arachnid orders. Results from this analysis indicate that absence of femoropatellar extensor muscles and the use of hydraulic leg extension are primitive for arachnids, thus refuting the widely held view that these features are uniquely derived in spiders. The analysis also reveals an association between the origin and elaboration of femoropatellar extensor muscles and reduction of the endosternite, an evolutionary pattern consistent with the view that endosternal suspensor muscles generate the pressures used by primitively "extensorless" arachnids during locomotion.

The functional predictions of the endosternite and musculi laterales models of hydraulic pressure generation were tested by recording muscle activity and prosomal pressure in freely walking whipscorpions, *Mastigoproctus giganteus* (Uropygi). The analysis revealed a correlation between prosomal pressure and the activity of endosternal suspensor muscles. In contrast, the musculi laterales displayed a cyclical pattern of discrete bursts,

a pattern that cannot account for the elevated pressure baseline observed during locomotion. Cyclical fluctuations in prosomal pressure occurred in walking whipscorpions but appeared to result from volume changes associated with leg movements, specifically rapid flexion of leg 4 during protraction, rather than contraction of the musculi laterales.

HISTORICAL ANALYSIS OF THE LOCOMOTOR APPARATUS

Our understanding of the evolution of structure and function has been enhanced through the integration of phylogenetic systematics and functional morphology. A well-corroborated phylogenetic reconstruction generated through cladistic analysis can serve as a historical framework for generating and testing hypotheses concerning the direction and relative timing of specific evolutionary transformations (Lauder, '81, '90). Because the viability of a transformational hypothesis generated through historical analysis is intimately linked with that of the cladogram upon which it is based, re-evaluation of phylogenetic reconstructions with additional characters provides a means by which transformational hypotheses can be tested and potentially falsified (Coddington, '88).

The present analysis attempts to test the evolutionary predictions of the musculi laterales and endosternite hypotheses of hydraulic pressure generation. Three components of the prosoma, specifically the femoropatellar joints and endosternite and extrinsic leg muscles, are examined in representatives from several recent arachnid orders, and the results are interpreted within the context of the most well-supported cladogram available. The direction and relative timing of evolutionary transformations predicted by the endosternite and musculi laterales models are compared to those indicated by the cladogram.

Arachnid phylogeny

The phylogenetic reconstruction of Arachnida employed in the present study was derived from a computer-assisted cladistic analysis of 64 morphological and behavioral characters (Shultz, '90) (Fig. 1). The phylogenetic relationships suggested by this cladogram differ substantially from previous interpretations (Pocock, 1893; Firstman, '73; Yoshikura, '75; Kraus, '76; Weygoldt and Paulus, '79; van der Hammen, '89), and sev-

eral of the relationships hypothesized here, particularly the placement of *Scorpiones*, remain controversial.

Comparative anatomy of the prosoma Femoropatellar joint

The typical arachnid walking leg is composed of seven segments: coxa, trochanter, femur, patella, tibia, tarsus (divided into a basitarsus and telotarsus), and pretarsus (= apotele) (Fig. 2C). There are substantial differences among arachnids in the structure of the articulations and the arrangement of muscular origins and insertions. The structure of the femoropatellar joint is of particular interest as it is the principal site of propulsive extension in most arachnids. Outgroup comparisons with xiphosurans and reconstructions of eurypterids (Selden, '81) and trilobites (Cisne, '81) suggest that the femoropatellar joint in arachnids was originally formed by a dorsal hinge articulation, an arrangement that permits flexion and extension but precludes effective use of extensor muscles. The apparent sequence of skeleto-muscular innovations associated with the evolution of the femoropatellar extensor muscles from the primitively "extensorless" condition encompasses much of the morphological diversity in arachnid legs (Shultz, '89) (Fig. 3).

The appendicular anatomy of *Limulus polyphemus* (Xiphosura) lends insight into the primitive arrangement of muscles at the femoropatellar joint in arachnids. In addition to a battery of flexors originating in the femur and trochanter, the femoropatellar joint in xiphosurans is traversed by paired muscles, the anterior and posterior transpatellar muscles, that arise on the distodorsal surface of the femur and walls of the patella and insert on the anterior and posterior tibial margins, respectively. Because the patella joins the tibia at a single dorsal pivot, the transpatellar muscles may function, at least in part, as promotor and remotor of the patellotibial joint, respectively. This arrangement of articulations and muscles is retained to a large extent in mites, spiders, paligrades, and, with some modifications, amblypygids and uropygids (Shultz, '89).

Femoropatellar extensor muscles are present in scorpions, pseudoscorpions, and many opilionids and appear to have evolved through modification of the posterior transpatellar muscle (Fig. 3). The extensor appears to be synapomorphic for these taxa. The arrangement of the transpatellar mus-

cles in palpator opilionids, which include the harvestmen or daddy-longlegs, represents a comparatively primitive stage in extensor evolution. The posterior transpatellar muscle has lost its connection to the patella, and its origin on the femur has shifted to a process that extends above the condyles of the femoropatellar joint, a reorganization that allows the muscle to act as a femoropatellar extensor. The muscle retains its primitive insertion on the posterior tibial margin and presumably its primitive function as a patellotibial remotor. The arrangement of the anterior transpatellar muscle in palpator opilionids is similar to that in *Limulus*, spiders, mites, and other arachnids that lack extensors.

The basic structure of the femoropatellar joint and posterior transpatellar muscle in scorpions and certain pseudoscorpions is essentially the same as in opilionids. However, the patella has apparently undergone a 90° rotation such that the anterior and posterior margins of the patellotibial joint correspond to the ventral and dorsal margins of opilionids and other arachnids. This modification changed the function of the posterior transpatellar muscle from a patellotibial remotor to a patellotibial extensor. Thus the posterior transpatellar muscle in scorpions and certain pseudoscorpions acts to extend the femoropatellar and patellotibial joints simultaneously. The posterior transpatellar muscle is absent in solifuges, the apparent sister group of pseudoscorpions (Weygoldt and Paulus, '79; van der Hammen, '89; Shultz, '90), but there is evidence that the patellotibial joint underwent the same 90° rotation that apparently occurred in the ancestors of scorpions and pseudoscorpions. Solifuges appear to extend their legs with an elastic mechanism (Shultz, '89).

Endosternite

The endosternite is a horizontal sheet of non-contractile connective tissue that occupies the ventral region of the prosoma and extends into the first opisthosomal segment (Firstman, '73) (Fig. 2). It is suspended within the hemocoel by a series of metamericly arranged muscles that correspond in arachnids to postoral segments III through VII. The endosternite is connected to the carapace within each segment via paired dorsal and dorsolateral suspensor muscles and to the sternum through paired ventral suspensors. The endosternite and its suspensor muscles appear to be homologous with the inter-

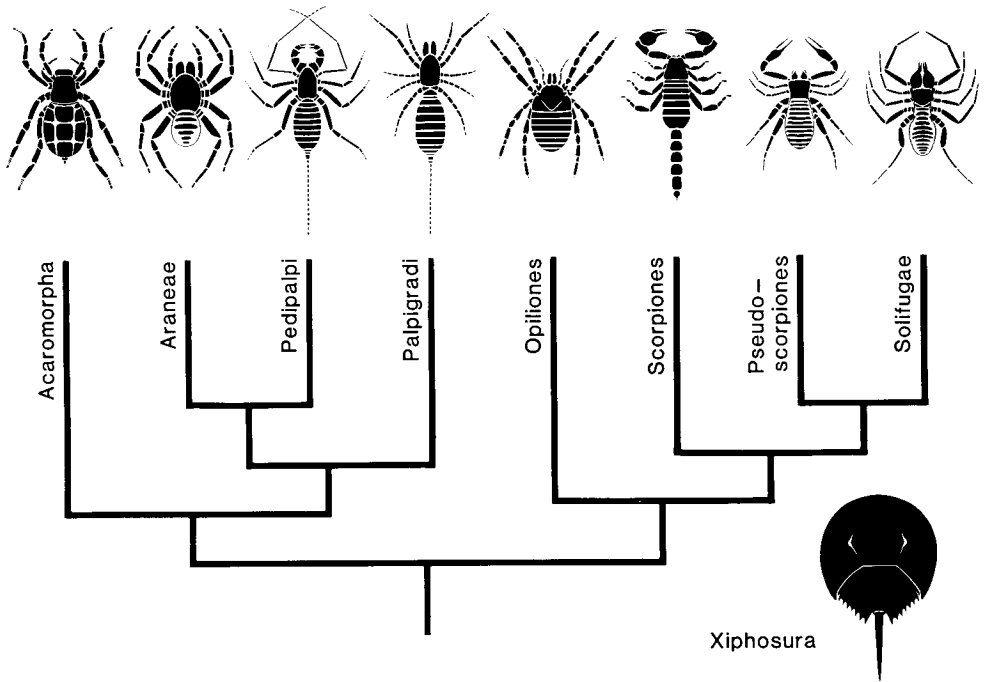


Fig. 1. Phylogenetic relationships of major arachnid lineages as suggested by computer-assisted cladistic analysis of 64 characters (Shultz, '90). Acaromorpha includes the orders Ricinulei and Acari; Pedipalpi includes the orders Amblypygi and Uropygi (= Schizomida + Thely-

phonida). Character polarity was established through outgroup comparisons with xiphosurans, eurypterids, pycnogonids, trilobites, and cephalocarid crustaceans. The cladogram has a consistency index of 0.59.

segmental tendon system of other arthropods (Boudreaux, '79).

