

Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications

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The morphological diversity of locomotor appendages in Arachnida is surveyed to reconstruct phylogenetic relationships and discover evolutionary trends in form and function. The appendicular skeleton and musculature of representatives from the ten living arachnid orders are described, and a system of homology is proposed. Character polarities are established through comparison with an outgroup, *Limulus polyphemus* (Xiphosura). Cladistic analysis suggests that Arachnida is monophyletic and that absence of extensor muscles is a primitive condition. Extensors are primitively absent in Araneae, Amblypygi, Uropygi, Palpigradi, Ricinulei and Acari. Most similarities in the appendages of these orders are symplesiomorphic so that phylogenetic relationships among the 'extensorless' groups cannot be resolved solely on the basis of appendicular characters. Extensor muscles appear to have evolved once, and their presence is considered a synapomorphic feature of Opiliones, Scorpiones, Pseudoscorpiones and Solifugae. Solifugae lack extensors, but a parsimonious interpretation of other characters indicates that this is a secondary, derived condition. The phylogenetic relationships among these four orders are clarified by modifications of the patellofibial joint. Cladistic analysis indicates that Opiliones may be the sister group of the other three orders and that Scorpiones is the sister group of Pseudoscorpiones and Solifugae. Conclusions concerning phylogenetic relationships and evolutionary morphology presented here differ substantially from those of earlier studies on the locomotor appendages of Arachnida.

KEY WORDS: Arachnida – appendages – evolution – phylogeny – morphology – locomotion – muscles.

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INTRODUCTION

Despite persistent attempts by arachnologists to accommodate the morphological diversity of Arachnida within a phylogenetic reconstruction, we are not much closer to understanding the history of these animals than we were a century ago (cf. Pocock, 1893; Weygoldt & Paulus, 1979a, b). This paper reports the results from a survey of the morphology of arachnid locomotor appendages, offers a phylogenetic hypothesis based largely upon newly discovered synapomorphies, and explores the functional implications of the evolutionary trends revealed by this information. These results and interpretations will provide necessary groundwork for an intensive study of the evolutionary morphology of arachnid locomotion.

There are ten living orders of terrestrial chelicerate arthropods collectively termed arachnids (Weygoldt & Paulus, 1979b). Each order is defined by unique characters (autapomorphies), but there are few shared derived features (synapomorphies) that systematists can use to establish phylogenetic relationships among the orders. The extreme age of Arachnida (over 350 million years) is frequently invoked to explain this situation. The long interval of independent phyletic evolution within each of the arachnid lineages is thought to have obliterated most synapomorphic features, even though most arachnid orders had apparently achieved their current grades of organization as early as the Devonian (Shear *et al.*, 1984). Whatever its cause, the apparent absence of synapomorphies has led some systematists to conclude that Arachnida is polyphyletic (e.g. Kraus, 1976); that is, different arachnid groups may have arisen independently from different marine ancestors, which, if known, would not be considered arachnids themselves. Others maintain that arachnids are derived from a single common ancestor, although the precise arrangement of the orders among themselves remains elusive (Firstman, 1973; Weygoldt & Paulus, 1979b).

The comparative anatomy of arachnid walking legs exemplifies the problem with which arachnologists are faced. The generalized arachnid walking appendage is composed of seven segments; coxa, trochanter, femur, patella, tibia, tarsus (divided into a proximal basitarsus and distal telotarsus) and pretarsus. Some arachnids are thought to have two trochanters or two femora; others appear to have two femora and no patella; some seem to have two trochanters, two femora and no patella. Arachnids such as spiders and mites lack extensor muscles and apparently use hydraulic pressure for leg extension. Scorpions and pseudoscorpions have extensor muscles, whereas solifuges may use joint elasticity for extending their legs. Joint structure also shows considerable variation. The patella and tibia, for instance, may be joined by dorsal monocondylar, vertical bicondylar or transverse bicondylar joints or a dorsal hinge, depending on the order. To date, none of the phylogenetic hypotheses that claim Arachnida to be monophyletic have been able to accommodate this diversity in a convincing manner.

The most active proponent of a polyphyletic origin for Arachnida, van der Hammen (1977, 1979, 1982, 1985a,b, 1986), derives support for this view from his extensive anatomical studies of arachnid walking appendages. Based on joint morphology and the arrangement of muscular insertions, van der Hammen divides the extant Chelicerata (excluding Pantopoda) into seven groups, which he considers sufficiently distinct to warrant separation into seven classes. He

reasons that none of these groups could have arisen from any of the others and each must have been derived from a different chelicerate ancestor.

There are several reasons for questioning van der Hammen's conclusions. First, his anatomical descriptions are not always accurate and are generally incomplete and oversimplified. This is particularly evident in his diagrams of joint structure, in which he illustrates arrangements of articulations and muscle insertions (see van der Hammen, 1977: 311; 1985b: 140). For example, he depicts the femoropatellar joint of scorpions as a bicondylar dorsal hinge without an extensor. Yet this joint never has a dorsal hinge, and an extensor is always present (Manton, 1958; Bowerman & Root, 1978; present study). In addition, the femoropatellar joint of pseudoscorpions, or 'basifemur-telofemur' joint in traditional terminology, is depicted as being immovable and without musculature when, in fact, it is fully operational, slightly movable or fused in different families and may be associated with as many as three muscles (Börner, 1921; Chamberlin, 1931; present study).

These shortcomings may be attributed, in part, to van der Hammen's anatomical methods. He generally studied the musculature by dissolving the muscle tissue and then observing the number and arrangement of the cuticular tendons that remained. Cuticular tendons are present only at the distal attachments, and any given muscle may possess more than one. Likewise, there is no way to determine the proximal attachment (origin) of a muscle or to reconstruct its precise function and position relative to other muscles. Van der Hammen's method eliminates most of the information needed to establish reasonable homologies in the musculature of different taxa.

Another problem with van der Hammen's conclusions lies in the subjective interpretation of characters used in generating his phylogenetic reconstruction. The relationships hypothesized are based on those similarities deemed to be important. He did not distinguish primitive from derived similarities, nor did he establish a consistent rationale for favouring some similarities and ignoring others. Clearly, arachnid appendicular anatomy and its phylogenetic and functional implications should be re-examined in a more complete and objective manner.

The information reported here was obtained from the examination of intact muscles via dissection, observations of whole mounts, or both. I examined *Limulus polyphemus* (L.) (Xiphosura), which I regard as an outgroup and to which I refer in establishing character polarities, and representatives from all arachnid orders. In contrast to van der Hammen's interpretations, the number and basic arrangement of appendicular muscles were found to be fairly conservative throughout Arachnida and between arachnids and Xiphosura. The discovery of a transformational sequence suggesting the evolutionary route by which muscular leg extension arose from the primitive 'extensorless' condition is also reported. The phylogenetic relationships implied by this sequence of character transformations were unexpected and, if corroborated, may substantially alter current views of arachnid evolution.

METHODS

Anatomical techniques

The body lengths of the arachnids examined in this study range from about 170 mm in the black emperor scorpion *Pandinus imperator* (Koch) to about 1 mm

in the palpigrade *Eukoenenia* sp. Standard dissection techniques were used whenever possible. In such smaller animals as schizomids, cyphophthalmids and pseudoscorpions I supplemented my dissections with microscopical examinations of isolated legs suspended in immersion oil. Specimens were placed into increasing concentrations of ethyl alcohol, followed by increasing concentrations of immersion oil and then transferred to a cavity slide, where they could be viewed under a compound microscope. The specimens could be repositioned at will and the viscosity of the oil held them in the desired orientation. The muscles were easy to observe through the transparent cuticle. The smallest arachnids, palpigrades and some mites, were not dissected; descriptions were based on observations of whole specimens suspended in immersion oil. Anatomical observations were limited to the joints and musculature associates with the trochanter, femur, patella, tibia, tarsus and pretarsus. The anatomy of the coxa will be discussed in a separate paper.

Terminology

To facilitate comparisons among arachnid groups, each walking appendage is described as though it extended perpendicular to the long axis of the animal's body. The leg has an anterior, posterior, dorsal and ventral face. In some groups, such as Amblypygi, the coxotrochanteral joint has rotated 90° from its primitive orientation so that the anatomical anterior face is directed dorsally. To facilitate comparison, these legs are described as though they had not undergone this rotation. Unless indicated otherwise, all figures depict the anatomical anterior view of a walking leg from the right-hand side of the body.

Each leg consists of several podomeres connected by joints that may be either fused or movable. Articulations are defined as cuticular specializations that connect adjacent podomeres at movable joints and determine the kinds of movement a joint can undergo. Most articulations take the form of pivot points (condyles) or broad hinges. Joints operated by muscles that insert on the rim of the distal podomere are called eudesmotic joints, and those without muscular insertions are adesmatic joints (Couzijn, 1976). Podomeres bordered by eudesmotic joints are termed segments. Adesmatic joints typically represent the subdivision of a segment.

No simple system of terminology can describe all the kinds of motions joints may undergo, but three basic types of movement are common in arachnid legs: protraction-retraction, flexion-extension and levation-depression. Protraction describes any motion in which the anterior angle between adjacent podomeres decreases; retraction occurs when the anterior angle increases. Flexion occurs whenever the ventral angle between adjacent podomeres decreases below 180°. Extension takes place when the ventral angle increases up to 180°. Levation describes a movement in which the dorsal angle between two podomeres decreases below 180°, and depression occurs when the dorsal angle increases up to 180°. In some cases, especially at monocondylar joints, movement may consist of a rotation or rocking about the long axis of the leg.

Muscles are frequently termed by their functional names such as extensors or depressors, or described as performing particular functions; the function of a given muscle often seems obvious from its anatomy. In many cases, however, the muscle may span more than one joint, have multiple origins or operate at a joint

along with other muscles. In these instances the function of a muscle cannot be derived solely from anatomical criteria. The functions ascribed to specific muscles should be regarded as hypothetical.

Criteria of homology

Many criteria have been used in hypothesizing homologies between podomeres and muscles of different arachnid taxa (reviewed in Couzijn, 1976), but no single criterion is regarded as totally reliable. In this study, hypotheses of homology are derived from several lines of evidence, and the principle of parsimony is invoked to select that which is consistent with the greatest amount of information. In retrospect, it is difficult to understand the problems earlier workers encountered when attempting to establish podomere homologies in Arachnida. The number of podomeres and the arrangement of muscle insertions are fairly conservative throughout the group. Early confusion in this area may have resulted from an excessive reliance on external characters along with repeated but unsuccessful attempts to design a system of homology that would accommodate all arthropods.

SURVEY OF APPENDICULAR MORPHOLOGY

Class Xiphosura

The appendicular morphology of *Limulus polyphemus* has been described by Börner (1921), Vachon (1945), Snodgrass (1952), Manton (1977) and van der Hammen (1986). Although there are no important differences in the descriptions of the skeletal and muscular components of the walking appendages, there has been confusion over how the podomeres in *Limulus* should be homologized with those of arachnids. Here the system advocated by Snodgrass (1952) and van der Hammen (1986) is adopted, an interpretation clearly supported by the arrangement of muscle origins and insertions. In this section, the musculature of the fourth walking leg is described. Leg 4 differs from the other legs and pedipalp in having a distinct tibia and tarsus. These segments are fused in other appendages, forming the palm and immovable digit of the chela.

The pretarsus of leg 4 forms the movable finger of the chela (Fig. 1A). It joins the tarsus at a transverse bicondylar joint that moves by levation-depression (opening-closing). Levation is accomplished by a single muscle (1) that arises along the dorsal surface of the tarsus and inserts on the dorsal rim of the pretarsus. The depressor (2) arises on the ventral surface of the tarsus and inserts on the ventral rim of the pretarsus.

The distal end of the tibia in leg 4 is modified into a digging organ that consists of a ring of four spatulate setae (not illustrated) and the tarsus. The tarsus occupies the posterior border of the ring. The tarsus and setae insert on a flexible arthrodial membrane, but their movements are constrained by a series of notches at the margins of the tibia. Two muscles (3a, 3b) insert on the base of the tarsus (Fig. 1A). Muscle 3a arises on the anterior and posterior surfaces of the tibia and inserts on the anterior margin of the tarsus, which lies near the centre of the flexible membrane. Muscle 3b arises from the anterior surface of the tibia

and inserts on the posterior margin of the tarsus. Contraction of 3a apparently causes protraction at the tibiotarsal joint and, in turn, pulls the arthrodial membrane proximally into the tibia and closes the ring of setae, as one would close an umbrella. Contraction of 3b (perhaps in combination with hydraulic pressure or elasticity of the arthrodial membrane) may serve to retract the tibiotarsal joint and thus open the ring of setae. This arrangement is unique to Xiphosura.

The patellotibial joint is formed by a strong dorsal monocondylar articulation (Figs 5A, 9A, 16). The articulation is bordered anteriorly by a large process that arises from the proximal rim of the tibia and extends well above the dorsal surface of the point of articulation. A similar but smaller process is situated on the posterior side of the condyle. These processes serve as attachment sites for a pair of muscles (4a, 5a) that arise on the anterior and posterior surfaces of the patella and insert on the anterior and posterior tibial processes, respectively (Figs 9A, 16). They appear to cause extension and, perhaps, protraction-retraction at the patellotibial joint. The processes and their associated muscles are unique to Xiphosura.

Flexion at the patellotibial joint is apparently brought about by four muscles. Muscles 4b and 5b arise broadly from the anterior and posterior surfaces of the patella and insert on the ventroanterior and ventroposterior margins of the tibia, respectively (Fig. 9A). Muscle 6 arises from the ventral and proximodorsal surfaces of the patella and the distodorsal surface of the femur. This muscle inserts on the ventroanterior rim of the tibia. Muscle 7 is the posterior mirror image of 6, arising from the femur and patella and inserting on the ventroposterior rim of the tibia (Figs 5A, 16). These four muscles may participate in protraction-retraction as well as flexion.

The femoropatellar joint is formed by a strong transverse bicondylar dorsal hinge, the anterior condyle being somewhat larger than its posterior counterpart. This joint is the principal site of flexion-extension in all legs of *Limulus*. Flexion is brought about by a muscular complex consisting of four main components (8a–8d) (Figs 5A, 15A). The flexors operate through a large Y-shaped patellar sclerite (Fig. 15A). The distal ends of the anterior and posterior arms of the sclerite attach to the anterior and posterior margins of the patella, respectively, and the third arm extends proximally through the entire length of the femur, where it terminates at a large muscle (8d) that arises broadly from the ventral surface of the trochanter. Another muscle (8a) arises broadly from the distoanterior surface of the femur and inserts on the anterior arm of the patellar sclerite. The mirror image of this muscle (8b) arises from the distoposterior surface of the femur and inserts on the posterior arm of the sclerite. The final muscle in this complex (8c) arises from the ventroposterior surface of the femur and inserts on the patellar sclerite at the proximal part of its posterior arm. There is no extensor at the femoropatellar joint.

The femur joins the trochanter at a transverse bicondylar joint (Fig. 9A) that permits levation-depression. Depression may be accomplished by as many as four muscles. Muscle 9 arises from the anterior surface of the trochanter and inserts on the ventroposterior surface of the femur just proximal to the origin of 8c. Muscle 10 arises from the anterior surface of the trochanter proximal to 9 and inserts on the posterior surface of the femur. A third depressor muscle (11) arises broadly from the ventral and posterior walls of the trochanter and inserts on the

ventral rim of the femur. Finally, 8d may also participate in the depression of this joint (Fig. 5A).

Levation at the trochanterofemoral joint is brought about by a large muscle (12) arising broadly from the proximoanterior and proximoposterior surfaces of the femur and inserts on the dorsal rim of the trochanter (Fig. 9A). Another part of 12 arises along the dorsal midline of the femur for nearly its entire length. This portion also inserts on the dorsal margin of the trochanter.

Class Arachnida

Order Araneae

Appendicular anatomy appears to be fairly uniform throughout the order. Studies to date have concentrated on members of the suborder Opisthothelae, those spiders bearing spinnerets at the posterior end of the opisthosoma. This group includes the 'tarantula' spiders (Mygalomorphae) as well as the more familiar 'true' spiders (Araneomorphae). Thorough examinations of appendicular musculature have been conducted on representatives from several araneomorph families: Agelenidae (Parry, 1957; Clarke, 1986), Araneidae (Dillon, 1952; Frank, 1957; Clarke, 1986), Theridiidae (Whitehead & Rempel, 1959; Clarke, 1986) and Heteropodidae (= Eusparassidae) (Clarke, 1984). Earlier studies tend to be less accurate or less complete (e.g. Gaubert, 1892; Petrunkevitch, 1909). In contrast, few mygalomorph species have been studied, all from the family Theraphosidae (= Aviculariidae) (Snodgrass, 1952; Rathmayer, 1966; Clarke, 1986). Ruhland & Rathmayer (1978) provided a detailed analysis of leg muscles in a mygalomorph and attempted to homologize them with the muscles of spiders described in earlier studies.

Liphistiomorph spiders (Suborder Mesothelae) form the monophyletic sister group of Opisthothelae (Platnick & Gertsch, 1976) and are thought to represent a primitive grade in spider evolution, retaining eight spinnerets near the middle of a clearly segmented opisthosoma. This description of the fourth walking leg is based on the dissection of a single specimen of *Liphistius sumatranus* Thorell (Liphistiidae). Despite the special position of *Liphistius* in spider phylogeny, its appendicular morphology does not differ substantially from that of other spiders.

The pretarsus of *Liphistius* is platelike and bears two large claws dorsally and a small median claw ventrally (Fig. 1B). The pretarsus joins the tarsus by means of a transverse bicondylar joint that undergoes levation-depression. The levator (1) arises from the dorsal surface of the basitarsus and inserts at the dorsal rim of the pretarsus. In *Liphistius*, depression is brought about by a muscular complex (2), consisting of paired heads arising from the distodorsal surface of the tibia and an unpaired head arising from the dorsal surface of the patella. These heads insert on a common tendon that terminates distally on the ventral rim of the pretarsus (Fig. 1B). The tibial component is present in all spiders studied so far but the patellar head is greatly reduced in mygalomorphs and araneomorphs (Ruhland & Rathmayer, 1978), and this may represent an apomorphic feature of Opisthothelae. The patellar head of muscle 2 is unlikely to play a role in operating the claws in non-liphistiomorph spiders, but it may have a sensory function (Ruhland & Rathmayer, 1978).

The telotarsus joins the basitarsus by means of arthrodial membranes. A sclerotized flange projects distally from the dorsal surface of the basitarsus and

apparently serves to prevent hyperextension of the intratarsal joint. Movement between the telotarsus and basitarsus includes protraction-retraction, flexion-extension and perhaps slight rotations around the long axis of the leg. No muscles insert on the telotarsus, but the tendons of muscles 1 and 2 traverse the intratarsal joint and may influence movement there.

The tibiotarsal joint (Fig. 1B) is formed by a transverse bicondylar dorsal hinge that undergoes flexion-extension. The flexor (3) consists of symmetrical anterior and posterior subdivisions that are separated by the tendon of muscle 2 and the pedal nerves. Each subdivision of muscle 3 normally consists of two heads, a short head arising from the distal part of the tibia and a long head arising from the proximal part. Extension at the tibiotarsal joint is apparently caused by a general increase in haemolymph pressure brought about by the compression of the prosoma (Parry & Brown, 1959; Wilson, 1970; Wilson & Bullock, 1973; Stewart & Martin, 1974; Anderson & Prestwich, 1975). The increased pressure causes the broad ventral arthrodial membrane to 'balloon', promoting extension of the joint (see Blickhan & Barth, 1985 for a detailed functional analysis of this process).