The endosternite is well developed in palpi-grades, spiders, amblypygids, and uropygids, where it retains a nearly full complement of suspensor muscles (Figs. 2, 5A-C). Outgroup comparisons indicate that a well-developed endosternite with many suspensor muscles is the primitive condition for arachnids. The endosternite in xiphosurans is primitive in being large but has lost several of the posterior suspensors (Fig. 4). As a consequence, the intersegmental tendon systems observed in cephalocarid crustaceans (Hessler, '64) and that hypothesized for trilobites (Cisne, '81) may be more appropriate models of the primitive arachnid condition (Shultz, '90). The prosomal endosternite is greatly reduced in opilionids, scorpions, and pseudoscorpions, retaining two pairs of suspensors at most (Fig. 6A-C), and is essentially absent in solifuges (Firstman, '73).

Extrinsic leg muscles

Comparative morphological studies indicate that each leg of the arachnid ancestor

was probably equipped with nine extrinsic muscles that inserted symmetrically along the coxal margin. Five of these muscles, the tergocoxals, originated on the carapace, and four, the endosternocoxals, originated on the endosternite (Fig. 2). This general arrangement of extrinsic leg muscles occurs in Xiphosura (Snodgrass, '52; Manton, '64; Wyse and Dwyer, '73) (Fig. 4) and several arachnid lineages, including spiders (Whitehead and Rempel, '59; Palmgren, '78, '81) (Fig. 5A), amblypygids (Fig. 5B), uropygids (Fig. 5C), and opilionids (Fig. 6A). A similar pattern is also present in reconstructions of trilobites, although the anterior and posterior tergocoxals may not have been differentiated into distinct medial and lateral components (Cisne, '81). The number of extrinsic muscles is reduced in scorpions (Beck, 1885) (Fig. 6B), pseudoscorpions, (Fig. 6C) and solifuges, a feature associated with reduction of coxal movement in these arachnids.

The lateral tergocoxals are modified in spiders and uropygid whipscorpions (Fig. 5AC) and are termed musculi laterales (Wilson,

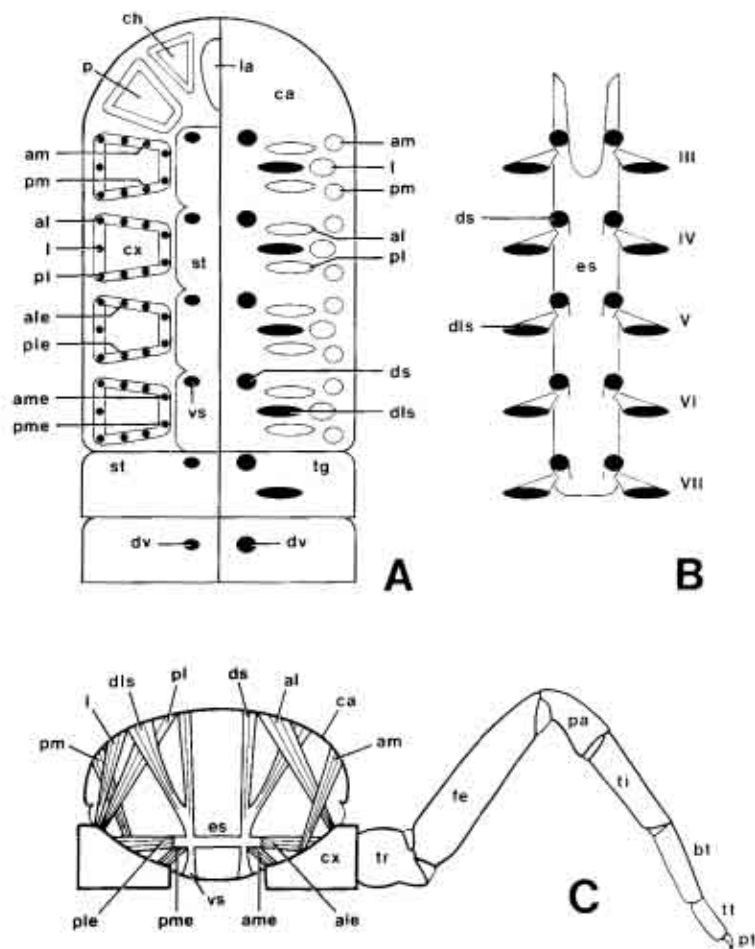


Fig. 2. Diagrammatic arachnid illustrating primitive features of the skeletomuscular system suggested by outgroup comparisons and parsimony analysis. The prosoma is formed by fusion of six postoral, appendage-bearing segments (I–VI). The anterior segment bears the feeding appendages or chelicerae (ch) and the second bears the pedipalps (p). The four remaining segments are equipped with walking legs (1–4). The dorsal surface of the prosoma is covered by a single large sclerite, the carapace (ca), and the ventral surface is formed by a sternum (st), a preoral labrum (la), and the proximal segments or coxae (cx) of the appendages. A horizontal sheet of noncontractile connective tissue, the endosternite (es), is suspended between the carapace and sternum and extends posteriorly into the first opisthosomal segment. There are five sets of endosternal suspensor muscles representing postoral segments III–VII, each set consisting of paired dorsal (ds), dorsolateral (dls), and ventral (vs) suspensors. The endosternite is replaced in most opisthosomal segments by paired dorsoventral muscles (dv) that link the dorsal tergite (tg) with the ventral sternite (st). Dorsoventral muscles are serially homologous with the dorsal and ventral endosternal suspensors. The coxa of each walking leg is equipped with nine extrinsic muscles, five tergoxal muscles originating

from the carapace, and four endosternocoxal muscles originating from the endosternite. **A:** Dorsal view of the prosoma and anterior opisthosoma. The right side shows sites where extrinsic leg muscles and endosternal suspensors attach to the carapace. The left side depicts the internal ventral surface of the body with the carapace, tergites, and endosternite removed to show attachments of extrinsic leg muscles and ventral endosternal suspensors. **B:** Dorsal view of the endosternite. **C:** Anterior view of a cross section through the prosoma showing arrangement of extrinsic leg muscles and the endosternite. The right side shows the anterior extrinsic leg muscles, and the left side shows the lateral and posterior extrinsic muscles with the anterior muscles removed. Abbreviations: bt, basitarsus; ca, carapace; ch, chelicera; cx, coxa; dv, dorsoventral muscle; es, endosternite; fe, femur; la, labrum; p, pedipalp; pa, patella; pt, pretarsus; st, sternite or sternum; tg, tergite; ti, tibia; tr, trochanter; tt, telotarsus. Endosternal suspensors: ds, dorsal suspensor; dls, dorsolateral suspensor; vs, ventral suspensor. Endosternocoxal muscles: ale, anterolateral; ame, anteromedial; ple, posterolateral; pme, posteromedial. Tergocoxal muscles: al, anterolateral; am, anteromedial; l, lateral; pl, posterolateral; pm, posteromedial.

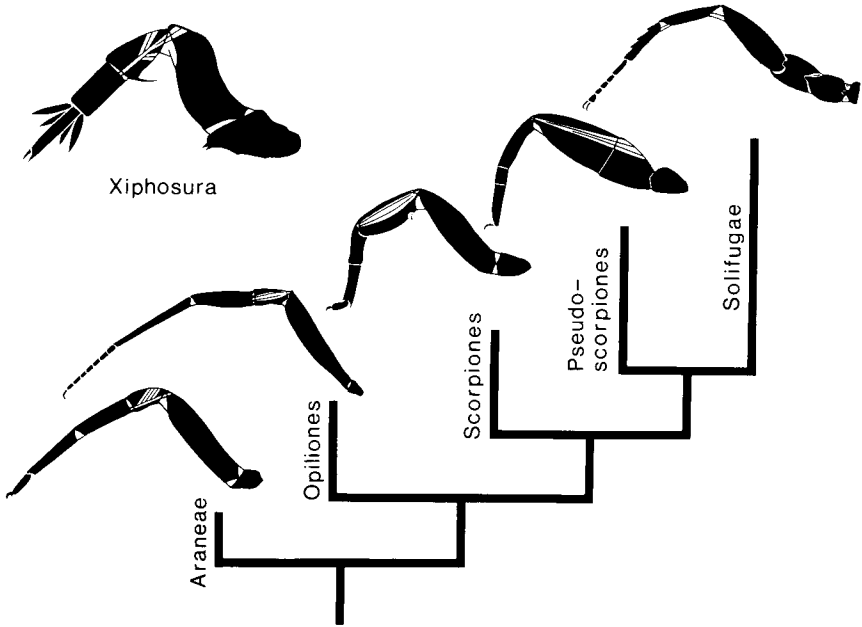


Fig. 3. Evolution of the posterior transpatellar muscle in arachnid walking legs. Each drawing depicts a posterior view of the fourth walking leg from the left side of the body; only the posterior transpatellar muscle is depicted. The femoropatellar joint in *Xiphosura* is traversed by symmetrically paired transpatellar muscles that originate in the femur and patella and insert on the tibia, an arrangement that is primitive for arachnids and is retained in *Araneae* and several other taxa. The posterior transpatellar muscle assumed the role of a femoropatellar extensor in the common ancestors of *Opiliones*, *Scorpiones*, *Pseudoscorpiones*, and *Solifugae* when its

origin shifted to a distodorsal process of the femur. The muscle retains its primitive insertion on the posterior tibial margin in palpator opilionids, but the patellotibial joint appears to have rotated 90° in the common ancestors of *Scorpiones*, *Pseudoscorpiones*, and *Solifugae* such that the primitive posterior tibial insertion assumed a dorsal position. This transition allowed the transpatellar muscle to extend the patellotibial and femoropatellar joints simultaneously. The muscle is absent in *Solifugae*, but evidence of the 90° rotation remains in the pattern of muscle insertions (Shultz, '89).

'70; Anderson and Prestwich, '75; Palmgren, '78). The *musculi laterales* apparently evolved when the insertion of the lateral tergocoxal shifted from the lateral coxal margin to the dorsally adjacent pleural membrane. The *musculi laterales* probably arose independently in spiders and uropygids, as the lateral tergocoxals retain the primitive coxal insertions in palpigrades (personal observation) and amblypygids (Fig. 5B). Palmgren ('78) noted that a portion of the *musculi laterales* attaches to the coxae in certain spiders and interpreted this as evidence for the derivation of the extrinsic coxal muscles from the *lateralis* complex. However, outgroup comparisons clearly indicate the reverse; the *musculi laterales* are derived from an extrinsic coxal muscle, the lateral tergocoxal.

The fluid pressure pump of arachnids

The observations discussed above are consistent with the view that hydraulic exten-

sion is primitive for arachnids and that fluid pressure used for extending the femoropatellar joint of the legs is generated by contraction of endosternal suspensor muscles. Phylogenetic analysis suggests that the arachnid ancestor lacked extensor muscles but had a well-developed endosternite. This grade of organization is retained, for the most part, in the arachnid lineage that includes spiders, palpigrades, and whipscorpions (*Micrura* in Shultz, '90) (Fig. 1), and it is known that spiders use hydraulic extension. A femoropatellar extensor muscle and a greatly reduced prosomal endosternite are synapomorphic for the lineage that includes opilionids, scorpions, and pseudoscorpions. The association between the appearance of extensors and reduction of the endosternite is consistent with the view that direct muscular contraction replaced the hydraulic mechanism powered by contraction of the endosternal suspensors.

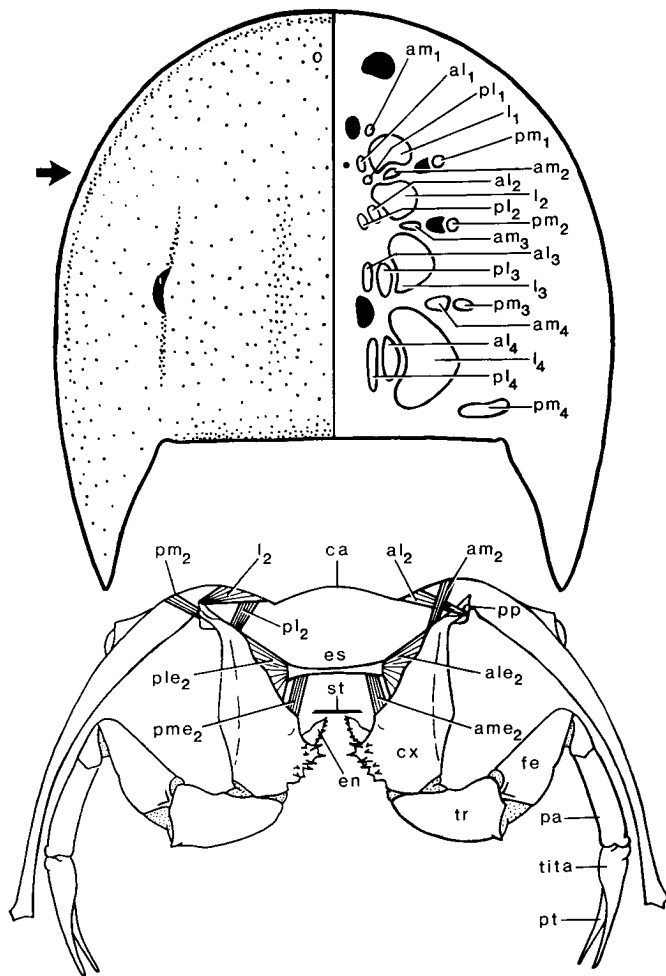


Fig. 4. Skeletomuscular anatomy of the prosoma of *Limulus polyphemus* (Xiphosura). The right side of the upper figure depicts the arrangement of carapacial insertions of the endosternal suspensors (black) and extrinsic muscles of the walking legs. The lower figure depicts a cross section of the prosoma from an anterior perspective (after Wyse and Dwyer, '73). The right side of the lower

figure shows the arrangement of anterior extrinsic leg muscles and the left side shows the arrangement of the lateral and posterior muscles with anterior muscles removed. The arrow near the upper figure indicates the approximate site of the section illustrated in the lower figure. en, endite; pp, pivot point; tita, tibiotarsus. Other abbreviations as in Figure 2.

In contrast, comparative studies of skeletomuscular anatomy provide little evidence consistent with Wilson's ('70) hypothesis that the musculi laterales generate fluid pressures for locomotion or the hypothesis that hydraulic extension is a derived feature unique to spiders. The musculi laterales appear to have evolved independently in spiders and uropygid whipscorpions from certain extrinsic leg muscles, the lateral tergoxoxals. As musculi laterales appear to be unique to these taxa, Wilson's proposal would require a

different method of extension or a different-fluid pressure pump in other "extensorless" arachnids. In addition, the appearance of extensor muscles in arachnids is not associated with changes in the lateral tergoxoxal muscle such as occurred in the evolution of the endosternite. In fact, certain palpatop opilionids, which have femoropatellar extensors, retain the primitive arrangement of extrinsic coxal muscles. These observations do not qualify as tests of the functional predictions of Wilson's hypothesis but point to the fact that