The patellotibial joint (Figs 5B, 9B, 16) is formed by a single dorsal condyle that permits mainly protraction-retraction, although some flexion-extension is possible, as well. Although van der Hammen (1986) describes a ventral condyle in *Liphistius*, his illustration shows only that the ventral arthrodial membrane is narrow and that the ventral margins of the patella and tibia are more heavily sclerotized than the adjacent cuticle. Four muscles insert on the proximal rim of the tibia (4–7). Muscle 4 arises broadly from the anterior surface of the patella and inserts on the anterior rim of the tibia (Figs 9B, 16), appearing to cause protraction. Muscle 5 arises from the posterior face of the patella, inserts on the posterior rim of the tibia and apparently causes retraction. The arrangement of muscles 4 and 5 described here is present in all spiders studied so far (Ruhland & Rathmayer, 1978; Clarke, 1986).

Two other muscles act across the patellotibial joint but arise, in part, in the femur (Figs 5B, 16). An anterior transpatellar muscle (6) and a posterior transpatellar muscle (7) arise on the distodorsal surface of the femur, traverse the patella ventrally and insert on the ventroanterior and ventroposterior margins of the tibia, respectively. Muscle 6 is simple and straplike, but the tendon of the muscle 7 receives fibres from the proximoposterior surface of the patella (Fig. 5B). In their study of a mygalomorph, Ruhland & Rathmayer (1978) indicate that muscle 7 is like 6 in lacking a direct connection to the patella, and this observation is supported by Dillon (1952). However, results from my dissections of theraphosids are consistent with the description of *Liphistius* given above. Frank's (1957) study of an orb weaver (Araneomorphae; Araneidae) also corroborates this observation. No other study of araneomorph appendages mentions the existence of the femoral heads of the transpatellar muscles, although the patellar head of muscle 7 is usually present.

The femoropatellar joint is complex in spiders, and the intricacies of its functional morphology are described by Manton (1958). The present description is more general. The femoropatellar joint (Figs 5B, 15B, 16) is formed by a transverse bicondylar dorsal hinge that permits flexion-extension. Only flexor muscles are present, and extension results from increased hydraulic pressure. Unlike the tibiotarsal joint, the flexors of the femoropatellar joint insert

primarily on a U-shaped sclerite patellar sclerite that, in turn, attaches to the patella via flexible ligaments (Fig. 15B). The flexor musculature is divided into three main components (8a, 8b, 8d –Figs 5B, 15B). A broad muscle (8a) arises along the anterior face of the femur and inserts on the anterior arm of the patellar sclerite and on the ventral rim of the patella. Muscle 8b is essentially the posterior mirror image of 8a but originates along the distal two-thirds of the posterior surface of the femur. The third component (8d) is a large muscle that arises from the distoventral portion of the trochanter and inserts through a strong tendon on the middle of the patellar sclerite. Muscle 8d typically has three or four subcomponents; see Parry (1957), Ruhland & Rathmayer (1978), or Clarke (1986) for detailed descriptions.

The trochanter joins the femur at a transverse bicondylar joint (Fig. 9B) that undergoes levation-depression. Depression is brought about, in part, by contraction of a large muscle (9) that arises from the ventroanterior surface of the trochanter and inserts broadly on the proximal third of the posterior surface of the femur. Contraction of muscle 8d, which arises just distal to 9, probably plays a role in depression as well. A small muscle (10) arises near the origin of 9 and crosses the trochanterofemoral joint diagonally to insert at the proximoposterior portion of the femur. It crosses the joint near the axis of rotation and would not be expected to play an important role in operating the joint directly. Levation of the femur is accomplished by two muscles. Muscle 12 arises from the anterior surface of the trochanter and inserts on the dorsal rim of the femur. Muscle 13 has two heads, one arising just posterior to the origin of 9 on the anterior surface of the trochanter, the other arising from the anterior surface of the coxa. Muscle 13 inserts with 12 at the dorsal rim of the femur.

Order Amblypygi

Amblypygids (or whipspiders) are thought to be closely related to Araneae and have been used to establish character polarities in a cladistic analysis of the spider suborders (Platnick & Gertsch, 1976). Yet these arachnids differ from spiders in several important respects. The first leg in amblypygids is antenniform and is used as a sensory organ. Amblypygids are therefore functional hexapods. In addition, all walking legs are laterigrade—the articulations of the coxotrochanteral joints are oriented in such a way that the primitive anterior face of each leg is directed dorsally. To simplify comparisons with other arachnids, amblypygid walking legs will be described here as though they maintained the primitive prograde orientation.

The appendicular morphology of Amblypygi has received relatively little attention. Wood (1926) described the joints and musculature associated with the coxa, trochanter, femur and patella in a North American amblypygid, *Phrynus marginemaculatus* Koch, but many of her observations appear to be inaccurate. Manton (1977) and van der Hammen (1986) describe the external anatomy of walking legs in representative species. The skeleton and muscles of the fourth walking leg in *P. marginemaculatus* are described here. The morphology of legs 2 and 3 is similar to that of leg 4 and although leg 1 is modified for use as a tactile organ its basic morphology is like that of the other legs. Several specimens of *Phrynus viridescens* Franganillo have also been examined, but they do not differ substantially from *P. marginemaculatus*.

The pretarsus bears two large claws but lacks the median claw found in most spiders. It joins the telotarsus at a transverse bicondylar joint (Fig. 1C) that undergoes levation-depression. The levator (1) arises from the dorsal surface of the basitarsus and inserts at the dorsal rim of the pretarsus. The depressor (2) arises from the proximal portion of the tibia and inserts with a long tendon at the ventral margin of the pretarsus.

The tarsus is divided into a three-segmented telotarsus and an unsegmented basitarsus (Fig. 1C). The joint between the telotarsus and basitarsus is similar to that found in spiders; a sclerotized flange projects distally from the dorsal surface of the basitarsus and apparently serves to prevent hyperextension of the joint. Likewise, the joint may undergo protraction-retraction, flexion-extension and rocking movements. The joints of the telotarsus are adesmatic and lack well-developed articulations.

The tarsus joins the tibia by means of arthrodial membranes (Fig. 1C). This joint resembles the telotarsus-basitarsus joint; a sclerotized flange projects from the dorsal surface of the tibia and apparently acts to prevent hyperextension. The flexor (3) arises largely from the proximal half of the tibia, although slips arise along the entire length of that segment, and inserts at the ventral rim of the basitarsus by means of a long tendon. There is no extensor muscle at the tibiotarsal joint.

The tibia of leg 4 is subdivided by three adesmatic dorsal hinge joints that allow flexion-extension (Fig. 1C). The distal joint is the most well developed and is the only intratibial joint present in legs 2 and 3. The structure of this joint is reminiscent of the tibiotarsal joint in having modifications to prevent hyperextension. In this case, however, a heavily-sclerotized flange projects proximally from the distal podomere and fits within a sclerotized shelf on the dorsal surface of the proximal podomere when the joint is fully extended. Based on external evidence alone, Millot (1949a), Manton (1977) and van der Hammen (1986) concluded that the distal intratibial joint corresponds to the tibiotarsal joint and homologized the distal portion of the tibia with the basitarsus of spiders and other arachnids. Analysis of the musculature, however, establishes the true homologies of these podomeres.

The patellotibial joint (Figs 5C, 9C) is largely immovable in amblypygids. The dorsal surface of this joint is V-shaped with the apex pointing proximally. A strong condyle unites the tibia and patella at the apex of the V, and there is a smaller condyle-like structure on the posterior face of the joint. A stiff hinge connects the dorsoposterior margins of the tibia and patella between the two 'condyles'. Four muscles insert on the proximal rim of the tibia (4–7). Muscle 4 arises broadly from the anterior surface of the patella and inserts on the anterior rim of the tibia (Fig. 9C). A transpatellar muscle (6) arises from the distodorsal surface of the femur and also inserts on the anterior margin of the tibia (Fig. 5C). Muscle 5 arises broadly on the posterior face of the patella and muscle 7 arises from the proximoposterior surface. Both muscles insert on the ventroposterior rim of the tibia. The patellotibial joint is the principal site of leg autotomy in *P. marginemaculatus* (personal observation).

The femoropatellar joint (Figs 5C, 15C) is formed by a transverse bicondylar dorsal hinge and movement is limited to flexion-extension. The patellar sclerite attaches to the anterior rim of the patella, and its posterior margin is free (Fig. 15C). As in *Limulus* and spiders, this joint is operated by flexors only.

Extension appears to result from hydraulic pressure. Muscle 8a arises broadly on the ventral rim of the patella, although some fibres insert on the patellar sclerite from the posterior surface of the distal half of the femur and inserts directly on the ventral rim of the patella, although some fibres insert on the patellar sclerite as well. Muscle 8c arises from the dorsoposterior surface of the proximal half of the femur and inserts on the patellar sclerite by means of a large tendon that it shares with 8d. Muscle 8d arises from the distoventral surface of the trochanter, traverses the entire length the femur and inserts on the patellar sclerite (Figs 5C, 15C).

The trochanter and femur are joined by a transverse bicondylar joint (Figs 9C, 17A) that permits levation-depression. Depression is brought about by two muscles (9, 11). Muscle 9 arises on the ventroanterior surface of the trochanter, as in spiders, and inserts broadly on the posterior surface of the proximal one-third of the femur. Muscle 11 arises on the ventral surface of the trochanter and inserts on the ventral rim of the femur. A small muscle (10) arises just proximal to the origin of 9, crosses the joint diagonally and inserts on the proximoposterior portion of the femur. Muscle 10 seems unlikely to influence movement at this joint to any great extent. Levation at the trochantero-femoral joint is brought about by two muscles (12, 13). Muscle 12 arises from the dorsoanterior wall of the trochanter and inserts along the dorsal midline of the femur. Muscle 13 arises from the dorsoanterior wall of the proximal part of the trochanter and the anterior surface of the coxa; it inserts on the dorsal rim of the femur.

Order Uropygi

Uropygids (or whipscorpions) are often considered the sister group of Amblypygi and Araneae (Weygoldt & Paulus, 1979b), but their appendages bear a stronger resemblance to those of amblypygids than to spiders. Whipscorpions, like amblypygids, are functional hexapods; the first leg pair is antenniform and is used as a tactile organ. Amblypygids and uropygids also share a unique and complicated arrangement of flexor muscles at the femoropatellar joint.

Uropygi is divided into two suborders differentiated by size, carapace morphology and certain aspects of their appendicular anatomy. Species within the suborder Thelyphonida are generally large with heavily sclerotized bodies and an undivided carapace. The walking appendages are laterigrade resembling those of amblypygids. Members of the suborder Schizomida are generally small (body length less than 5 mm) and the carapace is divided into several distinct plates; the appendages are prograde as in spiders. Unlike thelyphonids, which are typically slow and deliberate in their movements, schizomids are generally active and can jump. The femur of leg 4 and its associated muscles are enlarged and may enhance their jumping ability.

Little work has been done on the appendicular anatomy of uropygids. Börner (1904) provides a generally accurate illustration of muscles in a thelyphonid, and van der Hammen (1986) provides an illustration of the external anatomy and tendons from a representative of each suborder. The skeleton and muscles of leg 4 of a large thelyphonid, *Mastigoproctus giganteus* (Lucas), and a schizomid, *Schizomus* sp. (voucher: American Museum of Natural History) are described. The musculature of *Mastigoproctus* was revealed through dissection whereas the

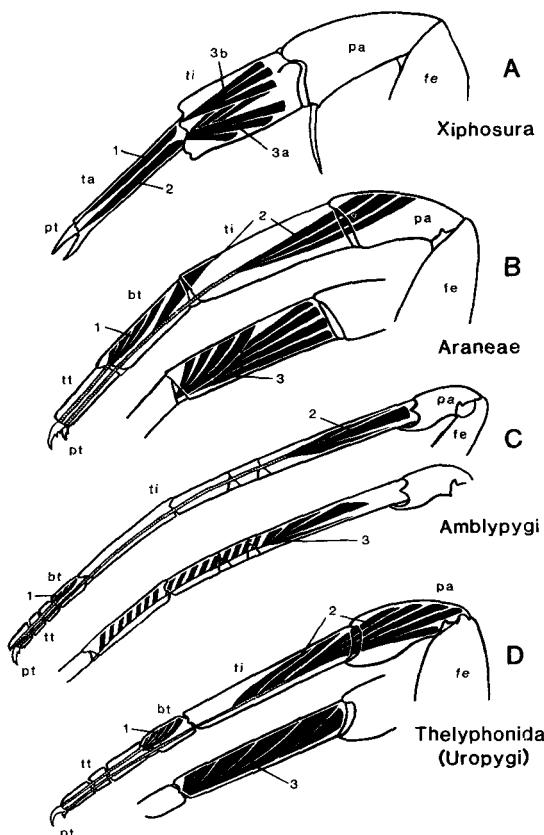


Figure 1. Anterior view of distal muscles (1-3) in leg 4. A, *Limulus polyphemus* (Xiphosura). B, *Liphistius sumatranaus* (Araneae). C, *Phrynus marginemaculatus* (Amblypygi). D, *Mastigoproctus giganteus* (Thelyphonida, Uropygi). Abbreviations: bt, basitarsus; fe, femur; pa, patella; pt, pretarsus; ta, tarsus; ti, tibia; tt, telotarsus.

results from the schizomid dissection were supplemented by observations of isolated appendages suspended in immersion oil.

Suborder Thelyphonida. The structure of the pretarsus in *M. giganteus* resembles that found in Araneae in taking the form of a claw-bearing plate with two large claws dorsally and one small median claw ventrally (Fig. 1D). The pretarsus joins the tarsus at a transverse bicondylar joint and undergoes levation-depression. Levation is brought about by a single muscle (1) that arises on the dorsal surface of the basitarsus and inserts on the dorsal rim of the pretarsus. The depressor (2) arises from the proximodorsal surface of the tibia and broadly on the posterior and dorsal walls of the patella.

The tarsus comprises a telotarsus with three tarsomeres and a basitarsus as in amblypygids. The telotarsus joins the basitarsus by means of arthrodial membranes that permit primarily flexion-extension.

The tibiotarsal joint (Fig. 1D) is formed by a strong transverse bicondylar articulation, the posterior condyle being larger than its anterior counterpart. Movement at this joint is limited to flexion-extension. A large flexor muscle (3)

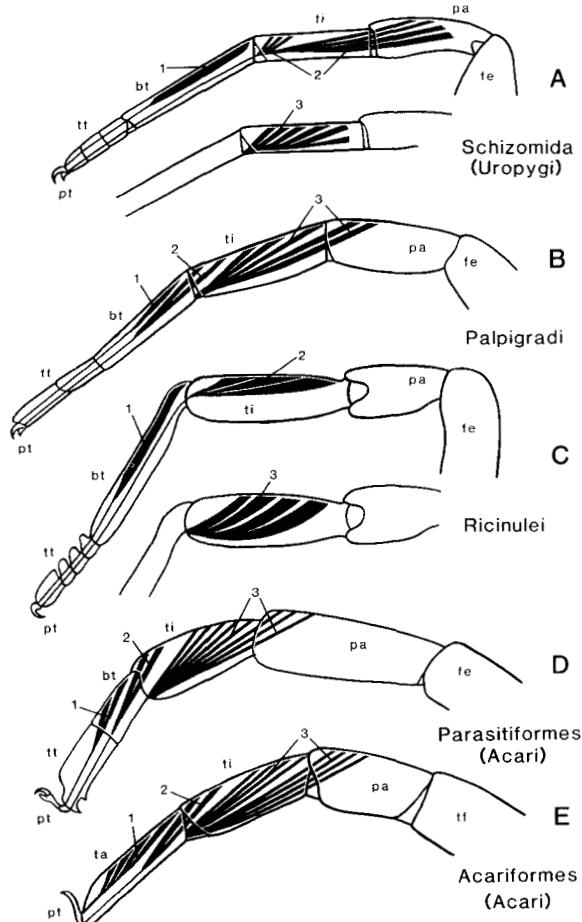


Figure 2. Anterior view of distal muscles (1-3) in leg 4. A, *Schizomus* sp. (Schizomida, Uropygi). B, *Eukoenia* sp. (Palpigradi). C, *Cryptocellus gamboa* (Ricinulei). D, *Amblyomma americanum* (Parasitiformes, Acari). E, *Dinothrombium* sp. (Acariformes, Acari). Abbreviations: bt, basitarsus; fe, femur; pa, patella; pt, pretarsus; ta, tarsus; tf, telofemur; ti, tibia; tt, telotarsus.

arises from the anterior and posterior walls of the tibia and inserts on the ventral margin of the basitarsus. There is no extensor muscle.

The patellotibial joint (Figs 5D, 9D) is formed by a strong dorsoanterior monocondylar articulation that largely permits flexion-extension, but some protraction-retraction and rocking movements are also possible. Movement at this joint is controlled by four muscles (4-7). Muscles 4 and 5 arise broadly on the distoanterior and distoposterior walls of the patella and insert on the anterior and posterior rims of the tibia, respectively (Fig. 9D). The remaining muscles (6, 7) are situated in the anterior half of the patella; the posterior half is occupied by a large component of the pretarsal depressor (2) (Fig. 1D). Muscle 6 arises from the ventral and dorsoanterior surfaces of the patella and the distodorsal surface of the femur. Muscle 7 arises on the ventroanterior surface of the patella and on the distodorsal surface of the femur just posterior to the origin of 6. Both insert on the ventral margin of the tibia.

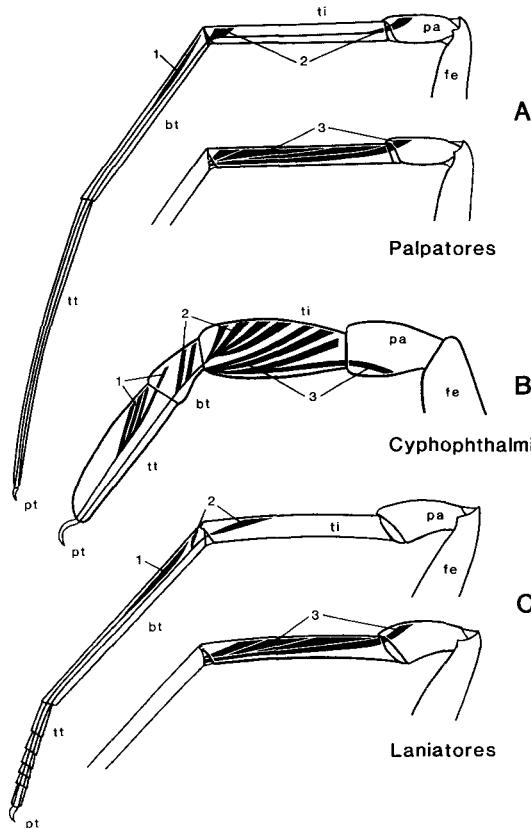


Figure 3. Anterior view of distal muscles (1–3) in leg 4 of the opilionids. A, *Leiobunum vittatum* (Palpatores). B, *Siro acaroides* (Cyphophthalmi). C, *Cynorta subserialis* (Laniatores). Abbreviations: bt, basitarsus; fe, femur; pa, patella; pt, pretarsus; ti, tibia; tt, telotarsus.

The femoropatellar joint (Figs 5D, 15D) is formed by a transverse bicondylar dorsal hinge and is only supplied with flexors. Attachment of the patellar sclerite is to the patella only at its anterior margin as in amblypygids (Fig. 15D). Muscle 8a arises broadly from the anterior wall of the femur and inserts on the patellar sclerite. Muscle 8b arises from the distal half of the posterior surface of the femur and inserts on the ventral rim of the patella. Muscle 8c is composed of several heads, which arise from the proximodorsal and posterior surfaces of the femur and insert with tendons onto the patellar sclerite jointly with the tendon of 8d. Muscle 8d arises from the ventroanterior surface of the trochanter near its distal end and inserts via a strong tendon onto the patellar sclerite. Observations of living specimens suggest that extension at the femoropatellar joint is accomplished by ballooning of the broad arthrodiyal membrane brought about by an increase in haemolymph pressure.

The trochanter joins the femur at a transverse bicondylar joint (Fig. 9D) that undergoes levation-depression. Depression is apparently brought about by two muscles, 8d (described above) and 11. Muscle 11 arises broadly from the ventral and ventroposterior surfaces of the trochanter and inserts on the ventral rim of the femur. A small muscle (10) arises from the anterior surface of the trochanter,

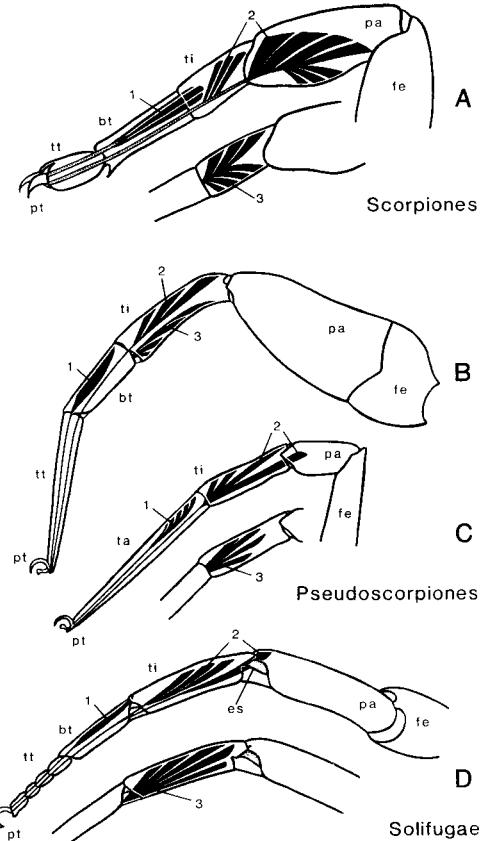


Figure 4. Anterior view of distal muscles (1-3). A, Leg 4 of *Pandinus imperator* (Scorpiones). B, Leg 4 of *Chthonius tetracheilatus* (Pseudoscorpiones). C, Leg 1 of *C. tetrachelatus*. D, Leg 2 of *Paragaleodes scalaris* (Solifugae). Abbreviations: bt, basitarsus; es, elastic sclerite; fe, femur; pa, patella; pt, pretarsus; ta, tarsus; ti, tibia; tt, telotarsus.

traverses the trochanterofemoral joint diagonally and inserts on the proximoposterior surface of the femur. The function of 10 is not apparent. Elevation at this joint is brought about by a single muscle (13), which arises broadly from the anterior and dorsal surfaces of the trochanter and coxa and inserts on the dorsal rim of the femur.

Suborder Schizomida. The pretarsus, with two large dorsal claws and a small median ventral claw (Fig. 2A), joins the tarsus at a transverse bicondylar joint that undergoes levation-depression. The levator (1) arises on the dorsal surface of the basitarsus and inserts on the dorsal rim of the pretarsus. Depression is brought about by contraction of muscle 2, which arises on the proximodorsal surface of the tibia and broadly on the posterior surface of the patella.

The telotarsus is composed of three subdivisions and joins the basitarsus at a dorsal articulation. Movement at this joint probably consists of flexion-extension and protraction-retraction. The basitarsus attaches to the tibia by way of a transverse bicondylar dorsal hinge (Fig. 2A) that permits flexion-extension. This joint is not supplied with an extensor but with a flexor (3) which arises primarily

from the anterior and posterior surface of the tibia. I could not confirm van der Hammen's (1986) observation that 3 extends into the patella.

The patellotibial joint (Figs 6A, 9E) is formed by a single dorsal condyle and undergoes protraction-retraction. Protraction is accomplished by a single muscle (4) arising from the anterior wall of the patella and inserting on the anterior rim of the tibia. There is no apparent retractor, but the patellar component of muscle 2 may fill this role. The transpatellar muscles (6, 7) are absent.

Except for the absence of the transpatellar muscles, the femoropatellar joint in *Schizomus* (Fig. 6A) is similar to that of *Mastigoproctus* (Fig. 5D). A transverse bicondylar dorsal hinge allows flexion-extension, but only flexors are present. The flexor is divided into four heads (8a–8d). Muscle 8a arises from the anterior face of the femur and inserts on the patellar sclerite, which, in turn, attaches to the ventroanterior margin of the patella. Muscle 8b arises from the distoposterior wall of the femur and inserts directly on the ventral margin of the patella. Muscle 8b lacks a direct connection to the patellar sclerite as in *Mastigoproctus*. Muscle 8c arises from the proximal part of the dorsoposterior wall of the femur and inserts on the patellar sclerite via a tendon that it shares with 8d. Muscle 8d arises from the ventral lip of the trochanter.

The trochanter joins the femur at a transverse bicondylar joint (Fig. 9E) that undergoes levation-depression. Two muscles may play a role in depression, 8d (described above) and 11. Muscle 11 arises from the ventral surface of the trochanter and inserts on the ventroposterior rim of the femur. A small muscle (10) arises on the anterior surface of the trochanter and inserts on the proximoposterior surface of the femur. The function of 10 is unknown. Levation of the trochantero-femoral joint is also brought about by two muscles (12, 13). Muscle 12 arises from the anterior wall of the trochanter and inserts broadly along the dorsoposterior surface of the femur. Muscle 13 arises from the dorsal surface of the trochanter and coxa and inserts on the dorsal margin of the femur.

Order Palpigradi

Palpigradi is a small order of minute, soil-dwelling arachnids that resemble thelyphonids (Uropygi), and bear a tail-like sensory flagellum at the posterior end of the opisthosoma. Unlike uropygids, however, the pedipalps of palpigrades are leg-like rather than raptorial, and the first walking leg, although used as a sensory organ, is not antenniferous. All walking legs in Palpigradi have the typical number of eudesmotic joints, but there is disagreement over how the segments should be homologized with those of other arachnids (reviewed by Rowland & Sissom, 1980). The most recent system by van der Hammen (1982) proposes that coxae are absent in this order and that the most proximal segment is the trochanter. The trochanter is followed by two femoral segments, a patella, a tibia and a divided tarsus. Other workers consider the most proximal segment to be a freely movable coxa, and the second segment is regarded as the trochanter. Present observations of the extrinsic leg muscles of Palpigradi and other arachnids support the latter view. Three sets of extrinsic leg muscles (anterior, lateral, posterior) arise from the proximal segment and insert on the carapace; two sets (anterior, posterior) arise from the proximal segment and insert on the endosternite. This arrangement is characteristic of the coxae in most arachnids, *Limulus* and even trilobites (Cisne, 1981). I therefore reject van der Hammen's

proposal and adopt the more traditional system advocated by Hansen & Sörensen (1897), Börner (1901) and Roewer (1934).

The external anatomy of palpigrade appendages has been described by Börner (1901) and Roewer (1934). Van der Hammen (1982) dealt with the musculature of *Eukoenenia mirabilis* (Grassi) but this was limited to the study of cuticular tendons. Here the muscles of the fourth walking leg of *Eukoenenia* sp. from Key Largo, Florida (voucher: Acarological Collection, Ohio State University) are described. The four pairs of walking legs differ primarily in overall size, length and in the number of tarsomeres. Present descriptions are based on the examination of unstained whole mounts and whole specimens suspended in immersion oil. The muscles were clearly visible through the transparent cuticle.

The pretarsus, bearing two large dorsal claws and one small median ventral claw (Fig. 2B), joins the tarsus at a transverse bicondylar joint that apparently undergoes levation-depression. The levator (1) arises from the proximodorsal surface of the tarsus and inserts on the dorsal rim of the pretarsus. The depressor (2) arises from the distodorsal surface of the tibia and inserts on the ventral rim of the pretarsus via a long tendon. In leg 4, the tarsus consists of three tarsomeres. Börner (1901) considered the proximal tarsomere to be equivalent to the basitarsus of other arachnids.

The tibiotarsal joint (Fig. 2B) is formed by a transverse dorsal hinge that permits flexion-extension. Flexion is accomplished by a paired muscle (3) that arises from the anterior and posterior surfaces of the tibia and the distodorsal surface of the patella. Muscle 3 inserts on the ventral rim of the tarsus.

The patellotibial joint (Fig. 6B) is formed by a single dorsal condyle that apparently permits protraction-retraction as well as flexion-extension. These movements are brought about by a paired transpatellar muscle that inserts broadly on the ventral rim of the tibia. The anterior half of this muscle probably corresponds to the anterior transpatellar muscle (6) of other arachnids and *Limulus*, the posterior half to the posterior transpatellar muscle (7). Muscle 6 arises from the anterior surface of the patella and distoanterior half of the femur. Muscle 7 is the posterior mirror image of 6. Muscles 4 and 5 appear to be absent in Palpigradi, although they may exist as undifferentiated components of muscles 6 and 7, respectively.

The femoropatellar joint (Fig. 6B) is formed by a transverse dorsal hinge articulation that appears to permit flexion-extension. Flexion is brought about by a large paired muscle (8) arising from the anterior and posterior surfaces of the femur and trochanter and inserting on the ventral rim of the patella. Van der Hammen (1982) described extensor muscles at the femoropatellar and patellotibial joints of leg 1 but his observations remain unconfirmed.

The trochanter joins the femur at a transverse dorsal hinge (Fig. 10A) that primarily undergoes flexion-extension. Flexion is brought about, in part, by a muscle (11) arising from the ventral surface of the trochanter and inserting on the ventral rim of the femur. The trochanteral heads of muscle 8 probably play a role in flexing the trochanterofemoral joint, as well. There is no extensor muscle.

Order Ricinulei

Ricinulei is a small order of unusual arachnids that are thought to be close relatives of Acari (Weygoldt & Paulus, 1979b; Lindquist, 1984). Several features

of ricinuleid walking appendages are noteworthy. The cuticle is extremely tough and thick and the condyles are large and strong suggesting that ricinuleids are capable of exerting large forces against the substrate, but it is not apparent how these forces might be produced. Ricinuleids have no extensor muscles, and they lack the well-developed arthrodial membranes typical of arachnids that use hydraulic leg extension. A more intensive study of locomotion in these animals is clearly needed. Another peculiarity of the ricinuleids is that the first and second pairs of walking legs have one trochanter (Fig. 10B), but the third and fourth appear to have two (Fig. 10C). From comparisons with other arachnids, the distal 'trochanter' is suggested to represent the proximal portion of a divided femur. This subject will be discussed in detail below.

The external morphology of ricinuleid walking appendages has been described by Hansen & Sörensen (1904) and Millot (1949b); van der Hammen (1979) has described the cuticular muscular insertions in *Ricinoides karschii* (Hansen & Sörensen). The appendicular skeleton and musculature of leg 2 are described from dissection of a single specimen of *Cryptocellus gamboa* Platnick & Shadab. The anatomy of the femur, patella, tibia, tarsus and pretarsus in leg 2 is similar in other walking legs, but the presence of an extra segment in legs 3 and 4 necessitates further description, and so an illustration of the proximal portion of leg 4 is also provided (Fig. 10C).

The pretarsus of leg 2 in ricinuleids bears a pair of large claws and joins the telotarsus at a transverse bicondylar joint (Fig. 2C) that undergoes levation-depression. The levator (1) arises on the proximodorsal surface of the basitarsus and inserts on the dorsal rim of the pretarsus via a tendon. The depressor (2) arises primarily from the dorsal surface of the tibia and basitarsus and inserts on the ventral rim of the pretarsus. I could not corroborate van der Hammen's (1979) observation that the tendon of muscle 2 extends into the femur.

The tarsus of leg 2 consists of a telotarsus composed of five tarsomeres and an undivided basitarsus. All joints within the tarsus are adesmatic. The basitarsus joins the tibia through a transverse bicondylar joint (Fig. 2C) that permits flexion-extension. Flexion is brought about by a single muscle (3) that arises broadly from the anterior and posterior surfaces of the tibia and inserts on the ventral rim of the basitarsus through a strong tendon. As in other arachnids, there is no extensor at this joint.

The patella joins the tibia at a strong vertical bicondylar anterior hinge (Figs 6C, 10B) that permits protraction-retraction. Retraction is accomplished by two muscles (4, 5). Muscle 4 arises from the anterior surface of the patella and inserts on the ventroposterior rim of the tibia. Muscle 5 arises broadly from the dorsal and posterior surfaces of the patella and inserts on the dorsoposterior rim of the tibia. It is unclear how protraction is accomplished.

The femur joins the patella by means of a strong transverse bicondylar dorsal hinge (Fig. 6C) that undergoes flexion-extension. Flexion is brought about by a muscular complex that consists of three components (8a-8c). Muscle 8a arises broadly from the anterior surface of the femur and inserts on the anterior margin of the patella. Muscle 8b is the mirror image of 8a, arising from the posterior surface of the femur and inserting on the posterior rim of the patella. The largest component (8c) arises from the proximal part of the femur and inserts by means of a strong tendon on a patellar sclerite. There is no extensor.

In legs 1 and 2, the trochanter attaches to the femur through a transverse

bicondylar joint (Fig. 10B) that permits levation-depression. Depression is brought about by a paired muscle (11) that arises from the anterior and posterior surfaces of the trochanter and inserts on the ventral margin of the femur. Levation is apparently brought about by a single muscle (13) that arises from the dorsal portion of the trochanter and coxa and inserts on the dorsal rim of the femur.

In legs 3 and 4, the distal 'trochanter' (basifemur) joins the 'femur' (telofermum) at a transverse bicondylar joint (Fig. 10C) that undergoes levation-depression. The depressor (10) arises from the anterior, ventral and posterior walls of the basifemur and inserts on the ventral rim of the telofemur. The levator (12) arises from the dorsal surface of basifemur and inserts on the dorsal rim of the telofemur.

The articulations and musculature of the trochanterobasifemoral joint of legs 3 and 4 are the same as described in the trochanterofemoral joint in the anterior legs (Fig. 10B, C), suggesting that these joints are serial homologues. A single levator (13) arises from the dorsal surface of the trochanter and coxa and inserts on the dorsal rim of the basifemur. The depressor (11) is paired and arises from the anterior and posterior walls of the trochanter. Muscle 11 inserts on the ventral rim of the basifemur.

Order Acari

Acari is composed of two principal lineages, Parasitiformes (= Anactinotrichida) and Acariformes (= Actinotrichida), but there is debate whether these lineages actually constitute a natural (monophyletic) group. Several authors suggest that Parasitiformes is more closely related to Ricinulei than to acariform mites and that Acari is therefore diphyletic (van der Hammen, 1979, 1982). In a critical review of this problem, Lindquist (1984) supports the view that Acari is monophyletic and that Ricinulei represents its sister group. A close phylogenetic relationship between Ricinulei and Acari is supported by similarities in postembryonic development, when they pass through a hexapod larval stage followed by several octopod nymphal instars, and by presence of a gnathosoma. Lindquist also notes that in opilioacarines, parasitiform mites that are thought to represent a primitive grade in mite evolution, legs 3 and 4 are equipped with two apparent trochanters as in ricinuleids, but this feature is absent in other mites.

The basic organization of walking appendages in Acari is fairly uniform, although several morphological trends are apparent. The femora of parasitiform mites, for example, are typically divided by a ring of reduced sclerotization associated with slit sensilla or lyrifissures. This 'joint' is largely immovable and is not equipped with muscles. The femoral ring is absent in Acariformes. The tarsi of Parasitiformes are typically divided by adesmatic joints, whereas the tarsi of acariform mites are usually undivided (van der Hammen, 1979, 1982; Lindquist, 1984). The walking legs of certain acariform mites are characterized by the appearance of a eudesmatic joint within the femur during postembryonic development, but this feature is probably not homologous with the femoral ring of parasitiform mites.

Differences in the joints and musculature of the walking appendages have generally provided few reliable characters for elucidating phylogenetic

relationships among the major acarine groups (Lindquist, 1984; Woodring & Galbraith, 1976).

Suborder Parasitiformes. The skeletal and muscular anatomy of representatives from several parasitiform families have been examined: Argasidae (Shoukrey & Sweatman, 1984), Haemogamasidae (Young, 1970), Ixodidae (Ewing, 1928), Macrochelidae (Ewing, 1928), Phytoseiidae (Akimov & Yastrebtsov, 1987) and Uropodidae (Woodring & Galbraith, 1976). The joints and musculature appear to be fairly uniform throughout this group. The joints and musculature of a common hard-bodied tick, *Amblyomma americanum* L. (Ixodidae), are described from dissection. The fourth walking leg is described, but the basic organization of all legs within individuals is similar.

The pretarsus in *A. americanum* comprises two claws located at the distal tip of an elongate, flexible process. A padlike organ (pulvillus) is situated ventrally between the claws. Articulations between the pretarsus and telotarsus were not observed, but in other parasitiform mites there is a distinct transverse bicondylar joint (van der Hammen, 1979). The claws are operated by two muscles (Fig. 2D). Muscle 1 arises from the dorsal surface of the basitarsus and muscle 2 arises from the dorsal surface of the basitarsus and tibia. The muscles insert on the pretarsus by means of separate tendons. The division of the tarsi by adesmatic joints unites most Parasitiformes with the majority of other arachnids. These joints are movable in opilioacarines and a few other groups, but there is a tendency for them to fuse in Ixodida, Holothyrida and Gamasida (Lindquist, 1984).

The tibiotarsal joint (Fig. 2D) is formed by a dorsal hinge articulation and primarily undergoes flexion-extension. The flexor (3) is a paired muscle with heads arising broadly from the anterior and posterior surfaces of the tibia and the distodorsal surfaces of the patella or 'genu' in acarological parlance. Muscle 3 inserts on the ventral rim of the tarsus. There are no extensor muscles at this joint, and the absence of extensors is apparently characteristic of all mites. Mitchell (1957) suggests that leg extension in mites is brought about by increased hydraulic pressure generated within the body.

The tibia joins the patella at a transverse dorsal hinge (Figs 2D, 6D) permitting flexion-extension. Flexion is accomplished by a paired transpatellar muscle that probably corresponds to muscles 6 and 7 of other arachnids. The anterior half (6) arises from the anterior surface of the patella and the distodorsal surface of the femur and inserts on the ventroanterior rim of the tibia. The posterior half (7) is the mirror image of 6, arising on the posterior surface of the patella and femur and inserting on the ventroposterior margin of the tibia. Muscles 4 and 5 appear to be absent but may be present as undifferentiated portions of 6 and 7 as in Palpigradi.