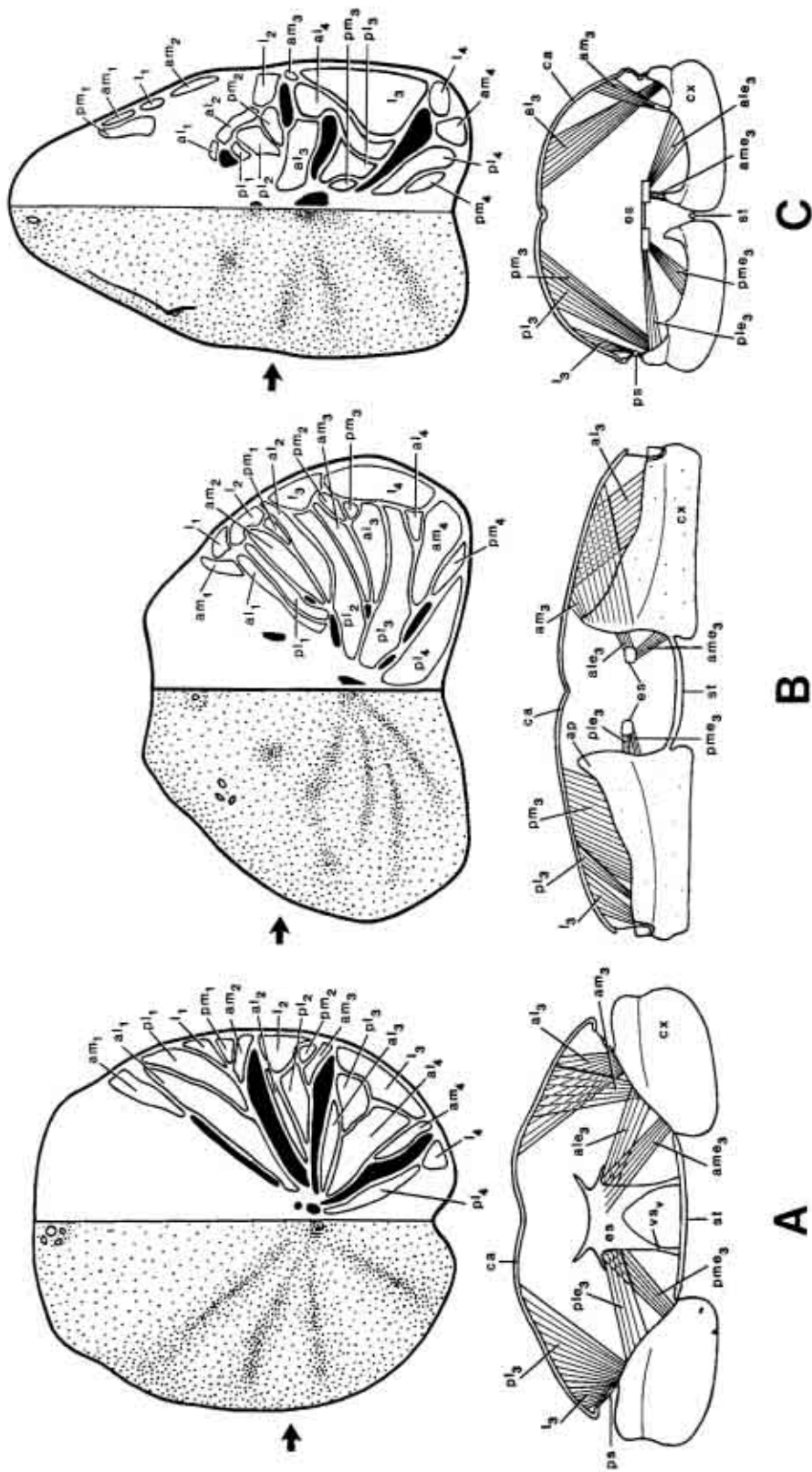


Fig. 5. Skeleto-muscular anatomy of the prosoma in **A**) a mygalomorph spider, *Eurypelma californicum* (Araneae), **B**) an amblypygid, *Phrynus marginemaculatus* (Pedipalpi, Amblypygi), and **C**) a whipscorpion, *M. giganteus* (Pedipalpi, Uropygi). The right side of each upper figure depicts the arrangement of carapacial insertions of endosternal suspensor muscles (black) and extrinsic muscles of the walking legs. Each lower figure depicts a cross section of the prosoma from an anterior perspective. The right side of the

lower figure shows the arrangement of anterior extrinsic leg muscles and the left side shows the arrangement of lateral and posterior muscles with the anterior muscles removed. The arrow near the upper figure indicates the approximate site of the section illustrated in the lower figure. Note that in the amblypygid contraction of am may cause coxal depression. ap, apodeme; ps, pleural sclerite. Other abbreviations as in Figure 2.

this mechanism, if valid, is not reflected in large-scale patterns of morphological diversity as is the endosternite model.

FUNCTIONAL ANALYSIS OF THE FLUID PRESSURE PUMP

This analysis is devoted to testing functional predictions of the endosternite and musculi laterales models of hydraulic pressure generation. If the endosternite model is correct, the level of activity in endosternal suspensor muscles in hydraulic arachnids should be positively correlated with the level of prosomal pressure. In contrast, the musculi laterales model predicts that the level of prosomal pressure is correlated with activity of the musculi laterales. These models were evaluated by recording prosomal pressure and muscle activity in the giant whipscorpion, *Mastigoproctus giganteus*, a hydraulic arachnid equipped with both endosternal suspensors and musculi laterales (Fig. 5C).

MATERIALS AND METHODS

Experimental animals

Electrophysiological analyses of locomotion were conducted on four large adult whipscorpions, *M. giganteus* (Uropygi, Thelyphonida), representing both sexes. The animals were collected near Portal, Arizona, and housed individually in plastic shoe boxes. Each whipscorpion was given one or two large mealworms or crickets per week, and water was provided ad libitum in open petri dishes. Each animal was used in two or three experiments. They were maintained for many weeks after the study and exhibited no ill effects from the procedure.

Electromyography

The skeletomuscular anatomy of *M. giganteus* facilitated tests of the endosternite and musculi laterales hypotheses by providing external landmarks to guide placement of electrodes for electromyography. The carapacial insertions of the endosternal suspensor muscles are broad and well-demarcated externally by fossae on the carapacial surface. In contrast, the carapacial insertions of endosternal suspensors in spiders are generally long and narrow, an organization that makes it difficult to isolate changes in extracellular electrical potential produced by endosternal suspensor activity from that generated by activity in adjacent muscles.

Although *M. giganteus* has four pairs of musculi laterales (one pair associated with each pair of legs), only the pair associated

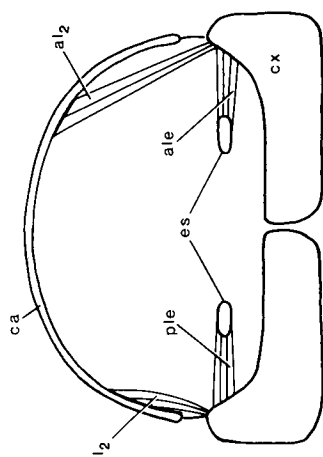
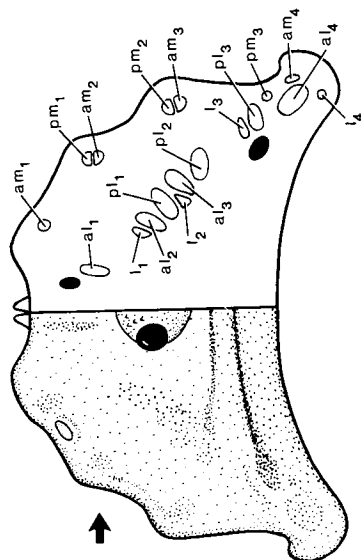
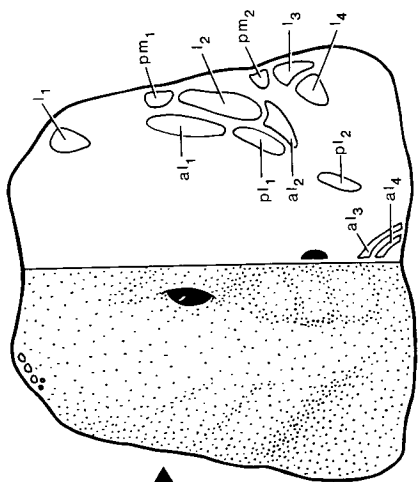
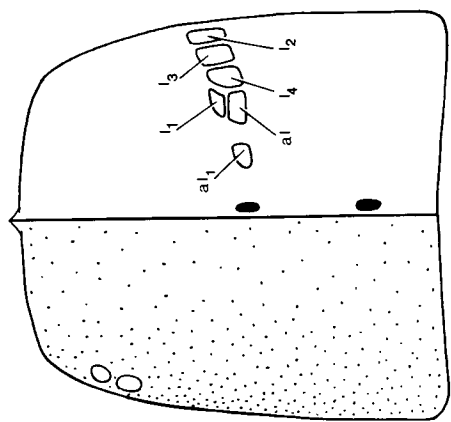
with leg 3 is well developed. Dissections revealed that attachments of these muscles correspond to elevated regions at the posterolateral surfaces of the carapace, another feature that facilitated accurate and consistent placement of electrodes. In contrast, all musculi laterales are well developed in most spiders, and there are typically no clear external features demarcating the insertion of each musculi lateralis.