The femoropatellar joint (Fig. 6D) is formed by a transverse dorsal hinge that permits flexion-extension. Flexion is accomplished by a paired muscle (8) that arises from the anterior and posterior surfaces of the femur and inserts broadly on the ventral margin of the patella.

The femur joins the trochanter at a transverse bicondylar joint (Fig. 10D) that undergoes levation-depression. The depressor (11) arises from the ventroanterior and ventroposterior surfaces of the trochanter and inserts on the ventral margin of the femur. Levation is accomplished by muscle 13, which arises from the

dorsal surface of the trochanter and coxa and inserts on the dorsal rim of the femur.

Suborder Acariformes. The major difference in walking legs of the two major acarine lineages is the tendency for some early derivative acariform mites to develop a eudesmotic joint within each femur, resulting in legs with eight segments rather than the typical seven. In some acariform mites, such as trombidiids, the femora of all walking legs are divided; such division is suppressed in some or all legs in other groups, such as higher Oribatida (van der Hammen, 1982; personal observation). Lindquist (1984) suggests that divided femora are primitive in Acariformes and that this feature gradually regressed in more derived groups. The broader significance of divided femora in mites and other arachnids is discussed later.

The appendicular anatomy of representatives from several acariform families have been examined: Labidostommatidae (Ewing, 1928), Hydryphantidae (Mitchell, 1957), Tetranychidae (Blauvelt, 1945), Trombiculidae (Mitchell, 1962) and Unionicolidae (Mitchell, 1955). This sample is small compared with the size and diversity of the group but it represents a fairly broad cross section. The anatomy of leg 4 in the trombidiid *Dinothrombium* sp. (voucher: Acarological Collection, Ohio State University) is described from dissection. Trombidiidae (velvet mites) are considered an early derivative group and have two femoral segments (basifemur, telofemur) in all walking legs. They share this feature with the water mites (Hydryphantidae, Unionicolidae) described by Mitchell (1955, 1957).

The pretarsus bears two claws and joins the tarsus at a transverse bicondylar joint (Fig. 2E) that undergoes levation-depression. The levator (1) arises from the dorsal surface of the tarsus and inserts on the dorsal margin of the pretarsus. The depressor (2) arises from the proximodorsal surface of the tarsus and the distodorsal surface of the tibia. It inserts on the ventral margin of the pretarsus.

The tarsus is undivided and joins the tibia at a transverse dorsal hinge (Fig. 2E) that permits flexion-extension. The flexor (3) is paired and arises broadly from the anterior and posterior surfaces of the tibia and the distodorsal surface of the patella. Muscle 3 inserts broadly on the rim of the tarsus.

The tibia joins the patella at a transverse dorsal hinge (Fig. 6E) and undergoes flexion-extension. The flexor is paired and arises from the anterior and posterior surfaces of the patella and the distodorsal surface of the telofemur. The anterior half of this muscle probably corresponds to the anterior transpatellar muscle (6) of other arachnids and *Limulus* and the posterior half to the posterior transpatellar muscle (7).

The patella joins the telofemur at a transverse dorsal hinge (Fig. 6E) and its movements are limited to flexion-extension. The flexor (8) is paired and arises broadly from the anterior and posterior surfaces of the telofemur and the distodorsal surface of the basifemur. Muscle 8 inserts on the ventral rim of the patella. The telofemur joins the basifemur at a transverse dorsal hinge that permits flexion-extension. The flexor arises broadly from the ventral surface of the basifemur and inserts on the ventral rim of the telofemur (Fig. 10E). This muscle is tentatively homologized with muscle 10 of other arachnids, and this view is upheld in the following discussion of double 'trochanters' and divided femora.

The basifemur joins the trochanter at a vertical bicondylar joint in which the

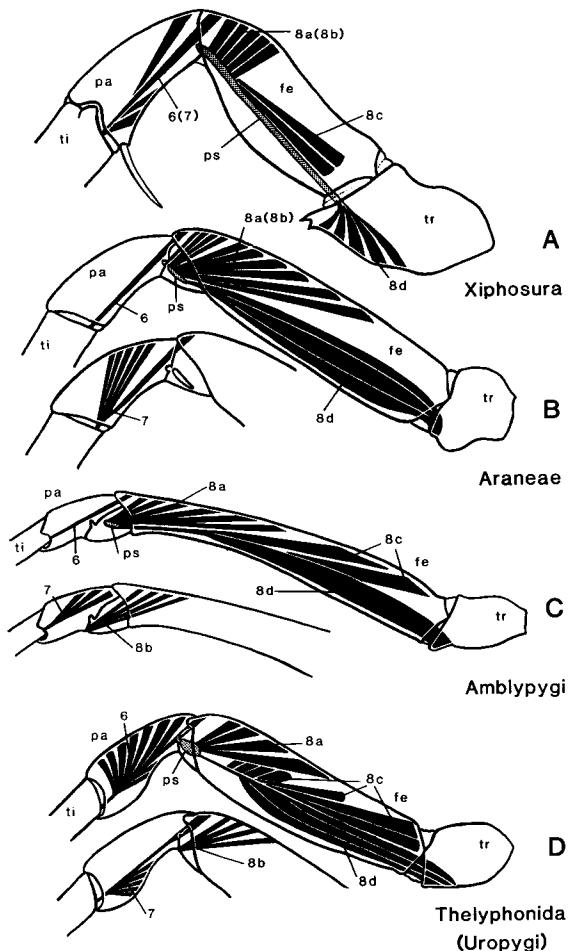


Figure 5. Anterior view of the transpatellar muscles (6, 7) and flexors of the femoropatellar joint (8a-8d) in leg 4. A, *Limulus polyphemus* (Xiphosura). B, *Liphistius sumatranaus* (Araneae). C, *Phrynos marginemaculatus* (Amblypygi). D, *Mastigoproctus giganteus* (Thelyphonida, Uropygi). Muscles indicated by numbers in parentheses are unillustrated posterior mirror images. Insets depict anterior view of muscle 7 with muscle 6 removed. Abbreviations: fe, femur; pa, patella; ps, patellar sclerite; ti, tibia; tr, trochanter.

dorsal condyle is distal to the ventral (Fig. 10E). The movement resulting from this arrangement cannot be described adequately as merely protraction-retraction but is more precisely an anterior-posterior rocking around the long axis of the leg. These movements are brought about by a pair of large muscles (11, 13). Muscle 11 arises broadly on the posterior surface of the trochanter and inserts on the posterior margin of the basifemur. Muscle 13 arises on the anterior face of the trochanter and inserts on the anterior rim of the basifemur.

Order Opiliones

Opiliones is traditionally divided into three suborders (Palpatores, Cyphophthalmi, Laniatores) distinguished by several appendicular features,

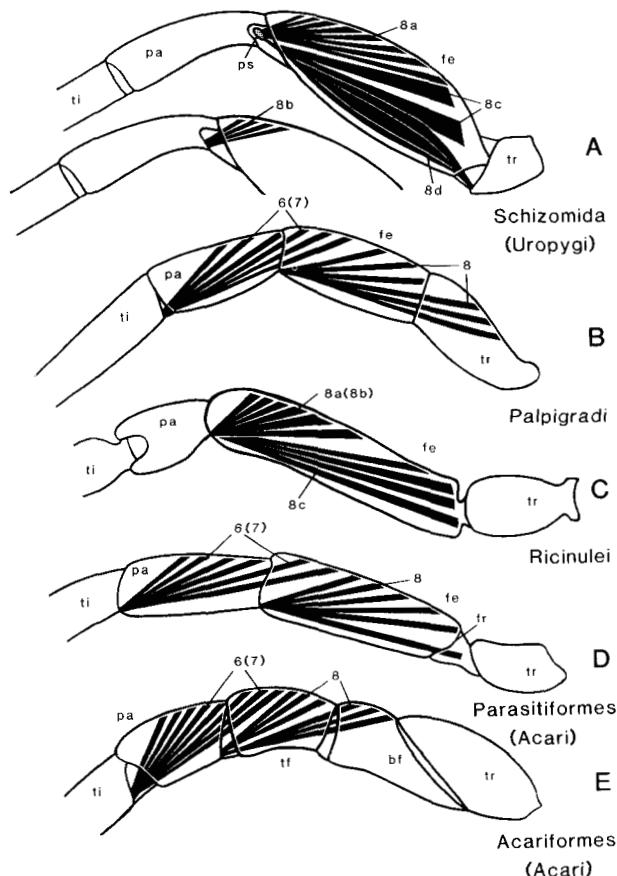


Figure 6. Anterior view of the transpatellar muscles (6, 7) and flexors of the femoropatellar joint (8a-8d). A, Leg 3 of *Schizomus* sp. (Schizomida, Uropygi). B, Leg 4 of *Eukoenenia* sp. (Palpigradi). C, Leg 2 of *Cryptocellus gamboa* (Ricinulei). D, Leg 4 of *Amblyomma americanus* (Parasitiformes, Acari). E, *Dinothrombium* sp. (Acariformes, Acari). Muscles indicated by numbers in parentheses are unillustrated posterior mirror images. Abbreviations: bf, basifemur; fe, femur; pa, patella; ps, patellar sclerite; tf, telofemur; ti, tibia; tr, trochanter.

notably the arrangement of the transpatellar muscles, and several non-appendicular characters (Shear, 1985). The external morphology of the walking legs in each suborder is well known, and several trends are apparent. The trochanter of all opilionids joins the femur at a vertical bicondylar joint rather than the transverse bicondylar joint characteristic of most other arachnids and *Limulus*. The patella, likewise, joins the tibia at a vertical bicondylar joint rather than the primitive dorsal monocondylar articulation. The second pair of walking legs is typically the longest and is used as a tactile organ. There is a tendency in many palpator and laniator groups for all walking legs to be long, inspiring the common name 'daddy-long-legs', and for the tarsi to be divided by numerous adesmatic joints. Prior to the present investigation, knowledge of appendicular musculature in Opiliones was derived from a few incomplete studies.

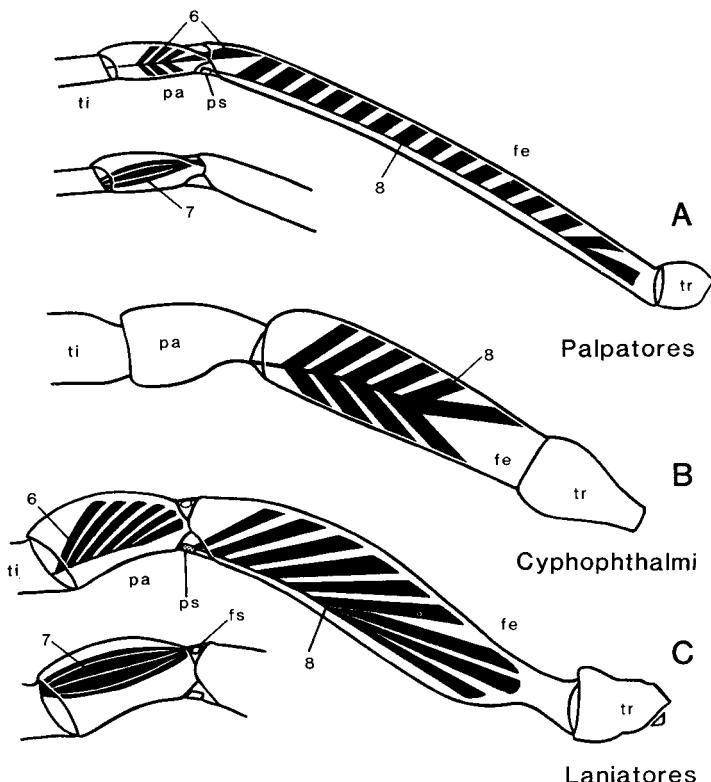


Figure 7. Anterior view of the transpatellar muscles (6, 7) and the flexor of the femoropatellar joint (8) in leg 4 of the opilionids. A, *Leiobunum vittatum* (Palpatores). B, *Siro acaroides* Cyphophthalmi. C, *Cynorta subserialis* (Laniatores). Insets depict anterior view of muscle 7 with muscle 6 removed. Abbreviations: fe, femur; fs, femoral sclerite; pa, patella; ps, patellar sclerite; ti, tibia; tr, trochanter.

Suborder Palpatores. Studies of palpator appendicular anatomy deal exclusively with larger North American or European representatives of the family Phalangiidae and Leiobunidae, commonly known as harvestmen. Gaubert (1892) stated incorrectly that the leg muscles of harvestmen are arranged essentially as in spiders. In a survey of arachnid leg autotomy mechanisms, Wood (1926) noted Gaubert's error and accurately described the muscles of the coxa, trochanter and femur in *Leiobunum* sp. Miller (1977) illustrated appendicular muscles in his study of the quivering movements made by the autotomized legs of *Paroligolophus agrestris* (Meade) and other Palpatores. Miller's illustration generally conforms to the present findings, but the origin of the phylogenetically important femoropatellar extensor (7) was noted incorrectly. The present description focuses upon the fourth walking leg of a common North American leiobunid, *Leiobunum vittatum* (Say).

The pretarsus in *L. vittatum*, as in all Palpatores, comprises a single claw and joins the telotarsus at a transverse bicondylar joint (Fig. 3A) that permits levation-depression. The levator (1) arises on the dorsal surface of the basitarsus and inserts on the dorsal portion of the pretarsus. Depression is accomplished by muscle 2, which arises on the dorsal surface of the tibia and distodorsal surface of

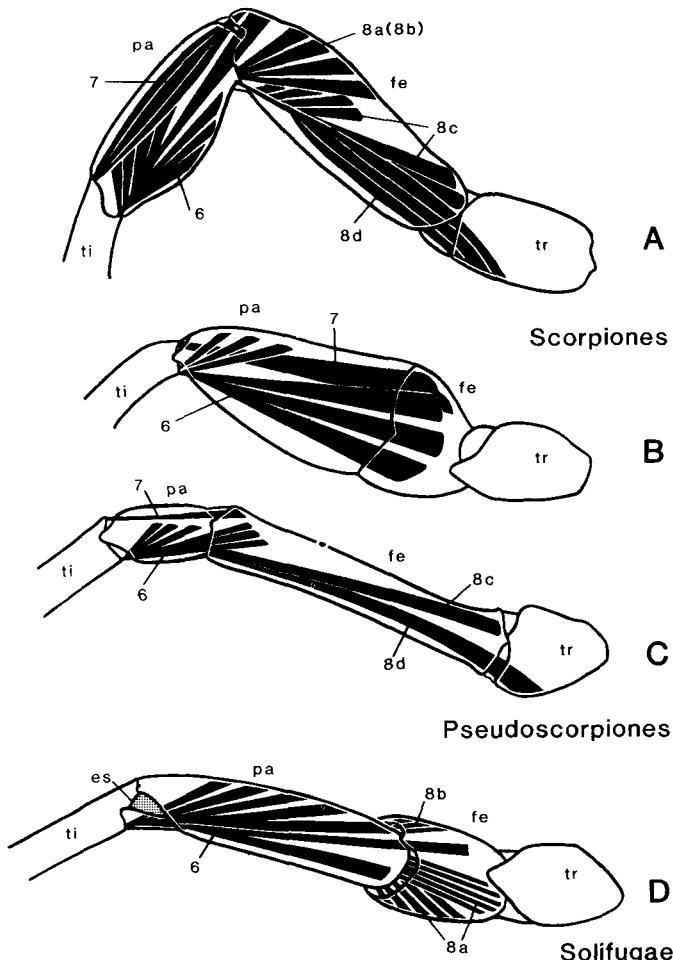


Figure 8. Anterior view of the transpatellar muscles (6, 7) and the flexors of the femoropatellar joint (8a-8d). A, Leg 4 of *Pandinus imperator* (Scorpiones). B, Leg 4 of *Cithonius tetrachelatus* (Pseudoscorpiones). C, Leg 1 of *C. tetrachelatus*. D, Leg 2 of *Paragaleodes scalaris* (Solifugae). Muscles indicated by numbers in parenthesis are unillustrated posterior mirror images. Abbreviations: es, elastic sclerite; fe, femur; pa, patella; ti, tibia; tr, trochanter.

the patella. Muscle 2 inserts on the ventral margin of the pretarsus via a long tendon.

The tarsus is long and divided by numerous adesmatic joints (not illustrated). The division between the basitarsus and telotarsus is distinguished by a sclerotized dorsal flange at the distal end of the basitarsus which limits movement largely to flexion-extension. The other adesmatic joints lack special articular features and are capable of a wider range of movements.

The tibiotarsal joint (Fig. 3A) is formed by a transverse bicondylar dorsal hinge that permits flexion-extension. The flexor (3) originates along the anterior and posterior walls of the tibia and the distodorsal surface of the patella. Muscle 3 inserts on the ventral rim of the basitarsus. There is no extensor.

The patellotibial joint (Figs 7A, 11A, 16) is bicondylar with one dorsoanterior

condyle and one ventroposterior condyle and primarily undergoes protraction-retraction.

Protraction is brought about by two muscles (4, 6). Muscle 4 arises from the distoanterior wall of the patella and inserts on the anterior margin of the tibia (Fig. 11A). Muscle 6 originates broadly on the anterior and ventral walls of the patella and on the distodorsal surface of the femur. The fibres and tendon of 6 traverse the femoropatellar joint ventral to the condyles and probably cause flexion at this joint in addition to protraction at the patellofibial joint (Figs 7A, 16). Retraction is also accomplished by two muscles (5, 7). Muscle 5 arises broadly on the posterior wall of the patella and inserts on the posterior rim of the tibia (Fig. 11A). Muscle 7 arises from a small process projecting from the distodorsal rim of the femur and inserts on the posterior rim of the tibia. Muscle 7 appears to be bifunctional, causing extension at the femoropatellar joint and retraction at the patellofibial joint. In contrast to 6, this muscle lacks direct connection to the patella (Figs 7A, 16).

The femur joins the patella at a transverse bicondylar joint (Fig. 7A) that permits flexion-extension. A patellar sclerite attaches to the ventral margin of the patella by means of a strong, flexible ligament. Flexion is partly brought about by muscle 8, which arises along the dorsal surface of the femur and inserts on the patellar sclerite via a long tendon. A transpatellar muscle (6) probably plays an additional role in flexing the femoropatellar joint. Extension is apparently accomplished by contraction of the other transpatellar muscle (7).

The trochanter joins the femur at a vertical bicondylar joint (Fig. 11A) that undergoes protraction-retraction. The protractor (13) arises from the anterior wall of the trochanter and inserts on the anterior margin of the femur. The retractor (11) arises from the posterior wall of the trochanter and inserts on the posterior margin of the femur.

Suborder Cyphophthalmi. Cyphophthalmi is a group of small opilionids, with adult body lengths ranging from 1 to 4 mm. The external anatomy of cyphophthalmid appendages has been described by Hansen & Sørensen (1904) and Ewing (1928), but until now our knowledge of the internal anatomy was limited to descriptions of tendinous insertions (van der Hammen, 1985a). The anatomy of leg 4 in *Siro acaroides* (Ewing) is described and illustrated both from dissection and examination of isolated appendages suspended in immersion oil.