Electromyograms (EMGs) were obtained via bipolar electrodes fashioned from insulated nichrome wire (A-M Systems Inc., No. 7620; 50 μ m bare). Each electrode consisted of two 50 cm wires glued in parallel, each with about 0.25 mm of insulation removed at one end. The bared ends were inserted just below the cuticle through a pair of closely spaced holes made with a sterilized minuten pin. A monopolar ground electrode was prepared in a similar way and was inserted through a single hole in the carapace. Once the electrodes were glued into place, their free ends were fastened together in parallel and anchored to the upper surface of the opisthosoma.

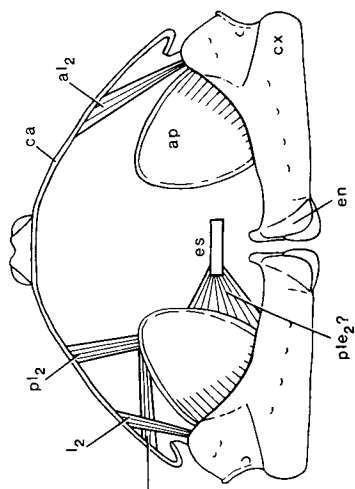
EMGs were obtained while the animal walked freely on the cardboard floor of a copper-screen Faraday cage. Signals from each bipolar electrode were patched into a differential pre-amplifier (Grass, Model 1509), and the monopolar electrode was connected to the common ground of the pre-amplifiers via the Faraday cage. Signals were treated similarly at each pre-amplifier; the low pass filter was generally set at 30 Hz and the high pass at 3 kHz. A 60 Hz notch filter was always in use. Amplification varied but generally ranged from 10,000 to 20,000. The treated signals were saved on paper using a multiple-speed chart recorder (Gould, Model 2400).

Pressure recordings

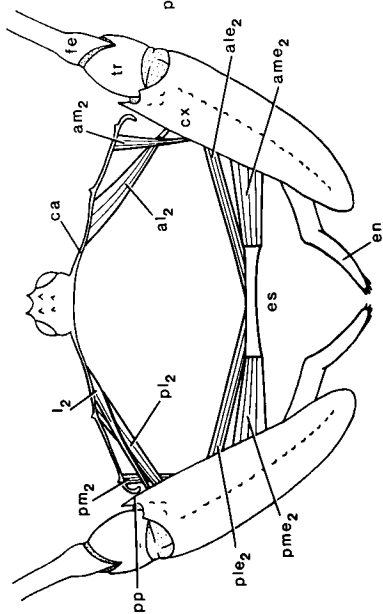
The morphology of *M. giganteus* also facilitated the measurement of prosomal pressure in freely walking animals. Members of the first leg pair are long, antenniform structures that are not used for propulsion, and the femoropatellar joint of each leg is equipped with a broad arthrodiol membrane that inflates as the joint is extended by hydraulic pressure. The fully expanded membrane of leg 1 provided a noninvasive means of measuring prosomal pressure, and immobilization of the leg had a minimal effect on the mechanics of locomotion. Recording techniques used in earlier investigations focusing



C



B



A

Figure 6

on spiders required either the amputation of a walking leg to gain access to the prosomal hemocoel (Anderson and Prestwich, '75; Prestwich, '88), a technique that makes normal locomotion impossible, or catheterization, which can damage musculature and is constrained by rapid clotting of the catheter bore (Stewart and Martin, '74; Paul et al., '89).

Measurements of prosomal pressure were obtained with a Millar catheter pressure transducer (Model PC-360). Although the transducer was designed for measuring intra-arterial pressure in large vertebrates, it has a small, subterminal active surface that proved to be well suited for obtaining pressure recordings at the femoropatellar membrane of leg 1 in *M. giganteus*. Flexibility of the transducer leads was improved by removing the protective plastic coating from the last 50 cm of the catheter. A transducer control unit (Millar, Model TCB-100) provided excitation voltage (6 V) and initial amplification ($10\times$) of the transducer signal.

With the animal restrained and leg 1 fully extended, the transducer surface was positioned against the arthrodistal membrane of the femoropatellar joint and bound in place with loops of thread. Tension on the thread was adjusted while the transducer signal was observed on an oscilloscope. Once the membrane covered the active surface of the transducer and a clear, stable trace of the animal's heartbeat was obtained, the orientation of the leg and transducer was stabilized by applying a coat of fast-drying epoxy. The leg and transducer were then anchored to the upper surface of the carapace and opisthosoma (Fig. 7). As the pressure recording technique was non-invasive and caused no apparent injury, it was possible to obtain measurements over a

prolonged period and experiments could be repeated in the same animal.

Statistical analysis

Statistical methods were used to determine possible functional relationships between cyclical firing of muscles and cyclical fluctuations of prosomal pressure. Many prosomal muscles were found to fire at a particular phase within the step cycle, and it was necessary to separate apparent covariation between muscle activity cycles and prosomal pressure cycles attributable to overall step period from covariation due to specific functional interactions. This was accomplished by conducting a least-squares regression to determine the relationship between a muscle timing parameter (e.g., burst duration) and step cycle period, as represented by the cycle period of a reference muscle. The procedure was repeated for the same sequence to determine the relationship between a timing parameter of the pressure cycle (e.g., trough-peak interval) and step cycle period as indicated by the period of the same reference muscle. Residuals from the muscle versus step period regression were plotted against residuals from the pressure versus step period regression. An Olmstead-Tukey corner test for association (Sokal and Rohlf, '81) was applied to determine whether a significant relationship existed between the residuals. Presence of a significant association was regarded as evidence for a functional relationship between muscle activity and pressure fluctuations beyond simple co-occurrence within a repeating cycle.

RESULTS

Shifts in the prosomal pressure baseline

EMGs and pressure recordings support the endosternite model of pressure generation and are inconsistent with the musculi laterales model. When the animals were at rest, endosternal suspensors showed continuous activity represented by trains of low-amplitude spikes. This pattern was interrupted occasionally by spontaneous increases in endosternal activity accompanied by temporary elevations in prosomal pressure (Fig. 8). The musculi laterales were silent during these resting periods and were often inactive during spontaneous pressure increases. Most prosomal muscles, including endosternal suspensors and musculi laterales, were strongly active during struggles or when the animal was startled. This activity was usually accom-

Fig. 6. Skeletomuscular anatomy of the prosoma in A) a harvestman, *Leiobunum vittatum* (Opiliones, Palpatores), B) a scorpion, *Centruroides vittatus* (Scorpiones), and C) a pseudoscorpion, *Microbisium parvulum* (Pseudoscorpiones). The right side of each upper figure depicts the arrangement of carapacial insertions of endosternal suspensor muscles (black) and extrinsic muscles of the walking legs. Each lower figure depicts a cross section of the prosoma from an anterior perspective. The right side of the lower figure shows the arrangement of anterior extrinsic leg muscles and the left side shows the arrangement of lateral and posterior muscles with the anterior muscles removed. The arrow near the upper figure indicates the approximate site of the section illustrated in the lower figure. ap, apodeme; en, endite; pp, pivot point. Other abbreviations as in Figure 2.

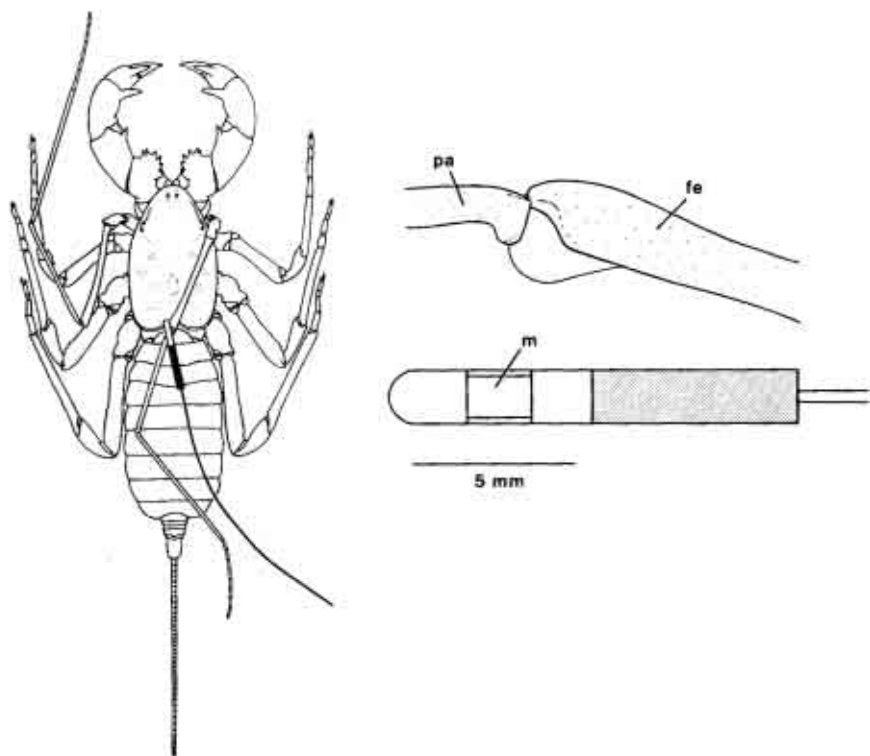


Fig. 7. Preparation used in obtaining measurements of prosomal pressure in freely walking whipscorpions, *M. giganteus*. Measurements were made with a Millar catheter pressure transducer (lower right). Flexibility of the transducer leads was improved by removing the last 50 cm of the catheter. With the animal restrained and leg 1 fully extended, the transducer surface (m) and arthrodial membrane of the femoropatellar joint (upper right) were