The pretarsus of each walking leg of *Siro* is like that of Palpatores, consisting of a single claw that attaches to the tarsus via a transverse bicondylar joint (Fig. 3B). Levation of the claw is accomplished by a single muscle (1) arising primarily from the proximodorsal surface of the telotarsus, although several fibres also arise from the dorsal portion of the basitarsus. Muscle 1 inserts on the dorsal margin of the pretarsus. Depression is brought about by muscle 2, which arises from the dorsal surface of the basitarsus and distodorsal surface of the tibia and inserts on the ventral margin of the pretarsus.

The tarsus in Cyphophthalmi is less complicated than that found in most other opilionids. Neither telotarsus nor basitarsus is subdivided by adesmatic joints, unlike most palpator and laniator groups, so that the basic organization of the tarsus is consistent with the majority of other arachnids. The joint between the telotarsus and basitarsus, however, lacks apparent articulations and is essentially immobile.

The tibiotarsal joint (Fig. 3B) consists of a transverse bicondylar dorsal hinge that permits flexion-extension. Flexion is brought about by a single muscle (3) that arises from the anterior and posterior walls of the tibia. A few fibres arise from the ventral surface of the patella. There is no extensor.

The tibia joins the patella at a vertical bicondylar joint (Fig. 11B) that permits protraction-retraction. Protraction is brought about by muscle 4 that arises from the dorsoanterior wall of the patella and inserts on the anterior margin of the tibia. Retraction is accomplished by muscle 5, which arises from the posterior wall of the patella and inserts on the posterior rim of the tibia. In contrast to other opilionids and most other arachnids, the transpatellar muscles (6, 7) are absent.

The femoropatellar joint (Fig. 7B) consists of a transverse bicondylar dorsal hinge and undergoes flexion-extension. Flexion is brought about by muscle 8, which arises from the dorsal and ventral surfaces of the femur and inserts on the ventral margin of the patella. There is no extensor.

The femur joins the trochanter at a vertical bicondylar joint (Fig. 11B) that permits protraction-retraction. Protraction is brought about by muscle 13, which arises from the anterior wall of the trochanter and inserts on the anterior rim of the femur. Retraction is accomplished by muscle 11, which arises from the posterior wall of the trochanter and inserts on the posterior rim of the femur.

Suborder Laniatores. The external anatomy and tendinous insertions of walking legs in a single laniator species, *Scotolemon lespei* Lucas, has been described by van der Hammen (1985a). A description of the joints and muscles in the fourth walking leg of *Cynorta subserialis* (Cambridge), revealed by dissection, is given here. The appendages of *Acromares banksi* Goodnight & Goodnight and an unidentified gonyleptid (voucher: American Museum of Natural History) have also been examined. There are no substantial differences among these species.

The pretarsi of the first and second walking legs resemble those of other opilionids in forming a single claw, but those of legs 3 and 4 have two claws. The pretarsus joins the tarsus by means of a transverse bicondylar joint (Fig. 3C) that allows levation-depression. The levator (1) arises from the dorsal surface of the basitarsus and inserts on the dorsal rim of the pretarsus. The depressor (2) arises from the proximodorsal surface of the basitarsus and the dorsal surface of the tibia and inserts on the ventral rim of the pretarsus via a long tendon.

The telotarsus is attached to the basitarsus through a flexible ventral arthrodial membrane. The dorsal lip of the basitarsus is sclerotized and appears to prevent hyperextension of the joint. Movement is limited primarily to flexion-extension, but some degree of protraction-retraction is also possible. The telotarsus is subdivided by several adesmatic joints that lack well-developed articulations.

The tibiotarsal joint (Fig. 3C) is formed by a bicondylar dorsal hinge that allows flexion-extension. The flexor (3) arises from the anterior and posterior surfaces of the tibia and the dorsal surface of the patella and inserts on the ventral rim of the basitarsus.

The patella joins the tibia at a vertical bicondylar joint (Figs 7C, 11C) that permits protraction-retraction. As in *Leiobunum*, protraction is brought about by two muscles (4, 6). Muscle 4 arises on the distoanterior surface of the patella and inserts on the anterior margin of the tibia (Fig. 11C). Muscle 6 arises broadly

from the anterior and ventral surfaces of the patella and inserts on the anterior rim of the tibia. Unlike *Leiobunum*, laniator opilionids apparently lack the femoral component of 6 (Fig. 7C). Retraction at the patellotibial joint is accomplished by a single muscle (5) that originates broadly on the posterior surface of the patella and inserts on the posterior margin of the tibia (Fig. 11C). A transpatellar muscle (7) originates on the femur as in *Leiobunum* but inserts at the dorsal condyle of the patellotibial joint rather than the posterior rim of the tibia (Fig. 7C). Contraction of 7 would not therefore be expected to cause motion at the patellotibial joint.

The femur joins the patella at a strong transverse bicondylar joint (Fig. 7C) that permits flexion-extension. The condylar surfaces are broad protruding into the joint space and dividing it into dorsal and ventral canals. A large, rounded femoral sclerite occupies the dorsal canal and attaches proximally to the dorsal margin of the femur by strong ligaments. Nerves and tracheae traverse the ventral canal. The femoropatellar extensor (7) originates from the distal end of the femoral sclerite and inserts on the tibia at its dorsal articulation with the patella. Flexion is brought about by muscle 8, which arises from the dorsal and ventral surfaces of the femur and inserts on the patellar sclerite by means of a long tendon. The patellar sclerite attaches to the ventral rim of the patella via ligaments.

The trochanter joins the femur at a vertical bicondylar joint (Fig. 11C) that permits protraction-retraction. Protraction is brought about by muscle 13, which arises from the anterior surface of the trochanter and inserts on the anterior margin of the femur. The retractor (11) arises from the posterior surface of the trochanter and inserts on the posterior margin of the femur.

Order Scorpiones

Knowledge of scorpion appendicular anatomy is based on studies of representatives from three families: Buthidae (Wood, 1926; Snodgrass, 1952; Couzijn, 1976), Scorpionidae (Manton, 1958; Alexander, 1967) and Vaejovidae (Bowerman & Root, 1978). Results from these studies are in general agreement, but there are a few inconsistencies. Manton (1958) stated that certain muscles in the patella consist of paired mirror images when, in fact, all muscles in the scorpion patella are unpaired or asymmetrical. In his description of *Centruroides* sp. (Buthidae), Snodgrass (1952) indicated that the phylogenetically significant transpatellar extensor (7) arises from the proximal portion of the patella, but examination of this genus shows that this muscle arises from the distal part of the femur as in other scorpions.

The appendicular muscles of a large scorpionid, *Pandinus imperator* Koch, are described. Several representatives of the family Buthidae were also examined but their musculature does not differ significantly from that found in *Pandinus*. There are few important differences between the legs of an individual, and this description of joints and muscles is based on the dissection of leg 4.

The walking appendages of scorpions are typical of most other arachnids terminating distally with a pretarsus in the form of a claw-bearing plate that attaches to the tarsus via a transverse bicondylar joint (Fig. 4A). Levation at this joint is controlled by a single muscle (1) arising on the distoanterior surface of the tibia and inserting on the dorsal rim of the pretarsus. Depression is brought about by the action of a muscular complex (2) with heads arising on the

proximoanterior surface of the tibia and the anterior and proximoventral surfaces of the patella. All muscle fibres of 2 insert on a long cuticular tendon that begins proximally in the patella and inserts on the ventral rim of the pretarsus.

The telotarsus joins the basitarsus at a large dorsoanterior condyle in the form of a ball and socket joint. This arrangement allows levation-depression as well as rotational movements around the long axis of the leg. Couzijn (1976) gives a detailed discussion of the functional morphology of this and other articulations in scorpion legs.

The tibiotarsal joint (Fig. 4A) consists of a vertical bicondylar articulation and an anterior hinge. Movement is limited to slight protraction-retraction. Retraction is apparently accomplished by a single muscle (3) that arises from the posterior, dorsal and ventral surfaces of the tibia. There is no protractor.

The patellotibial joint and its associated muscles (Figs 8A, 12A, 16) differ substantially from those found in most other arachnids and *Limulus*. The joint is formed by a transverse bicondylar articulation and undergoes flexion-extension rather than protraction-retraction. Extension is apparently brought about by a large spindle-shaped muscle (7) that arises from a dorsal process extending from the distal end of the femur and inserts on the dorsal rim of the tibia. Flexion at the patellotibial joint is brought about by two muscles. The larger of these (6) consists of two heads, one arising from the posterior and ventral surfaces of the patella and another arising on dorsal surface of the femur proximal to the origin of 7 (Figs 8A, 16). Both heads insert on a single cuticular tendon that attaches to the ventroposterior rim of the tibia. The second flexor (4) arises from the ventroanterior surface of the patella just ventral to the origin of 2 and inserts on the ventroanterior rim of the tibia (Fig. 12A).

The femur and patella are joined by a transverse bicondylar joint (Figs 8A, 16) that undergoes flexion-extension. Two muscles arising from the distal part of the femur (6, 7) traverse this joint but pass through the patella to insert on the tibia (Figs 8A, 16). Muscle 7 arises from a femoral process dorsal to the condyles, and its contraction is expected to cause extension. Muscle 6 traverses this joint near the level of the condyles. This muscle probably does not greatly influence movement at the femoropatellar joint but it may play some role in flexion.

Most muscles associated with the femoropatellar joint are flexors (Figs 8A, 15E). The arrangement of the flexor complex (8) resembles that found in other arachnids (especially Uropygi and Amblypygi), but the patellar sclerite is absent in scorpions, and the flexors insert directly on the ventral rim of the patella. Muscles 8a and 8b are mirror images arising on the anterior and posterior surfaces of the femur, respectively. Muscle 8c arises from the posterior surface of the femur and is usually divided into two or more heads. These heads all insert on a common tendon that merges distally with that of 8d before inserting on the ventral rim of the patella. Muscle 8d arises from the distal ventroanterior wall of the trochanter by means of a strong noncuticular tendon and traverses the entire length of the femur to insert on the patella in the company of 8c.

The trochanter joins the femur at a transverse bicondylar joint (Fig. 12A) that permits levation-depression. Depression is brought about, in part, by muscle 11, which arises from the ventral surface of the trochanter and inserts on the ventral rim of the femur. Muscle 8d may also participate in depression of the joint. A small muscle (10) arises from the anterior wall of the trochanter just dorsal to

the origin of 8d and inserts on the proximoposterior surface of the femur. Muscle 10 traverses the trochanterofemoral joint at the level of the condyles and probably has little direct influence over movement. Levation is brought about by a single muscle (13) that arises from the dorsal surface of the trochanter and anterior surface of the coxa and inserts on the dorsal rim of the femur.

Order Pseudoscorpiones

The appendicular anatomy of pseudoscorpions has been described several times. Börner (1921) provided an accurate illustration of muscles in the first and fourth walking legs of a garypoid pseudoscorpion. Ewing's (1928) description of the fourth leg of a cheliferoid pseudoscorpion is generally accurate although the important transpatellar extensor (7) was omitted. Chamberlin (1931) illustrated the musculature of the first and fourth walking legs from a representative from each of the six pseudoscorpion superfamilies; the drawings and descriptions are generally accurate, despite some minor omissions noted below.

The first and fourth walking legs of *Chthonius tetrachelatus* (Preyssler) (Chthonioidea) are illustrated in Fig. 4. There are important morphological differences between the anterior and posterior pairs of legs of chthonioid pseudoscorpions. The femur and patella in legs 1 and 2 resemble those of certain other arachnids, especially Opiliones and Scorpiones, but the tarsus is undivided (monotarsate). The femur and patella of legs 3 and 4 have essentially fused to form a composite 'femur', a common arrangement in pseudoscorpions which inspired a controversy over the existence of the patella in this order. In addition, the tarsi in legs 3 and 4 are diplotarsate, divided into a proximal basitarsus and distal telotarsus. Representatives from other superfamilies have also been examined and reference is made to them where appropriate.

The pretarsus of most pseudoscorpions is equipped with a pair of claws dorsally and an empodium ventrally. The empodium is an eversible organ that facilitates climbing. The pretarsus joins the tarsus at a transverse bicondylar joint (Fig. 4B, C) that undergoes levation-depression. The levator (1) arises on the proximodorsal surface of the tarsus (or basitarsus in those legs with divided tarsi). Depression of the claws is brought about by muscle 2, which arises broadly on the anterior wall of the tibia and the distoanterior wall of the patella. The patellar head is apparently absent in legs 3 and 4 of *C. tetrachelatus* but is present in the corresponding legs of other pseudoscorpions (Chamberlin, 1931; personal observation).

Segmentation of the tarsi varies among pseudoscorpions and serves as a basis for arranging the superfamilies into larger groupings (Chamberlin, 1931). Legs 1 and 2 of the Heterosphyronida are monotarsate, but legs 3 and 4 are diplotarsate, as in Chthonioidea. All other pseudoscorpions are placed in the Homosphyronida, because the tarsi are similar in all walking legs. The Homosphyronida encompasses the Diplosphyronida (all legs diplotarsate) and Monosphyronida (all legs monotarsate). The character of 'tarsal homogeneity' emphasized by Chamberlin is clearly artificial. Comparisons with other arachnids indicate that the diplotarsate condition is plesiomorphic, suggesting that the Diplosphyronida is paraphyletic and that the Homosphyronida is not monophyletic.

The tarsus of *Chthonius* joins the tibia at a dorsoanterior bicondylar hinge

(Fig. 4B, C) that permits movement intermediate between flexion-extension and protraction-retraction. This arrangement is common in less derived groups but the tibiotarsal joint in many cheliferoids comprises a transverse bicondylar dorsal hinge and undergoes flexion-extension. Movement at the tibiotarsal joint is accomplished by a single muscle (3) that arises from the posterior or ventral surface of the tibia, depending on the orientation of the articulations.

The tibia joins the patella at a transverse bicondylar joint (Figs 8B, C, 16) that allows flexion-extension. Extension is brought about by a single transpatellar muscle (7) that arises on the distodorsal surface of the femur and inserts on a process at the dorsal rim of the tibia. Fibres also arise from the dorsal part of the patella in some pseudoscorpions. Flexion is brought about by another transpatellar muscle (6). Muscle 6 of *Chthonius* and other chthonioids, inserts on the ventral margin of the tibia via three tendons (Chamberlin, 1931; van der Hammen, 1986). Fibres inserting on the anterior and posterior tendons arise from the anterior and posterior walls of the patella; those inserting on the median tendon arise from the femur. In most other superfamilies, muscle 6 inserts via one tendon, but the paired patellar and unpaired femoral components are present (Chamberlin, 1931).

The size, shape and articulations between the patella and femur vary greatly throughout Pseudoscorpiones. Some taxa show variation between legs within an individual. The femoropatellar joint may be freely mobile with a long femur and short patella as in other arachnids, such as leg 1 of *Chthonius*. More commonly, the joint may consist of a vertical bicondylar articulation or it may be virtually immobile or totally fused, as the fourth leg of *Chthonius*, with reduced femur and greatly expanded patella.

The femoropatellar joints in legs 1 and 2 of *Chthonius* (Fig. 8C) are formed by transverse bicondylar articulations that permit flexion-extension. Flexion is brought about by muscle 8, with two principal heads which both insert on the ventral rim of the patella. Muscle 8c arises from the proximodorsal portion of the femur, and 8d arises from the distoventral surface of the trochanter. The femoropatellar joints of legs 3 and 4 (Fig. 8B) are formed by weakly defined transverse bicondylar articulations that permit little movement. Muscle 8 is not present in legs 3 and 4 of *Chthonius*, but it occurs in the corresponding legs of representatives from other superfamilies (Chamberlin, 1931; personal observation).

The trochanter joins the femur at a transverse bicondylar joint (Fig. 12B, C) that primarily permits levation-depression. Depression is partly brought about by a muscle (11) that arises from the ventral and posterior surfaces of the trochanter and inserts on the ventral margin of the femur. Muscle 8d may also play a role in depression. A small muscle (10) arises on the anterior surface of the trochanter, traverses the joint diagonally and inserts on the proximoposterior surface of the femur. Its function is not apparent. Chamberlin consistently overlooked 10, although Börner (1921) depicted this muscle in *Garypus* sp. (Garypoidea), and it has been observed here in *Chthonius* and several chernetids and cheliferids. Levation is brought about by a muscle (13) that arises on the dorsoanterior surface of the trochanter and in the coxa. Both heads insert on the dorsal margin of the femur.

Many arachnologists maintain that the walking legs of pseudoscorpions differ from those of other arachnids in having two femoral segments and lacking a

patella (Gaubert, 1892; Chamberlin, 1931; Vachon, 1947, 1976; van der Hammen, 1986). That the distal femoral segment or telofemur is homologous with the patella of other arachnids is the obvious alternative which had suggested itself to Chamberlin, but he rejected this view in his influential 1931 monograph. Systematists subsequently working on pseudoscorpions continue to use the terms 'telofemur' and 'basifemur' in their descriptions of these arachnids. The idea that the patella is absent in pseudoscorpions is now so entrenched that van der Hammen (1977, 1986) proposed that this order be placed in a new class, the Apatellata, to distinguish it and its relatives, the Solifugae, from other chelicerates. On the other hand, Weygoldt & Paulus (1979a) revived the notion that the telofemur is actually the patella. Proponents of each view claim support from the arrangement of the appendicular musculature. I conclude, with Weygoldt & Paulus, that the 'telofemur' of pseudoscorpions is homologous with the patella of other arachnids.

The conclusion that pseudoscorpions possess a patella is apparent when comparing walking leg musculature with that of scorpions. Similarities between the patella of scorpions and the 'telofemur' of pseudoscorpions are as follows. (1) Both constitute the fourth segment of the walking leg. (2) The proximal joint in each consists of a transverse bicondylar articulation. (3) Flexion at the proximal joint, when possible, is accomplished by muscle 8 with heads arising from the trochanter and femur. (4) Both are traversed by a pair of muscles that arise in the proximal segment (femur) and insert on the distal segment (tibia). The dorsal muscle (7) extends the distal and proximal joints and the ventral muscle (6) flexes the distal and, perhaps, proximal joints. (5) The distal joint in each is formed by a transverse bicondylar articulation. (6) The proximal head of muscle 2 originates on the anterior surface of both segments. There is little doubt that pseudoscorpions retain the patella, indicating that the basic organization of the pseudoscorpion walking appendage does not differ substantially from that of other arachnids and that van der Hammen's proposal to erect a new class, the Apatellata, should be abandoned. When describing pseudoscorpions, systematists should replace the terms basifemur and telofemur with femur and patella, respectively.

Order Solifugae

The appendicular anatomy of solifuges (wind scorpions) is generally thought to differ from that of most other arachnids in several important respects. Solifuges, like pseudoscorpions, are generally believed to lack patellae and to possess divided femora in all walking legs. Solifuges also appear to have two trochanters on legs 3 and 4. The previous section concluded that the traditional view of the absent patella in pseudoscorpions is apparently wrong; the distal 'femur' is actually the patella. The same reasoning applies to solifuges, and, in addition, the distal 'trochanters' of legs 3 and 4 appear to be the proximal portions of divided femora (basifemora).

The external anatomy of solifuge walking legs has been described by Barrows (1925), Ewing (1928) and Manton (1977). The anterior two pairs of legs are similar, but leg 1 serves as a tactile organ so that solifuges are functional hexapods. The posterior pairs of walking legs differ from the anterior pairs in having two apparent 'trochanters'. The coxae and 'trochanters' of leg 4 are equipped with unique sensory organs, the malleoli or racket organs (Fig. 12E).

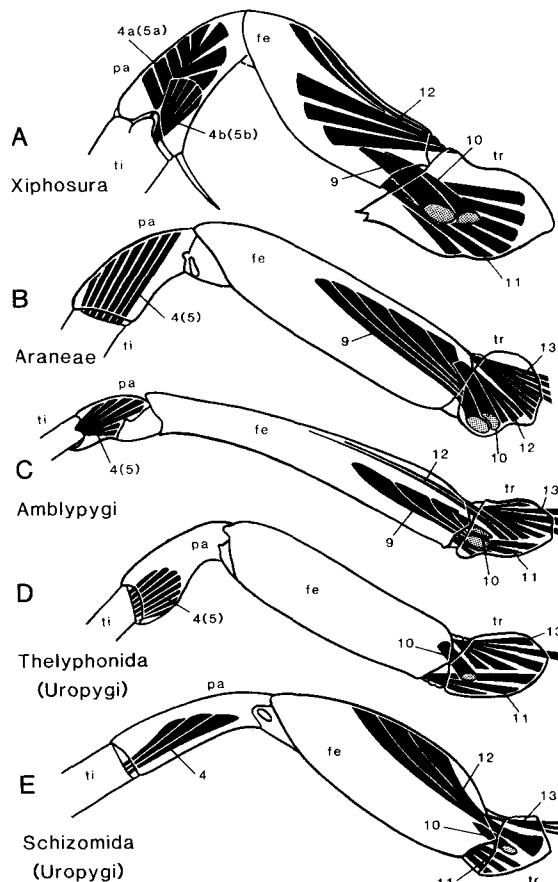


Figure 9. Anterior view of muscles at the patellofibial joint (4, 5) and the trochanterofemoral joint (9–13) in leg 4. A, *Limulus polyphemus* (Xiphosura). B, *Liphistius sumatranus* (Araneae). C, *Phrynum marginemaculatus* (Amblypygi). D, *Mastigoproctus giganteus* (Thelyphonida, Uropygi). E, *Schizomus* sp. (Schizomida, Uropygi). Muscles indicated by numbers in parentheses are unillustrated posterior mirror images. Abbreviations: fe, femur; pa, patella; ti, tibia; tr, trochanter.

Roewer (1934) depicted the muscles of leg 4 of a rhagodid solifuge and his figure has been redrawn several times by other authors, occasionally with considerable, but unjustified, modifications (Millot & Vachon, 1949). The creative reinterpretations of Roewer's drawing are particularly inaccurate because the original was itself partly in error. Roewer depicted extensors at the patellofibial (telofermur-tibia) joint, yet all solifuges presently examined lack extensor muscles. Ewing (1928) provided a more accurate illustration of the distal segments, but muscles of those situated proximally do not correspond to present observations.

The second and fourth walking legs of a large male *Paragaleodes scalaris* (Koch) (Galeodidae) are described and illustrated. The muscles of a large unidentified female galeodid (voucher: Museum of Comparative Zoology, Harvard University) and those of several specimens of *Branchia* sp. (Ammotrechidae) (voucher: American Museum of Natural History) have also been examined. There are slight differences in the orientation of the proximal articulations, but the basic organization of the walking legs is the same in all specimens examined.

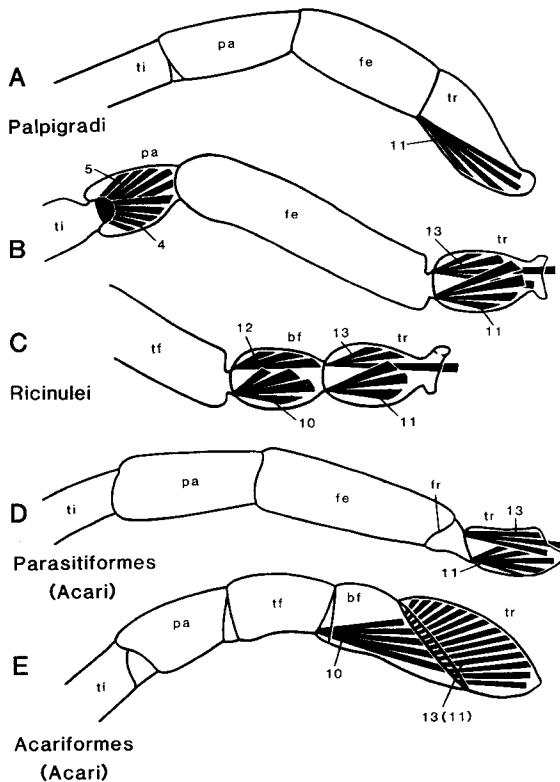


Figure 10. Anterior view of muscles at the patellofibial joint (4, 5) and the proximal joints (9–13). A, Leg 4 of *Eukoenenia* sp. (Palpigradi). B, Leg 2 of *Cryptocellus gamboa* (Ricinulei). C, Leg 4 of *C. gamboa*. D, Leg 4 of *Amblyomma americanum* (Parasitiformes, Acari), and (E) *Dinothrombium* sp. (Acariformes, Acari). Muscles indicated by numbers in parentheses are unillustrated posterior mirror images. Abbreviations: bf, basifemur; fe, femur; fr, femoral ring; pa, patella; tf, telofemur; ti, tibia; tr, trochanter.

The pretarsus of all legs bears two large claws dorsally and a median eversible empodium ventrally. The empodium is apparently homologous with the median claw of other arachnids (Roewer, 1934). The pretarsus joins the tarsus at a transverse bicondylar joint (Fig. 4D) that allows levation-depression. The levator (1) arises primarily from the dorsal surface of the basitarsus, although a few fibres arise from the distodorsal surface of the tibia, and inserts on the pretarsus. The depressor (2) consists of two heads, one arising on the proximoposterior wall of the tibia and another on the dorsal portion of the extreme distal end of the patella. The two heads of muscle 2 insert on the ventral rim of the pretarsus via a common tendon.

The telotarsus is composed of one or more tarsomeres, depending on the species, and attaches to the basitarsus by a flexible joint that lacks apparent articulations. Movement at this joint is limited primarily to flexion-extension. Extension is apparently brought about by the resilience of the arthrodial membrane. A sclerotized flange projects distally from the basitarsus and may serve to prevent hyperextension of the joint.

The tibiotarsal joint (Fig. 4D) is formed by a transverse bicondylar dorsal

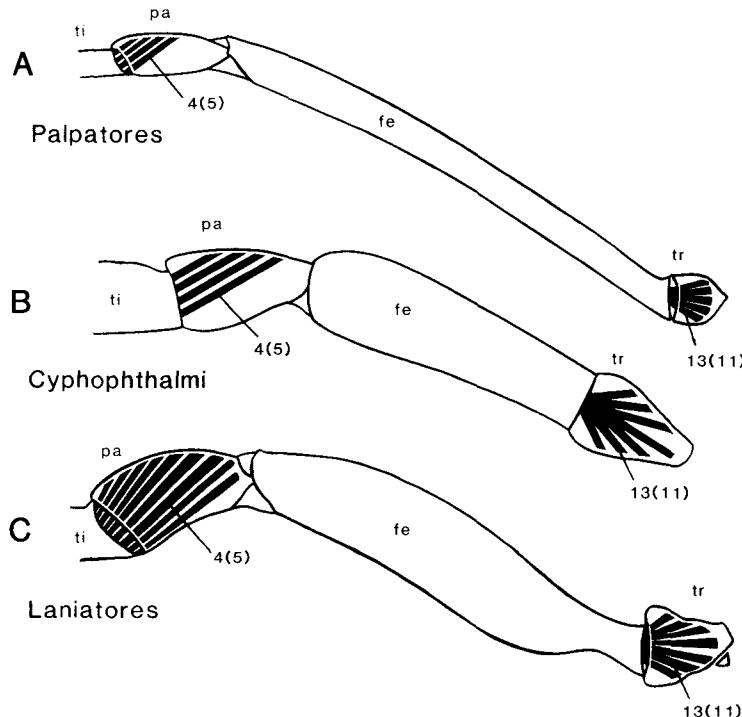


Figure 11. Anterior view of muscles at the patellofemoral joint (4, 5) and the trochanterofemoral joint (11, 13) in leg 4 of the opilionids. A, *Leiobunum vittatum* (Palpatores). B, *Siro acaroides* (Cyphophthalmi). C, *Cyrtora subserialis* (Laniatores). Muscles indicated by numbers in parentheses are unillustrated posterior mirror images. Abbreviations; fe, femur; pa, patella; ti, tibia; tr, trochanter.

hinge that permits flexion-extension. Flexion is accomplished by contraction of a single muscle (3) that arises from the anterior and posterior walls of the tibia and inserts on the ventral rim of the basitarsus. Extension may be brought about, at least in part, by elastic sclerites that traverse the anterior and posterior surfaces of the articular space just ventral to the condyles (Fig. 4D). The patellofemoral joint has a similar arrangement, a transverse bicondylar dorsal hinge with elastic sclerites (Figs 4D, 8D), but flexion is brought about by two muscles (4, 6). Muscle 4 arises broadly from the anterior surface of the patella and inserts at the ventroanterior margin of the tibia (Fig. 12D). Muscle 6 arises from the posterior and proximoanterior walls of the patella and the dorsal surface of the femur, or telofemur in legs 3 and 4. It inserts on the ventroposterior rim of the tibia (Figs 8D, 16).

The femoropatellar joint in solifuges (Fig. 8D) differs greatly from the corresponding joint in other arachnids. It is formed by a strong dorsoanterior monocondylar articulation that permits flexion-extension, protraction-retraction and perhaps rotational movements (rocking) about the long axis of the leg. The joint is operated by four muscles that are arranged symmetrically about the articulation. One muscle arises on the ventroanterior wall of the femur of legs 1 and 2 or the telofemur of legs 3 and 4 and inserts on the ventroanterior margin of the patella near the condyle. This muscle's mirror image arises on the

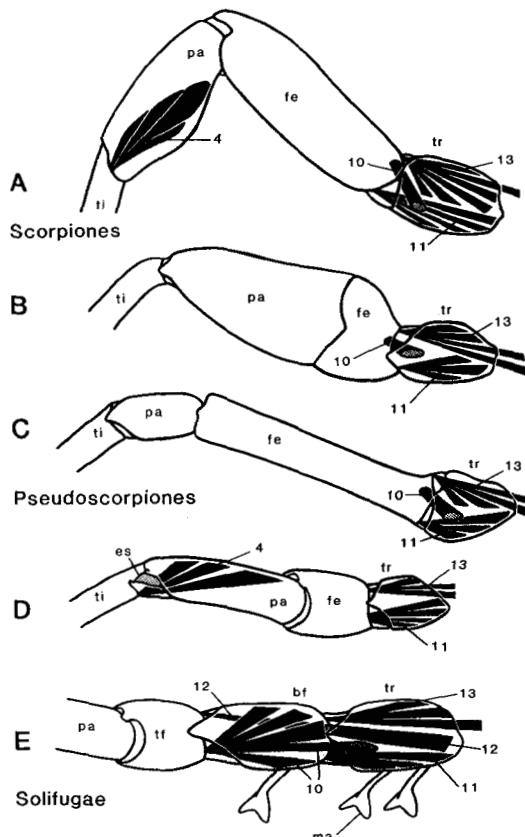


Figure 12. Anterior view of muscles at the patellotibial joint (4) and the proximal joints (10–13). A, *Pandinus imperator* (Scorpiones). B, Leg 4 of *Chthonius tetrachelatus* (Pseudoscorpiones). C, Leg 1 of *C. tetrachelatus*. D, Leg 2 of *Paragaleodes scalaris* (Solifugae). E, Leg 4 of *P. scalaris*. Abbreviations: bf, basifemur; es, elastic sclerite; fe, femur; ma, malleolus; pa, patella; tf, telofemur; ti, tibia; tr, trochanter.

dorsoposterior wall of the femur or telofemur and inserts on the dorsal rim of the patella. These muscles appear to cause protraction and retraction, respectively. A third muscle arises on the ventroanterior and proximoanterior surfaces of the femur or telofemur and inserts on the ventroanterior rim of the patella. Its mirror image originates on the ventroposterior and proximoposterior walls of the femur or telofemur and inserts on the ventroposterior rim of the patella. These muscles apparently serve to flex the femoropatellar joint and may also participate in protraction-retraction. I tentatively designate the two anterior muscles 8a and the two posterior muscles 8b.

The telofemur and basifemur ('distal trochanter') of legs 3 and 4 are joined by transverse bicondylar joints in which the anterior condyle is distal to the posterior (Figs 12E, 17B). The joint apparently undergoes levation-depression. Depression is brought about by a large muscle (10) that arises from the anterior wall of the trochanter and broadly from the posterior, ventral and anterior surfaces of the basifemur. Muscle 10 inserts on the ventral rim of the telofemur. Levation is brought about by a single muscle (12) that arises on the

dorsoanterior surface of the trochanter, traverses the basifemur and inserts on the dorsal rim of the telofemur. The homologies implied by designating these muscles 10 and 12 are tentative; the rationale for this usage will be discussed below.

The articulations and muscles associated with the trochanterofemoral joints of legs 1 and 2 and the trochanterobasifemoral joints of legs 3 and 4 are similar (Figs 12D, E, 17B). In each case, the trochanter joins the femoral segment by means of a transverse bicondylar joint that permits levation-depression. Levation is accomplished by muscle 13, which arises from the posterior surface of the trochanter and anterior surface of the coxa and inserts on the dorsal margin of the femur or basifemur. In legs 3 and 4, muscle 12 may also play a role in levation at this joint. Depression is brought about by muscle 11, which arises from the ventral surface of the trochanter and inserts on the ventral rim of the femur or basifemur.

Throughout this description of solifuge walking appendages, the term patella is used when referring to that segment traditionally termed 'telofemur' or 'femur 2'. Solifuges and pseudoscorpions are generally thought to differ from most other arachnids in lacking a patella and in possessing two femoral segments ('basifemur' and 'telofemur') for each walking leg. In the discussion of pseudoscorpions, I argued that the telofemur corresponds to the patella of scorpions. A similar argument applies to solifuges. The patella of scorpions and the 'telofemur' of solifuges share the following features. (1) Both constitute the fourth segment of the walking appendage, except in legs 3 and 4 of solifuges, which bear an extra 'trochanter'. (2) Both articulate with the tibia via a transverse joint that undergoes flexion-extension. (3) Flexion at the tibial joint is controlled by two muscles (Figs 8A, D, 16). One muscle (4) arises from the anterior surface of each segment and inserts on the ventroanterior margin of the tibia. The other muscle (6) arises from the dorsal surface of the femur (Scorpiones) or 'basifemur' (Solifugae) and inserts on the ventroposterior margin of the tibia. (4) Both serve as the origin for the proximal head of muscle 2 (Fig. 4A, D). These similarities suggest that the 'telofemur' in Solifugae is homologous with the patella of Scorpiones and other arachnids.

I further suggest that the distal 'trochanter' of legs 3 and 4 in Solifugae represents the basal portion of a divided femur and not the duplication or subdivision of the primitive trochanter. This conclusion is based on the arrangement of the musculature. In most arachnids and *Limulus*, the trochanterofemoral joint is traversed by a muscle (10) that arises from the anterior surface of the trochanter and inserts on the proximoposterior surface of the femur (Figs 9A-E, 12A-C, 17A). In most arachnids, this muscle has no tendon and no apparent function. The depressor of the proposed intrafemoral joint has the same origin as muscle 10 (Figs 12E, 17B) and, if the intrafemoral joint were fused, it would have a similar insertion (Fig. 17A, B). Another unusual muscle with potential significance to this problem is found in amblypygids and schizomids. This muscle (12) arises from the proximoanterior surface of the trochanter and inserts along the dorsal surface of the femur but lacks an apparent tendon (Figs 9C, 17A). The levator of the intrafemoral joint in Solifugae also arises from the anterior wall of the trochanter (Fig. 12E) and, if the intrafemoral joint were fused, the levator would have an insertion similar to that described in Amblypygi (Fig. 17A, B). The arrangement of the muscles

operating the proposed trochanterobasifemoral joint in Solifugae is essentially identical with those found at the trochanterofemoral joints in legs 1 and 2 (Fig. 12D, E) and in the walking legs of most other arachnids.

The traditional terms used in describing legs 3 and 4 in Solifugae (coxa, trochanter 1, trochanter 2, basifemur, telofemur, tibia, tarsus, pretarsus) should therefore be changed to coxa, trochanter, basifemur, telofemur, patella, tibia, tarsus and pretarsus.

PHYLOGENETIC IMPLICATIONS

Cladistic analysis of characters described in this survey reveals several new insights but fails to resolve the relationships of the arachnid orders completely (Fig. 13, Table 1). The usefulness of this data set is not limited by difficulties in establishing reasonable homologies of leg segments or muscles, problems that plagued previous investigations (Weygoldt & Paulus, 1979a), but by a high incidence of symplesiomorphy in appendicular characters. Although the large number of primitive features revealed here is disappointing from the standpoint of phylogenetic reconstruction, it does indicate that most similarities in arachnid walking appendages represent elements retained from a common, though perhaps distant, ancestor. There are many autapomorphic features, but this does not warrant a pantheon of hypothetical proto-arachnids to 'explain' the diversity. The phylogenetic significance of the eight fundamental types of chelicerate appendages invented by van der Hammen (1977, 1985b) is questionable and may reflect a preoccupation with autapomorphies.

At present, there is no convincing evidence that Arachnida is polyphyletic; each order appears to be more closely related to some other arachnid lineage than to any known non-arachnid group. This view was first stated explicitly by Weygoldt & Paulus (1979b) and defended on the basis of four synapomorphies, namely the presence of five pairs of simple lateral eyes derived from paired compound eyes, preoral digestion, slit sensilla and endodermal Malpighian tubules. However, some of these synapomorphies are not convincing. Many fossil scorpions have well-developed compound eyes at the anterolateral margins of their carapaces (Kjellesvig-Waering, 1986), indicating that reduction to simple eyes must have occurred at least twice, once in scorpions and once in other arachnids. Preoral digestion is not universal in Arachnida and may not be primitive for the group. *Limulus*, opilionids and many mites ingest solid food and digest it internally. The structure of the preoral cavities in which preoral digestion typically occurs differs in the various arachnid lineages, suggesting that this feature also arose independently several times.

Despite objections to some of the characters used by Weygoldt & Paulus, the hypothesis that Arachnida is monophyletic is supported by the results of this study. With *Limulus* as an outgroup, cladistic analysis of appendicular characters provides four potential synapomorphies: a pretarsus with three claws, a pretarsal depressor muscle (2) with heads arising in the tibia or patella, a trochanterofemoral levator (13) arising in the trochanter and coxa, and a tarsus divided into a proximal basitarsus and a distal telotarsus by an adesmatic joint.