juxtaposed and fastened together temporarily with thread. Tension on the thread was adjusted while observing the transducer signal on an oscilloscope. Once a clear trace of the animal's heartbeat was obtained, the orientation of the leg and transducer was stabilized by applying a coat of fast-drying epoxy (not illustrated). The leg and transducer surface were then anchored to the upper surface of the carapace and opisthosoma. Pa, patella; fe, femur.

panied by dramatic increases in prosomal pressure that reached levels far above those observed during resting or normal locomotion.

Suspensor activity, as indicated by spike amplitude and frequency, increased substantially at the onset of locomotion, and this level continued as long as the animal remained active (Fig. 8). The EMGs revealed a spike train with no apparent internal pattern, such as cyclical fluctuations in spike amplitude. In contrast, the musculi laterales showed a cyclical firing pattern consisting of discrete bursts interrupted by silent periods. The firing pattern was clearly coupled with the step cycle (Fig. 9). A new baseline pressure was also established with the onset of locomotion and did not vary substantially within the range of sustained step periods (0.8–1.2 sec). However, puffs of air often elicited temporary increases in endosternal

suspensor activity and prosomal pressure. The animal continued to walk during these periods and pressure eventually returned to its normal level.

A strong cyclical fluctuation in prosomal pressure was superimposed on the elevated pressure baseline during locomotion (Figs. 8, 9). Pressure fluctuations were clearly coupled with the step cycle but displayed a cycle period half that of the step cycle. Possible causes of these fluctuations are discussed below.

Step-coupled fluctuations in prosomal pressure

The level of endosternal suspensor activity was correlated with the baseline level of prosomal pressure but did not display cyclical changes that might account for step-coupled pressure fluctuations. Two hypotheses are presented as possible explanations for

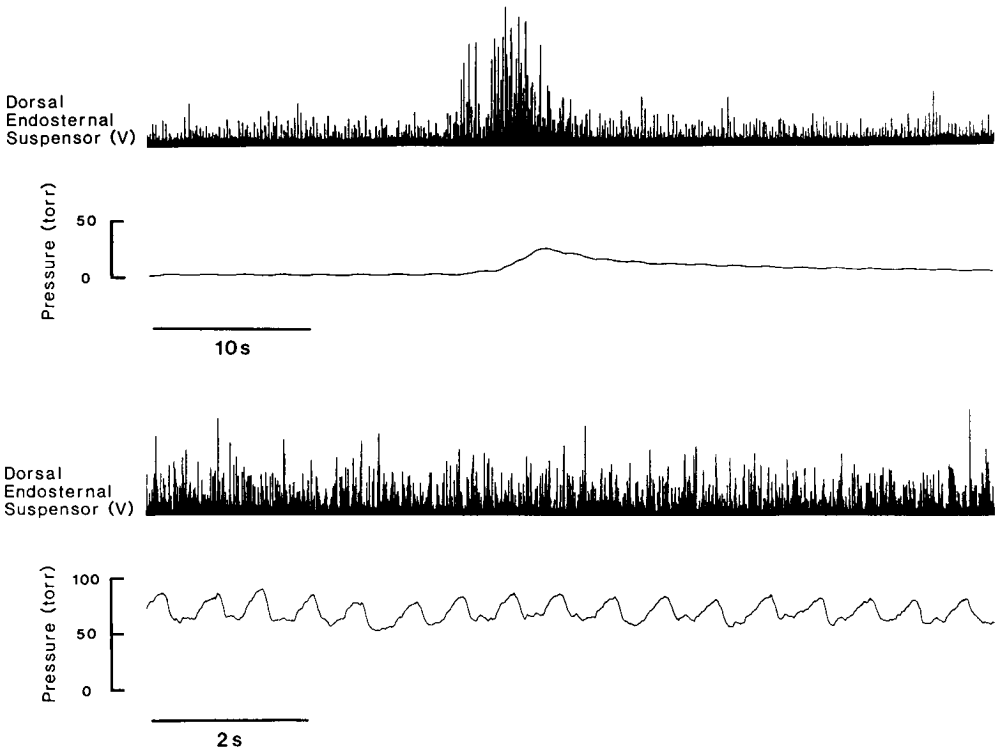


Fig. 8. Simultaneous records of activity in a dorsal endosternal suspensor muscle (segment V) and relative prosomal pressure during inactivity (upper traces) and locomotion (lower traces). All signals were obtained from

the same preparation; amplification and filtering of EMGs are identical. The baseline (0) in each pressure trace represents minimum sustained resting pressure at diastole.

this phenomenon, the musculi laterales hypothesis and the femoropatellar flexion hypothesis. The musculi laterales hypothesis is derived from Wilson's proposal that the musculi laterales generate hydraulic pressure used in propulsive leg extension. Although the cyclical firing pattern of these muscles cannot readily explain the elevated pressure baseline observed during locomotion, it might account for step-coupled fluctuations. The musculi laterales on the two sides of the animal fire 180° out of phase, a pattern that could produce two pressure pulses during each step cycle. The musculi laterales hypothesis predicts that the duration of the musculi laterales burst covaries with the trough-peak interval of the pressure waveform (Fig. 11).

Alternatively, cyclical pressure fluctuations may stem from flexion of the femoropatellar joints of the fourth leg pair. The volume of the femoropatellar joint increases as the joint is extended during the propulsive phase and decreases rapidly during the shorter recovery phase. The other walking

legs move in a different manner; femoropatellar extension is not as important during retraction nor is flexion as important during protraction. As the members of the fourth leg pair step 180° out of phase (Fig. 10), femoropatellar flexion could account for the occurrence of two pressure pulses during each step cycle. This hypothesis predicts that prosomal pressure should increase at the onset of femoropatellar flexor activity during the recovery phase of leg 4 and that the pressure peak should occur at the onset of the propulsive phase, when the femoropatellar joint begins to extend and the trochanterofemoral joint undergoes depression. Although there is no femoropatellar extensor muscle in *M. giganteus*, the onset of activity in the trochanterofemoral depressor can be used to indicate the onset of the propulsive phase. In summary, the femoropatellar flexion hypothesis predicts that the duration of the recovery phase in leg 4, as measured by the interval between the onset of flexor activity and the onset of depressor activity, should covary

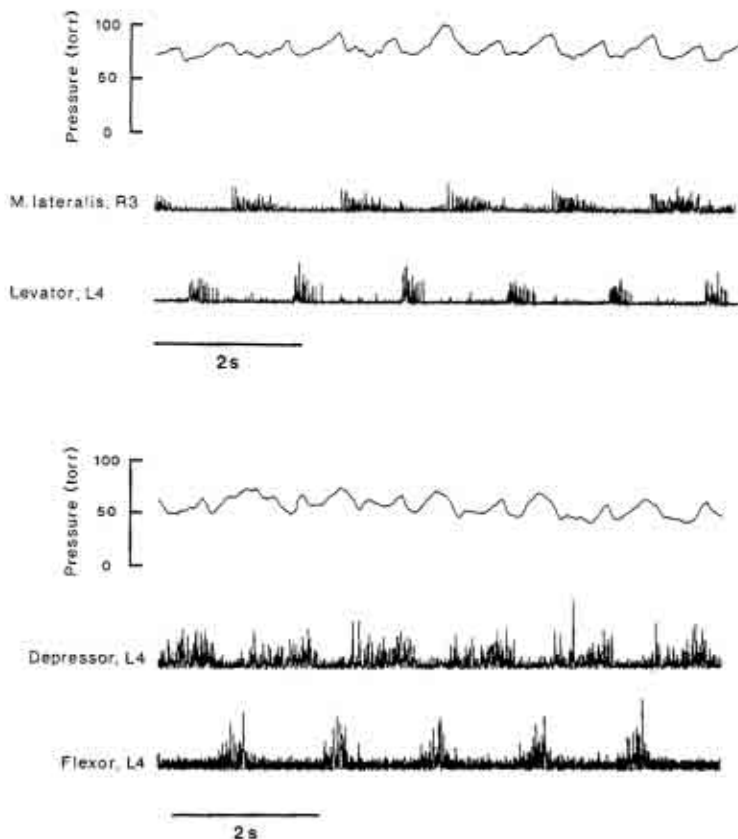


Fig. 9. Prosomal pressure and activity patterns of selected muscles in freely walking *M. giganteus*. Upper records depict simultaneous activity in a musculus lateralis and a trochanterofemoral levator (muscle 13 in Shultz, '89) during locomotion. Note that the m. lateralis burst begins near the peak of the pressure fluctuation cycle and that activation of the levator occurs in the trough just before pressure begins to increase. Lower records depict simultaneous activity in the trochanterofemoral depressor and a femoropatellar flexor in leg 4