By combining these synapomorphic features with those that are apparently symplesiomorphic for arachnids (shared by *Limulus*), reconstruction of a hypothetical appendage to represent the walking leg of the arachnid ancestor is

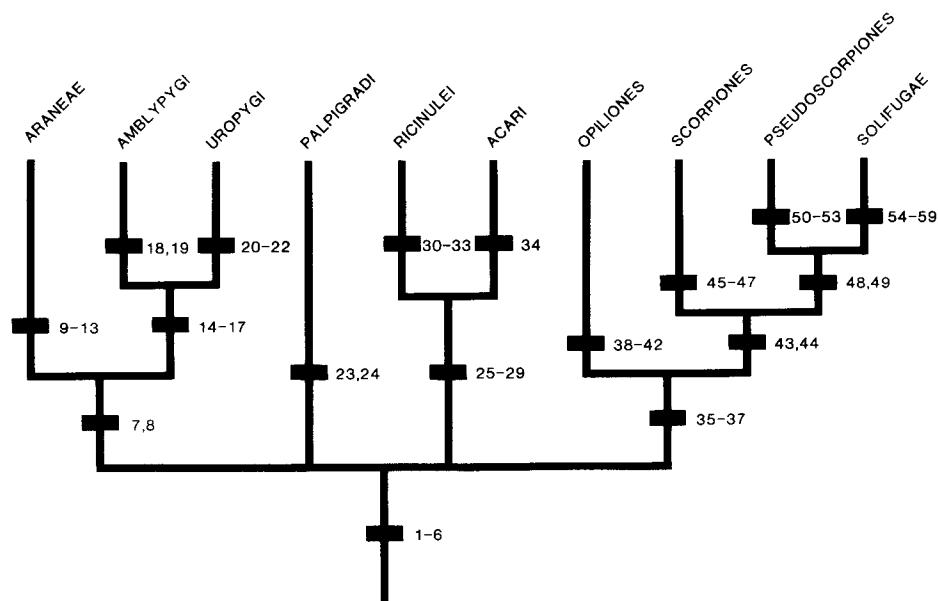


Figure 13. Cladogram showing the phylogenetic relationships of the arachnid orders as suggested by characters revealed in this study. Relationships cannot be resolved completely due to the high incidence of symplesiomorphy in appendicular characters. The characters on which this cladogram is based are listed in Table 1.

possible (Fig. 14). The proportions of the segments are open to speculation, but the basic organization of the joints and muscles is more convincing. Joint structure of this hypothetical appendage bears a striking resemblance to that of certain Eurypterida (cf. Selden, 1981), the apparent sister group of Arachnida (Weygoldt & Paulus, 1979b). Among living arachnids, Araneae approximates the hypothetical primitive condition most closely.

The primitive arachnid appendage once comprised seven segments: coxa, trochanter, femur, patella, tibia, tarsus and pretarsus. There were thirteen muscle groups distal to the coxa (1-13). The pretarsus took the form of a claw-bearing plate (two large claws dorsally and one median claw ventrally) that joined the tarsus at a transverse bicondylar joint. The tarsus was divided into a basitarsus and telotarsus by an adesmatic joint. Two muscles (1, 2) inserted on the pretarsus. Muscle 1 arose from the dorsal surface of the basitarsus and inserted on the dorsal rim of the pretarsus. Muscle 2 arose from the dorsal surface of the basitarsus and tibia, and perhaps patella, and inserted on the ventral rim of the pretarsus.

The basitarsus joined the tibia at a transverse dorsal hinge and was operated by one muscle (3). This muscle arose from the anterior and posterior surfaces of the tibia, and perhaps patella, and inserted on the ventral rim of the basitarsus. The patellotibial joint was formed by a dorsal monocondylar articulation operated by four muscles (4-7). Muscles 4 and 5 arose from the anterior and posterior surfaces of the patella and inserted on the anterior and posterior rims of the tibia, respectively. Muscles 6 and 7 were transpatellar. Muscle 6 arose from the anterior wall of the distodorsal part of the femur and the anterior wall of the

TABLE 1. Polarities of characters used in reconstructing phylogenetic relationships among the arachnid orders (see Fig. 13). Nonappendicular characters were obtained from Weygoldt & Paulus (1979b), Lindquist (1984) and Shear *et al.* (1987)

Plesiomorphic State	Apomorphic State
1. Pretarsus without claws	Pretarsus with three claws
2. Pretarsal depressor (2) arising in tarsus only	Muscle 2 arising in tibia and/or patella
3. Tarsus undivided	Tarsus divided into basitarsus and telotarsus
4. Trochanterofemoral levator (13) absent	Muscle 13 present (except Palpigradi)
5. Slit sensilla absent	Slit sensilla present
6. Malpighian tubules absent	Malpighian tubules present
7. Chelicerae chelate	Chelicerae subchelate
8. Spermatozoan axoneme without 9 + 3 microtubule arrangement	Spermatozoan axoneme with 9 + 3 microtubule arrangement
9. Posterior head of femoropatellar flexor (8c) present	Muscle 8c absent
10. Trochanterofemoral depressor (11) present	Muscle 11 absent
11. Opisthosomal spinning apparatus absent	Opisthosomal spinning apparatus present
12. Cheliceral venom glands absent	Cheliceral venom glands present
13. Male copulatory organ on pedipalp absent	Male copulatory organ on pedipalp present
14. Leg 1 leglike, ambulatory	Leg 1 antenniform, tactile
15. Femoropatellar flexor (8) inserting on patella symmetrically	Muscle 8 inserting on patella asymmetrically; 8a, 8c, 8d via anterior patellar sclerite, 8b directly on ventral rim of patella
16. Telotarsus undivided	Telotarsus divided into three tarsomeres
17. Pedipalps leglike	Pedipalps raptorial
18. Patellotibial joint movable	Patellotibial joint immovable
19. Tibia undivided	Tibia divided by one or more adesmatic joints
20. Pretarsal depressor (2) inserting dorsally on tibia and/or patella	Muscle 2 inserting on tibia and broadly on posterior surface of patella
21. Pedipalpal coxae not fused medially	Pedipalpal coxae fused medially
22. Female does not grasp male opisthosoma during mating	Female grasps male opisthosoma during mating
23. Trochanterofemoral joint with transverse bicondylar articulation; levator present	Trochanterofemoral joint with dorsal hinge articulation; levator absent
24. Respiratory organs present	Respiratory organs absent
25. All instars octopodal	Hexapod larval stage
26. Femur undivided	Femur divided into basifemur and telofemur (legs 3 and 4 in Ricinulei and opilioacarines; variable in less derived acariform Acari)
27. Patellotibial joint with dorsal monocondylar articulation	Patellotibial joint with transverse dorsal hinge articulation
28. Labrum not roughened, scaly or denticulate	Labrum roughened, scaly or denticulate
29. Gnathosoma absent	Gnathosoma present
30. Transpatellar muscles (6, 7) present	Transpatellar muscles absent
31. Patellotibial joint with transverse dorsal hinge articulation	Patellotibial joint with vertical anterior hinge articulation (90° rotation)
32. Male copulatory organ on leg 3 absent	Male copulatory organ on leg 3 present
33. Coupling mechanism between prosoma and opisthosoma absent	Coupling mechanism between prosoma and opisthosoma present
34. Hexapodal prelarva present (see Lindquist, 1984 for additional characters)	Hexapodal prelarva present
35. Transpatellar muscle (7) arising on dorsoposterior surface of femur, traverses femoropatellar joint ventral to axis of rotation	Muscle 7 arising on dorsal process of femur, traverses femoropatellar joint dorsal to axis of rotation
36. Muscle 7 with fibers arising from patella	Muscle 7 without fibers arising from patella
37. Patellotibial joint with dorsal monocondylar articulation	Patellotibial joint with vertical bicondylar articulation
38. Femoropatellar flexor (8) with four major subdivisions, one arising in trochanter	Muscle 8 without major subdivisions or connection to trochanter
39. Trochanterofemoral joint with transverse bicondylar articulation	Trochanterofemoral joint with vertical bicondylar articulation
40. Leg 2 ambulatory	Leg 2 elongate, tactile

TABLE 1. (continued)

Plesiomorphic State	Apomorphic State
41. Penis/ovipositor absent	Penis/ovipositor present
42. Prosomal repugnatorial glands absent	Prosomal repugnatorial glands present
43. Patellotibial joint not rotated 90°	Patellotibial joint rotated 90°
A. Vertical bicondylar articulation	Transverse bicondylar articulation
B. Muscle 7 with posterior insertion on tibia	Muscle 7 with dorsal insertion on tibia
C. Muscle 6 with anterior insertion on tibia	Muscle 6 with ventroposterior insertion on tibia
D. Muscle 4 with dorsoanterior insertion on tibia	Muscle 4 with ventroanterior insertion on tibia
44. Patellotibial muscle (5) present	Muscle 5 absent
45. Pretarsal levator (1) arising primarily from dorsal surface of tarsus	Muscle 1 arising from anterior surface of tibia
46. Pectines absent	Pectines present
47. Opisthosomal stinging apparatus absent	Opisthosomal stinging apparatus present
48. Chelicerae with three segments	Chelicerae with two segments; hinged ventrolaterally
49. Tracheal stigmata on opisthosomal segments 3 and 4 absent	Tracheal stigmata on opisthosomal segments 3 and 4 present
50. Patellotibial muscle (4) present	Muscle 4 absent
51. Muscles 8a, 8b present	Muscles 8a, 8b absent
52. Cheliceral spinning apparatus absent	Cheliceral spinning apparatus present
53. Pedipalpal venom glands absent	Pedipalpal venom glands present
54. Transpatellar muscle (7) present	Muscle 7 absent
55. Elastic sclerites absent or rudimentary	Elastic sclerites present at patellotibial and tibiotarsal joints
56. Femoropatellar joint with transverse bicondylar articulation	Femoropatellar joint with dorsoanterior moncondylar articulation
57. Malleoli absent	Malleoli present
58. Leg 1 ambulatory	Leg 1 tactile
59. Femora undivided	Femora of legs 3 and 4 divided into basifemur and telofemur

patella, and muscle 7 arose from the posterior wall of the distodorsal part of the femur and the posterior wall of the patella. Muscle 6 inserted on the anterior margin of the tibia, and muscle 7 on the posterior margin.

The femoropatellar joint consisted of a transverse bicondylar dorsal hinge and movement was controlled by four flexors (8a–8d). These muscles inserted

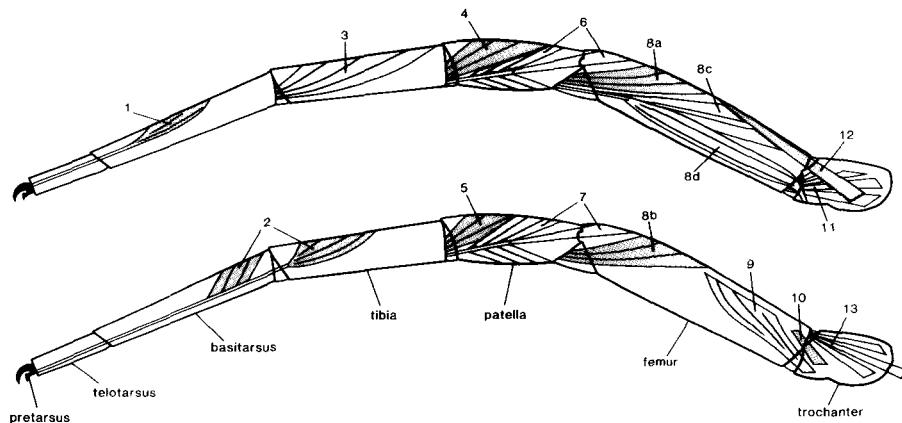


Figure 14. Anatomy of the primitive arachnid walking leg as suggested by a cladistic analysis of appendicular characters. See text for details.

directly on the ventral rim of the patella or indirectly through a patellar sclerite that attached to the patella via flexible ligaments. Muscles 8a and 8b were mirror images. Muscle 8a arose from the anterior wall of the femur and 8b arose from the posterior wall. Muscle 8c arose from the proximoposterior wall of the femur and 8d arose from the distoventral surface of the trochanter. Muscles 8c and 8d inserted on the patella together via a common tendon.

The femur joined the trochanter at a transverse bicondylar joint. Five muscles traversed this joint, in addition to 8d. Muscles 9 and 10 arose on the anterior wall of the trochanter and traversed the trochanterofemoral joint diagonally to insert on the posterior wall of the femur. Muscle 9 was broad and fan-shaped; muscle 10 was small and narrow. Muscle 11 arose on the ventral and posterior walls of the trochanter and inserted on the ventral margin of the femur. Muscle 12 arose on the anterior wall of the trochanter and inserted on the dorsal surface of the femur. Muscle 13 arose from the dorsal and anterior walls of both trochanter and coxa and inserted on the dorsal margin of the femur.

Most features of the primitive appendage have been either retained or replaced by apomorphies unique to individual orders. The comparative morphology of arachnid walking appendages provides only a few characters to establish relationships between orders. The phylogenetic significance of these features are discussed below and an attempt to integrate this information with previous views or current controversies in arachnid phylogeny is made.

Most arachnologists acknowledge a close phylogenetic relationship between Araneae, Amblypygi and Uropygi. This conclusion is supported by the structure and of the chelicerae and by an unusual 9+3 microtubule arrangement within the axoneme of the spermatozoa (Weygoldt & Paulus, 1979a, b). There is disagreement, however, over the precise relationship of the three orders among themselves. Kaestner (1968) argued that Amblypygi is more closely related to Araneae than to Uropygi, a view that has received widespread acceptance. Amblypygids and spiders are thought to be united by the possession of a postcerebral pharynx (sucking stomach) and narrow juncture (pedicel) between the prosoma and opisthosoma. In contrast, Shear *et al.* (1987) have advocated a return to the much older view that Amblypygi and Uropygi are closely related, forming a sister group to Araneae. According to their proposal, uropygids and amblypygids are united by the presence of raptorial pedipalps and by modification of the first walking leg for use as a tactile organ. They also argue that similarities between Amblypygi and Araneae do not indicate a close relationship; the postcerebral pharynx is symplesiomorphic and the pedicel is a superficial resemblance.

The results of this study corroborate the phylogenetic hypothesis of Shear and his co-workers. Uropygids and amblypygids are characterized by a patellar sclerite that attaches to the patella only on its anterior margin, not both anteriorly and posteriorly, as found in spiders and *Limulus* (Figs 5C, D, 6A, 15). The flexors of the femoropatellar joint (specifically 8a and 8b) are asymmetrical; 8a inserts on the patellar sclerite and 8b inserts primarily on the ventral rim of the patella itself (Fig. 15C, D). In spiders and *Limulus*, 8a and 8b are symmetrical and attach primarily to the anterior and posterior arms of the patellar sclerite, respectively (Fig. 15A, B). Asymmetrical femoropatellar flexors may represent a convergence brought about by the use of laterigrade locomotion in amblypygids and thelyphonid uropygids, but those who uphold this view

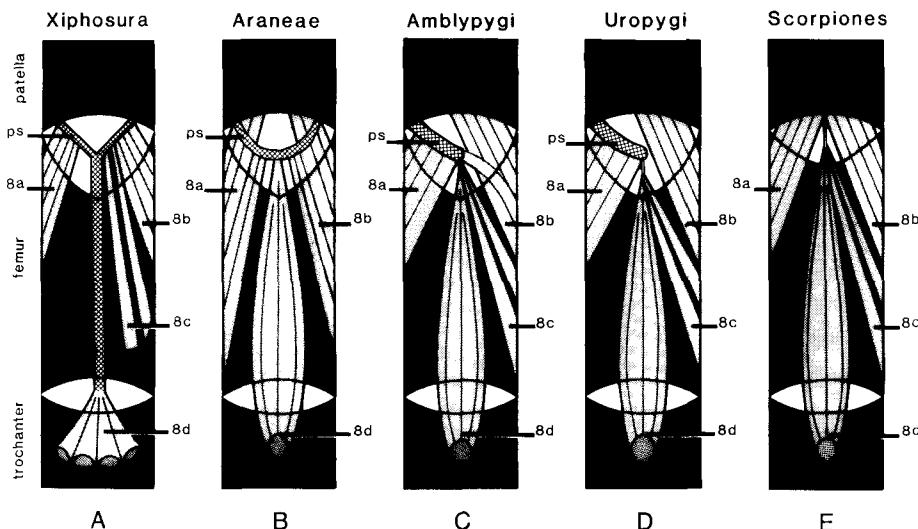


Figure 15. Diagrammatic ventral views of the flexor muscles at the femoropatellar joint. A, *Limulus polyphemus* (Xiphosura). B, *Liphistius sumatranaus* (Araneae). C, *Phrynx marginemaculatus* (Amblypygi). D, *Mastigoproctus giganteus* (Uropygi). E, *Pandinus imperator* (Scorpiones).

must account for the presence of asymmetrical femoropatellar musculature in schizomid uropygids, which are not laterigrade.

The structure of the tarsi in legs 2-4 of uropygids and amblypygids is also similar and differs from that found in spiders. Each telotarsus is divided into three principal tarsomeres by adesmatic joints (Figs 1C, D, 2A); the telotarsus in spiders is primitively undivided. The basitarsus is entire in all three orders but is much shorter relative to the leg length in thelyphonid Uropygi and Amblypygi (Fig. 1C, D). Amblypygids were formerly thought to differ from uropygids in having a long basitarsus and a four-segmented telotarsus. Earlier workers had mistaken the adesmatic intratibial joint of amblypygids with the tibiotarsal joint, but the podomere they interpreted as the basitarsus is actually the distal portion of the tibia. The divided tibia is an autapomorphic feature of Amblypygi.

The position of Palpigradi within arachnid phylogeny is open to speculation. These animals are traditionally thought to be closely related to Uropygi, because they both possess a sensory flagellum at the posterior end of the opisthosoma, a similarity that inspired the common name 'micro-whipscorpions'. Van der Hammen (1982), however, considered them to be most closely related to acariform mites; Firstman (1973) and Weygoldt & Paulus (1979b) suggested that Palpigradi is the sister group of all tracheate arachnids. None of these arrangements is convincing at present, nor is the information derived from this study helpful in resolving the problem. Ignorance of the phylogenetic position of Palpigradi within Arachnida is reflected in the cladogram (Fig. 13).

Ricinulei and Acari are often considered sister taxa (Weygoldt & Paulus, 1979b; Lindquist, 1984), but several workers, including van der Hammen (1977, 1979, 1982, 1985b), feel that parasitiform mites are more closely related to ricinuleids than to acariform mites. According to this view Acari is diphyletic or, from a somewhat different perspective, ricinuleids are merely primitive 'mites'

with several obvious autapomorphies. The appendicular characters from this study cannot resolve this issue, so the cladogram follows the conclusions of Weygoldt & Paulus (1979b) and Lindquist (1984), that Ricinulei and Acari are closely related but separate orders.

The relationship of Ricinulei and Acari to the other arachnid orders is also open to speculation. Several workers suggest a close relationship between Acari and Opiliones because of a resemblance between opilioacarine mites and certain opilionids, but this hypothesis has never been thoroughly assessed. The precise phylogenetic position of Ricinulei and Acari within Arachnida is uncertain.