(muscles 10 and 8a in Shultz, '89). Note that surges in prosomal pressure are correlated with the recovery phase of the step cycle, as indicated by silent periods in the depressor trace. This suggests that some feature of the recovery phase in leg 4, most probably flexion at the femoropatellar joint, causes cyclical changes in prosomal pressure during locomotion. The unusual pressure trace illustrated here (cf. Fig. 8) results from atypical protraction (foot-dragging) in leg R4. Abbreviations: R, right; L, left; 3, leg 3; 4, leg 4.

with the duration of the trough-peak interval of the pressure waveform (Fig. 11).

Visual comparison of the pressure waveform and EMGs appears to favor the femoropatellar flexion hypothesis. Activation of the femoropatellar flexor in leg 4 generally occurs in the pressure trough just before prosomal pressure increases (Fig. 9). In contrast, onset of activity in the musculi laterales occurs as prosomal pressure is decreasing but continues through the subsequent trough into the next pressure increase (Fig. 9). Although these observations are suggestive, several complicating factors should be noted. The nearly simultaneous occurrence of two

events within a repetitive cycle may reflect mere coincidence rather than a functional relationship. In addition, activation of the muscle that causes cyclical fluctuations in prosomal pressure may not occur simultaneously with pressure increases because of damping or a period of isometric contraction. In order to take these complicating factors into account, functional relationships between muscle firing patterns and pressure fluctuations were established through the statistical procedure summarized in "Materials and Methods."

The musculi laterales hypothesis was tested by investigating possible covariation in mus-

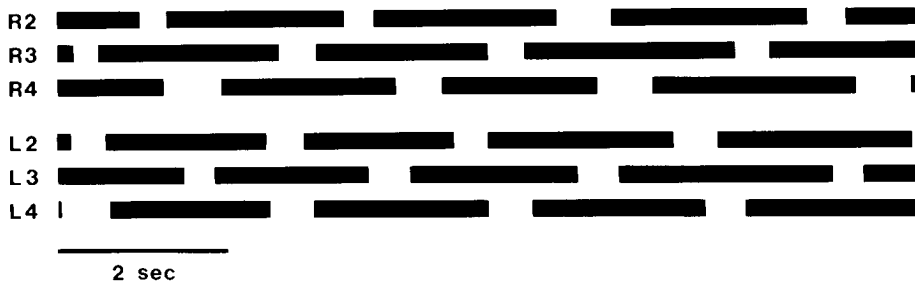


Fig. 10. Step diagram of a slow walk in *M. giganteus* derived from frame-by-frame analysis of video tape. Dark bars represent the propulsive phase of the step cycle (retraction). Note that the step pattern approximates an alternating tripod gait; that is, sets of diagonally adjacent contralateral legs (R2-L3-R4 and L2-R3-L4) step in near

synchrony and each leg steps about 180° out of phase with its contralateral counterpart and ipsilateral neighbors. The first leg pair in whipscorpions is antenniform and is used as a sensory organ rather than for propulsion (Fig. 7).

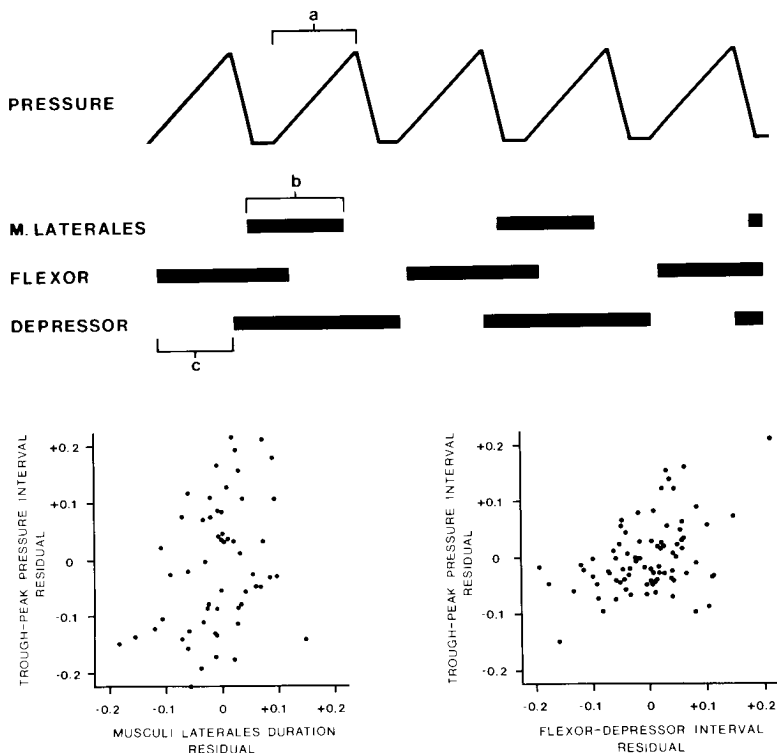


Fig. 11. Analysis of step-coupled fluctuations in prosomal pressure in *M. giganteus*. Two hypotheses are proposed to explain cyclical changes in pressure during locomotion, the musculi laterales hypothesis and the femoropatellar flexion hypothesis. The musculi laterales hypothesis predicts that value *a*, the trough-peak pressure interval, should covary with value *b*, the burst duration of the *m. laterales*. The flexion hypothesis predicts that value *a* covaries with value *c*, the flexor-depressor interval of leg 4. Covariation due to changes in step period was taken into account by calculating least-squares regressions for *a* and *b* against the cycle period of a reference muscle and then plotting the residuals from

the regressions against one another. The Olmstead-Tukey corner test for association found no significant relationship between trough-peak interval and musculi laterales duration ($P > .1$). This indicates that contraction of the *m. laterales* does not contribute substantially to the pressure cycle. The procedure was repeated for values *a* and *c* and analysis of residuals revealed a significant relationship between trough-peak interval and flexor-depressor interval ($P < .001$). This suggests that flexion during protraction in leg 4 generates the pressure cycle observed during locomotion. See text for details.

culi laterales burst duration and duration of the trough-peak interval of the pressure waveform. The effect of step cycle period was established by conducting a least-squares regression on musculi laterales burst duration (y) and levator cycle period (x) (slope = 0.603; y -intercept = -0.128; $r = 0.912$; $n = 51$; range(x) = 0.81-1.73) and on trough-peak pressure interval (y) and levator cycle period (x) (slope = 0.300; y -intercept = -0.0406; $r = 0.632$). All measurements were made in seconds and were accurate to within ± 5 msec. Slopes were significant at the .001 level. Residuals from the two regressions were plotted against one another (Fig. 11) and the Olmstead-Tukey corner method was used to test for association. As the test revealed no significant relationship between the residuals ($P > .1$), it was concluded that the musculi laterales do not contribute significantly to cyclical fluctuations in prosomal pressure during locomotion in *M. giganteus*.

The femoropatellar flexor hypothesis was tested in a similar manner. The effect of step cycle period was established by conducting a least-squares regression on the flexor-depressor interval (y) and flexor cycle period (x) (slope = 0.171; y -intercept = 0.0937; $r = 0.681$; $n = 83$; range(x) = 0.89-2.67) and on trough-peak pressure interval (y) and flexor cycle period (x) (slope = 0.168; y -intercept = 0.0932; $r = 0.744$). Slopes were significant at the .001 level. The residuals showed a significant level of association ($P < .001$) (Fig. 11). The analysis revealed significant covariation between femoropatellar flexion in leg 4 and fluctuations in prosomal pressure beyond that which can be attributed to differences in step period. This suggests that there is a functional relationship between the recovery phase of leg 4 and the pressure cycle and thus corroborates the femoropatellar flexion hypothesis.

DISCUSSION

The results of this investigation support the endosternite model of pressure generation and refute the musculi laterales model. The activity of the endosternal suspensor muscles, as indicated by amplitude and frequency of the spike train, increases substantially at the onset of locomotion in *M. giganteus* and persists at this level as long as the animal is active. This suggests that contraction of the suspensors causes compression of the prosoma and thereby establishes the elevated pressure baseline that powers hydraulic leg extension. In contrast, the musculi

laterales fire in discrete bursts that are coupled with the step cycle, and it is unlikely that this pattern could maintain the pressure baseline observed during locomotion.

This interpretation is supported by evidence derived from spontaneous increases in resting prosomal pressure and pressure increases produced when the animal is startled during locomotion. Changes in resting pressure are usually correlated with similar changes in suspensor activity but the musculi laterales are often inactive. Similarly, prosomal pressure and endosternal suspensor activity increase markedly when the animal is startled during locomotion, but the musculi laterales continue to fire in their usual step-coupled pattern.

Although endosternal suspensor activity probably establishes the general level of pressure in the prosoma, it does not appear to generate the cyclical fluctuations observed during locomotion. The timing of the fluctuation is apparently coupled with leg movements but has a peak-period half that of the step cycle. Visual comparison and statistical analysis of prosomal pressure and EMG records suggest that the pressure wave is generated primarily by changes in femoropatellar joint volume associated with movements of the fourth pair of walking legs. The step cycle in leg 4 consists of a propulsive phase (retraction) during which the femoropatellar joint extends under the influence of hydraulic pressure and a recovery phase (protraction) in which the femoropatellar joint is rapidly flexed. Thus femoropatellar joint volume increases gradually during retraction due to extension of the joint and inflation of the large arthroal membrane, and flexion during protraction causes a comparatively rapid reduction in joint volume that is translated into a surge in prosomal pressure. As each member of a segmental leg pair normally steps 180° out of phase with the other member, two apparent pressure cycles are observed within each step cycle.

Given the alternating step pattern of segmental leg pairs, it is tempting to speculate that the rise in pressure caused by flexion in one leg contributes to extension of the other and thereby increases the efficiency of the hydraulic mechanism. This does not appear to be the case, however, as the recovery phase is much shorter than the propulsive phase at normal, sustained step periods, which is about 1 sec in *M. giganteus* (personal observation). At these step periods, prosomal pressure de-

creases at the onset of retraction in a leg, increases briefly during protraction in the other member of the pair, and then drops again before retraction ends. I regard such fluctuations as a potential hinderance to hydraulic locomotion rather than a mechanism for increasing locomotor efficiency.

Pressure fluctuations may have a deleterious effect on intraleg coordination by altering the rate of extension during the propulsive stroke. Coordination between femoropatellar extension and trochanterofemoral depression in the fourth leg pair is essential for normal locomotion. If extension were to outpace depression, the tarsus would tend to lift from the substrate, thereby removing support and propulsive force provided by that leg. However, the legs of *M. giganteus* and many other arachnids are equipped with a muscle that may function to maintain proper coordination between the trochanterofemoral and femoropatellar joints. It originates in the trochanter, spans the femur and inserts on the ventral rim of the patella. This transfemoral muscle (muscle 8d in Shultz, '89) appears to maintain a relatively constant length during retraction (personal observation) and may establish an internal linkage that maintains coordination between depression and extension in the face of external perturbations such as fluctuation in prosomal pressure. The femoropatellar flexor muscles could also play a role in reducing the deleterious effects of pressure fluctuations on joint coordination, but recent electromyographic analyses of freely walking *M. giganteus* show that flexor activity diminishes gradually during the propulsive phase. There is no evidence that flexor activity changes during retraction in response to pressure fluctuations (personal observation).

The conclusion that endosternal suspensors generate the pressure used in hydraulic leg extension was anticipated by Gaubert (1892) in his impressive comparative study of the locomotor apparatus in arachnids. Following Blanchard (1864), he noted that spiders, whipscorpions, and certain other arachnids lack extensor muscles and suggested that extension was accomplished by hydraulic ("turgor") pressure. He hypothesized further that this pressure was generated through compression of the prosoma through contraction of muscles associated with the endosternite or "aponeurosis."

Gaubert's insights were either overlooked or rejected by subsequent workers (Petrun-

kevitch, '09; Ellis, '44; Parry and Brown, '59). Wilson ('70) dismissed the endosternite hypothesis in his search for the fluid pressure pump in spiders and opted instead for the musculi laterales. The endosternite in most araneomorph spiders attaches to the carapace dorsally and to the coxae ventrally by means of extrinsic coxal muscles. True ventral suspensors are absent in most araneomorphs but are present in most mygalomorphs or "tarantula-like" spiders (Fig. 5A). Wilson argued that contractions of the endosternal suspensors would interfere with coxal movement and that the musculi laterales, which insert on the pleural membrane, would not. It should be noted in this context that the ventral suspensors in *M. giganteus* attach to coxal apodemes (Fig. 5C), although one pair (vs IV) retains a primitive sternal attachment (cf. Fig. 2) (Firstman, '73; personal observation).

Wilson's hypothesis has received widespread acceptance and dissenting views have been largely ignored. For example, Palmgren ('81) noted that medial extrinsic coxal muscles, such as those attaching to the endosternite, have a low mechanical advantage at the prosoma-coxa joint and would not be expected to influence coxal movement greatly even when exerting relatively large forces. This observation challenges Wilson's contention that contraction of endosternal muscles would have deleterious effects on coxal movement. In addition, Wilson's reasoning fails to account for the absence of musculi laterales in other hydraulic arachnids such as amblypygids and palpigrades, both of which retain lateral tergo-coxal muscles (the primitive form of the musculi laterales) and a nearly full complement of endosternal suspensors.

In contrast to Wilson's hypothesis, activity of the musculi laterales does not appear to contribute significantly to prosomal pressure during locomotion in *M. giganteus*. The cyclical activity pattern in these muscles cannot account for the elevated baseline in prosomal pressure observed during walking, and there is no convincing evidence that this pattern is functionally linked to step-coupled fluctuations in prosomal pressure. Based on their morphology, I suggest that the musculi laterales function in controlling coxal movement by acting as an antagonist to prosomal pressure at the prosoma-coxa joint. This hypothesis is consistent with the apparent evolutionary derivation of these muscles from extrinsic coxal muscles (lateral tergo-coxals)

and the correlation noted by Wilson ('70) between levels of activity and development of the musculi laterales in different spider taxa.

In most arachnids and reconstructions of trilobites (Cisne, '81) and eurypterids (Selden, '81), the coxa is suspended within a flexible membrane; there are no condyles at the prosoma-coxa joint. As a consequence, coxal movement probably depends on the action of muscles against the tension of the pleural membrane produced by fluid pressure. The orientation of the lateral tergo-coxal muscle (Fig. 2) suggests that it functions as a coxal levator. It is likely that increased prosomal pressure promotes coxal depression through expansion of the dorsal pleural membrane and that the lateral tergo-coxal serves as an antagonist to this action.

The musculi laterales evolved in spiders and uropygids when the insertion of the lateral tergo-coxals shifted from the lateral coxal margin to the dorsally adjacent pleural membrane. The derived pleural insertion would seem to allow the muscle to work directly against tension in the pleural membrane, a mechanism that seems more effective in counteracting the effects of high prosomal pressures. This reasoning implies that those arachnids with musculi laterales generate greater pressures than do other hydraulic arachnids. In fact, the dorsal endosternal suspensors in uropygids and spiders are generally larger than in related arachnids that lack musculi laterales such as amblypygids (Fig. 5A-C).

The hypotheses presented here concerning the evolution and function of the lateral tergo-coxals and musculi laterales may be tested by comparative functional studies of living arachnids. Among those arachnids large enough for standard electromyographic investigation, amblypygids and palpatopilionids retain the lateral tergo-coxal in an essentially primitive form. The hypothesis proposed here suggests that coxal depression in these arachnids should result from increases in hydraulic pressure (although amblypygids may use direct muscular contraction—Fig. 5B), and that activity within the lateral tergo-coxal should occur during coxal levation or periods when hydraulic pressure is sufficiently high that coxal depression would occur in the absence of an antagonistic force. The musculi laterales of spiders and *M. giganteus* probably retain the function of the more primitive lateral tergo-coxals. Thus coxal levation may

be a functional homology of the lateral tergo-coxals in arachnids.

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