The most important conclusion of this study, that Opiliones, Scorpiones, Pseudoscorpiones and Solifugae appear to form a monophyletic group, is based on a unique arrangement of the femoropatellar joint, in particular, the specializations of the posterior transpatellar muscle (7). In *Limulus*, muscle 7 arises from the distodorsal surface of the femur and traverses the patella to insert on the posterior rim of the tibia. It passes ventral to the axis of rotation at the femoropatellar joint and receives fibres from the walls of the patella (Figs 5A, 16). This arrangement is also present in Araneae (Figs 5B, 16), Palpigradi (Fig. 6B) and Acari (Fig. 6D, E) and is considered here to be a primitive condition (Fig. 14). Muscle 7 arises from a distal process of the femur and traverses the femoropatellar joint dorsal to its axis of rotation in Opiliones, Scorpiones and Pseudoscorpiones. In contrast to the primitive state, 7 does not receive fibres from the walls of the patella in these orders (Figs 7A, C, 8A-C).

Relationships between the members of this clade can be resolved further by the morphology of the patellofibial joint. In *Limulus*, this joint is formed by a

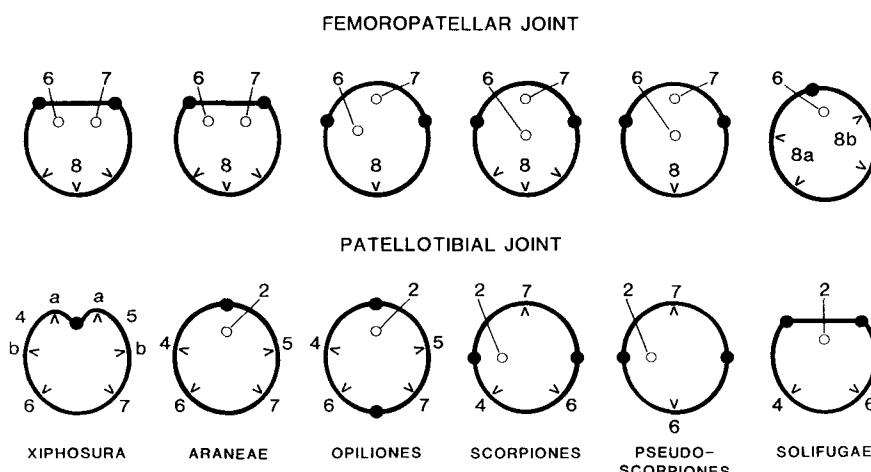


Figure 16. Diagrammatic cross sections through the femoropatellar and patellotibial joints of walking legs in *Limulus polyphemus* (Xiphosura), *Liphistius sumatranaus* (Araneae), *Leiobunum vittatum* (Opiliones), *Pandinus imperator* (Scorpiones), *Chthonius tetrachelatus* (Pseudoscorpiones) (leg 1), and *Paragaleodes scalaris* (Solifugae). Each diagram depicts the proximal rim of the distal segment of each joint, patella (femoropatellar joint) and tibia (patellotibial joint). The solid circles represent articulations (condyles), the open circles depict muscles that traverse the joint but do not insert on the distal segment, and the arrows (V) indicate approximate sites of tendinous insertions. The left-hand and upper sides of each diagram represent the anterior and dorsal surfaces of the joint, respectively.

single dorsal condyle and movement is controlled by four muscles (4–7). Muscles 4 and 5 arise on the anterior and posterior walls of the patella and insert on the anterior and posterior rims of the tibia, respectively (Figs 9A, 16). This arrangement is also found in Araneae, Uropygi and Amblypygi (Figs 9B–D, 16). Muscles 6 and 7 are transpatellar muscles, arising from the anterior and posterior surfaces of the femur and patella and inserting on the ventroanterior and ventroposterior rims of the tibia, respectively (Figs 5A, 16). This arrangement is also found in Araneae (Figs 5B, 16), Palpigradi (Fig. 6B), Acari (Fig. 6D, E) and, with some modifications of muscle 7 in Amblypygi (Fig. 5C) and Uropygi (Fig. 5D).

The patellotibial joint of Opiliones retains the primitive configuration of articulations and muscular insertions found in *Limulus* and spiders, but a ventral condyle joins the primitive dorsal, resulting in a vertical bicondylar joint (Figs 7, 11, 16). This arrangement is regarded as primitive for the four orders in this clade. The remaining orders (Scorpiones, Pseudoscorpiones and Solifugae) retain basic elements of this organization, but the entire joint (including articulations and muscular insertions) has rotated 90° from the primitive orientation, so that the dorsal surface of this joint corresponds to the posterior surface in Opiliones (Fig. 16). The vertical bicondylar joint in Opiliones corresponds to the transverse bicondylar joint of Scorpiones, Pseudoscorpiones and Solifugae. The muscles that insert on the anterior and posterior rims of the tibia in Opiliones correspond with the ventral and dorsal muscles of Scorpiones, Pseudoscorpiones and Solifugae. These orders also differ from opilionids and most other arachnids in lacking muscle 5. I hypothesize that the 90° rotation of the patellotibial joint and the absence of muscle 5 are synapomorphies of Scorpiones, Pseudoscorpiones and Solifugae and that Opiliones is the sister group to these three orders taken together.

The apparent rotation of the patellotibial joint is also reflected in the distal portion of the leg, especially in Scorpiones and many early derivative pseudoscorpions. The tibiotarsal joint of the hypothetical primitive arachnid appendage (Fig. 14) takes the form of a transverse bicondylar dorsal hinge, and the flexor at this joint (3) arises, in part, from the anterior and posterior walls of the tibia. The muscles controlling the claws (1, 2) also arise from the dorsal surface of the leg. The tibiotarsal joint of scorpions, however, is formed by a vertical bicondylar anterior hinge, and muscle 3 arises primarily from the ventral, posterior and dorsal surfaces of the tibia (Fig. 4A). Muscles 1 and 2 arise from the anterior surface of the leg. This pattern is less pronounced in pseudoscorpions (Fig. 4B, C) and is essentially absent in Solifugae (Fig. 4D). Although the morphology of the distal portions of the walking legs in scorpions is congruent with the hypothesis of a 90° rotation at the patellotibial joint, the pattern of change within the distal segments is not consistent enough to be regarded as synapomorphic for Scorpiones, Pseudoscorpiones and Solifugae.

Cladistic analysis of the morphology of walking appendages in Scorpiones, Pseudoscorpiones and Solifugae provides autapomorphic features for each order. In addition to traditional autapomorphies, such as pectines, Scorpiones is unique in that muscle 1 originates from the anterior surface of the tibia (Fig. 4A) rather than the dorsal surface of the basitarsus as in the primitive arachnid appendage (Fig. 14). Pseudoscorpions are characterized by the absence of muscle 4 and possessing a cheliceral spinning apparatus. Solifugae have several appendicular

autapomorphies (Table 1), but the absence of muscle 7 has special significance because its presence is considered here to be a synapomorphic feature of Opiliones, Scorpiones, Pseudoscorpiones and Solifugae.

The conclusion that a derived form of muscle 7 was present in the ancestors of Solifugae is supported by the following argument. The derived form of 7 is found in Pseudoscorpiones, the apparent sister group of Solifugae. These two orders are united by unusual features of the chelicerae and tracheal systems (Weygoldt & Paulus, 1979b). There are other similarities, such as the morphology of the preoral cavity and coxal region, but these features require further study. The arrangement of the patellotibial joint of solifuges appears to be the product of the same 90° rotation experienced by the ancestors of scorpions and pseudoscorpions. The joint is formed by a transverse articulation and the flexor muscles (4, 6) have essentially the same derived arrangement found in scorpions (Fig. 16). The patellotibial joint in solifuges is bicondylar like those of Opiliones, Scorpiones and Pseudoscorpiones. A derived form of muscle 7 exists in these three orders indicating that the ancestors of Solifugae also possessed this feature.

The most controversial result of this study is that scorpions are derived. These animals have traditionally occupied a special phylogenetic position in Arachnida since widespread opinion suggests that they are more primitive or archaic than other arachnids. This view is inspired by the extreme age of the group, the oldest known arachnids, and by their general resemblance to eurypterids. Although scorpions retain certain primitive features, including four pairs of booklungs, a series of opisthosomal ganglia and flagellate spermatozoa, plesiomorphic features are of limited value in elucidating phylogenetic relationships. Owing to lack of contrary evidence, the traditional opinion that scorpions are somehow 'more primitive' has been incorporated into the most recent cladistic analysis of Arachnida (Weygoldt & Paulus, 1979b). To my knowledge, this study is the first to use cladistic methodology to show that scorpions may be derived arachnids, but this hypothesis requires corroboration from other lines of evidence.

THE PROBLEM OF DOUBLE TROCHANTERS AND DIVIDED FEMORA

Although there is no compelling reason to reject Xiphosura as a legitimate outgroup of Arachnida, there is evidence suggesting that outgroup comparisons should be extended beyond *Limulus* in order to elucidate certain aspects of the evolutionary morphology of arachnid appendages, namely the occurrence of an extra segment in the walking legs of ricinuleids, solifuges, opilioacarines and certain acariform mites. It has become standard practice to dismiss these similarities as convergences, as reflected by the different names given to the extra segment in different lineages. Several lines of evidence indicate that the primitive chelicerate appendage consisted of eight segments rather than seven, the number in the walking legs of spiders, scorpions and most other arachnids. For example, the legs of pycnogonids (Chelicerata; Pantopoda) are composed of eight segments (Fig. 18). King (1970) stated the pycnogonids have nine 'segments', but the 'tarsus-propodus' joint is adesmatic and probably represents a divided tarsus. Reconstructions of appendages in certain eurypterids have revealed an extra podomere in legs 3 and 4 (Selden, 1981), a pattern shared with ricinuleids, opilioacarines and solifuges. The thoracic appendages of trilobites also appear to contain eight podomeres (Cisne, 1981).

The presence of eight rather than seven segments in the primitive chelicerate appendage necessitates an explanation for the absence of the 'extra' segment in *Limulus* and most arachnids. The unusual muscle arrangement crossing the trochanterofemoral joint in these animals may provide an answer. In the discussion of Solifugae, the depressor muscle at the basifemur-telofemur joint was hypothesized to be homologous with a small muscle (10) found in *Limulus* and most arachnids. In its typical form, 10 arises on the anterior wall of the trochanter, traverses the trochanterofemoral joint diagonally, and inserts on the proximoposterior wall of the femur (Fig. 14). This muscle is unusual in lacking an obvious tendinous insertion and its functional significance is obscure. Another muscle (9) has a similar origin and insertion and lacks obvious tendons, as well. It occurs in *Limulus* (Fig. 9A), Araneae (Fig. 9B) and Amblypygi (Fig. 9C) and appears to serve as a depressor at the trochanterofemoral joint. Another unusual muscle (12) occurs in amblypygids and schizomids (Uropygi). It arises on the anterior wall of the trochanter, crosses the trochanterofemoral joint and inserts along the dorsal midline of the femur (Figs 9C, E, 17A). It does not insert by means of a tendon but may assist in levitating the joint. Based on similarities in origin and placement with respect to other muscles (Fig. 17), I have tentatively homologized 12 with the levator of the basifemur-telofemur joint in Solifugae.

These observations suggest that the femora of amblypygids and most other arachnids are actually composed of two segments that fused in the course of evolution. The unusual pattern of muscle insertions within the femur could indicate the site of a primitively mobile joint that these muscles once operated. Reconstructions of walking appendages of certain trigonotarbrids, extinct relatives of spiders, amblypygids and uropygids, do, in fact, show an extra podomere ('annulus') between the trochanter and femur (Shear *et al.*, 1987).

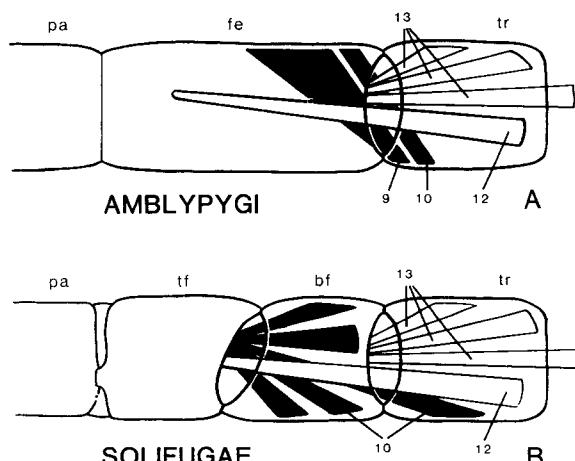
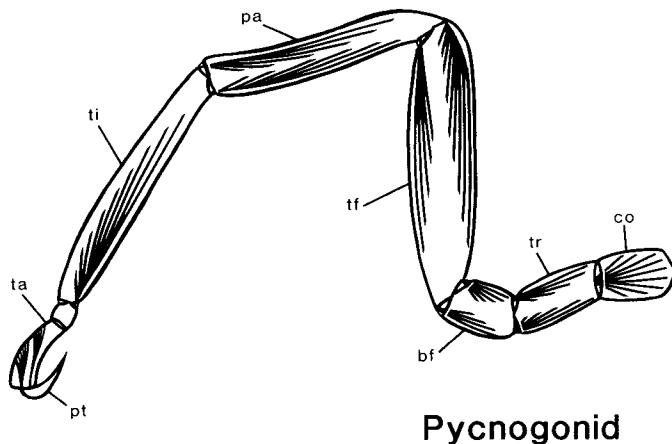


Figure 17. Comparison of musculature associated with A, the trochanterofemoral joint in *Phrynos marginemaculatus* Amblypygi and B, the trochanterofemoral and basifemur-telofemur joints in leg 4 of *Paragaleodes scalaris* (Solifugae). Each diagram shows a dorsal view of a walking leg from the right-hand side of the body. The unusual insertions of muscles 9, 10 and 12 in Amblypygi suggest that the femur of this and most other arachnid orders represents two segments (telofemur, basifemur) which have either fused many times in the course of evolution or fail to differentiate during ontogeny in all but a few arachnid lineages (e.g. legs 3 and 4 in Solifugae). Abbreviations: bf, basifemur; fe, femur; pa, patella; tf, telofemur; tr, trochanter.



Pycnogonid

Figure 18. Anterior view of leg 4 of an unidentified pycnogonid (Chelicerata: Pantopoda). Abbreviations: bf, basifemur; co, coxa; pa, patella; pt, pretarsus; ta, tarsus; tf, telofemur; ti, tibia; tr, trochanter.

This scenario is feasible but would require multiple fusions of the basifemur and telofemur in different lineages with similar morphological consequences. A more parsimonious solution can be found in the postembryonic development of certain mites. Legs 3 and 4 of early opilioacarine instars resemble the legs of other arachnids in having only seven segments but add an eighth, the second 'trochanter', as they mature. Van der Hammen (1979) suggested that the second 'trochanter' is present in early instars as an undifferentiated portion of the femur. A similar process occurs in certain acariform mites. The femur appears to divide during the course of development to form a basifemur and telofemur (Lindquist, 1984).

A synthesis of results from comparative anatomy, palaeontology, and ontogenetic studies provides a potential explanation for the sporadic appearance of double 'trochanters' and divided femora in Arachnida. The walking appendage of chelicerates could be hypothesized to have contained eight segments originally: coxa, trochanter, basifemur, telofemur, patella, tibia, tarsus, pretarsus. A 'femoral' segment would be divided to form the basifemur and telofemur at some point during ontogeny. The division of the femoral segment may have been suppressed in the common ancestors of *Limulus* and arachnids, but this reappeared in certain arachnid lineages from changes in the developmental programme. An extra segment in Ricinulei, Acari and Solifugae could be partly attributed to a symplesiomorphic developmental programme rather than homoplasy and the divided femur could be considered as atavistic. This hypothesis requires corroboration from ontogenetic studies of appendicular joints and musculature of pycnogonids, ricinuleids, opilioacarines and solifuges.

EVOLUTIONARY TRENDS IN LEG EXTENSION

Despite the morphological diversity of walking appendages in Arachnida, studies of the functional morphology of locomotion have dealt almost exclusively with spiders due, primarily, to the spiders' use of hydraulic pressure for leg

extension. The absence of extensors in spiders was first noted by Blanchard (1851–1864), but this was not recognized by most other arachnologists until later (Petrunkevitch, 1909). Gaubert (1892) was the first to propose that hydraulic pressure is used by arachnids in leg extension and that this pressure is generated within the prosoma, but his insight was overlooked by subsequent workers. Parry & Brown (1959) eventually 'rediscovered' the model proposed by Gaubert and provided experimental evidence to support it. The general conclusion that hydraulic pressure is generated in the prosoma has been reaffirmed several times (Wilson & Bullock, 1973; Stewart & Martin, 1974; Anderson & Prestwich, 1975), but the precise mechanism by which this is achieved has not been firmly established, even though several models have been proposed (Wilson, 1970; Palmgren, 1981).

Ideas on the evolutionary origin of hydraulic leg extension in spiders fall into two categories. In one widely accepted scenario, hydraulic extension and the absence of extensor muscles are considered derived features that evolved to provide space needed for the powerful flexors used in prey capture (Rovner, 1980). The supposed costs of this mechanism are perturbations to normal circulation, lack of locomotor stamina, inability to withstand desiccation or bleeding and are thought to be offset by the evolution of web-building and cheliceral venom, features that would minimize active locomotion and prolonged exertion (Wilson, 1970; Anderson & Prestwich, 1975). The reasoning is inconsistent with the results of this study. Extensors in Arachnida typically arise distal to their site of action at the femoropatellar joint and would not compete for space with the flexors. Most other arachnids that lack extensors namely mites, amblypygids, uropygids, ricinuleids, palpigrades, do not appear to use their legs in the direct manipulation of large prey. Any physiological or behavioural detriment imposed by use of hydraulic leg extension has not proven disastrous to the evolutionary success of the other 'extensorless' order, all of which lack cheliceral venom and silken snares.

In a second scenario, the absence of extensors in spiders is hypothesized to be a primitive feature inherited from a protoarthropod ancestor similar to Onychophora (Parry, 1960). Many wormlike invertebrates use hydrostatic skeletons for locomotion (Trueman, 1975). The parapodia of polychaetes and the lobopodia of onychophorans and tardigrades lack extensors but are equipped with flexors and other muscles that work against pressure generated in the body. Parry suggests that the situation observed in spiders is a retention or enhancement of this primitive mechanism.

Results from this study are consistent with the proposal that the absence of extensors in spiders and certain other arachnids is a primitive condition. Extensors are absent in *Limulus*, and the presence of dorsal hinge joints in Eurypterida (Seldon, 1981) and trilobites (Cisne, 1981) indicate that extensors were probably absent in these ancient arthropods, as well. Hydraulic leg extension may be a primitive feature of all arthropods (Manton, 1977). The absence of extensors and the use of hydraulic leg extension could be regarded as primitive features of arachnids, including spiders, although the available evidence is insufficient to homologize these features with those of protoarthropods or annelids.

The route by which muscular leg extension arose from the primitive 'extensorless' condition has not received much attention from arachnologists. As

exemplified by the scenario for the loss of extensors in spiders, arachnids have been generally assumed to use sets of antagonistic muscles to operate their joints. Faith in this notion appears to have been so strong, in fact, that some anatomists described and illustrated extensors where none exist (Schimkewitsch, 1884; Roewer, 1934; Sonenshine, 1970). The situation has been further confused by the failure of some anatomists to notice extensors in those arachnids which actually have them (Gaubert, 1892; Ewing, 1928; Snodgrass, 1952; Miller, 1977).

The apparent evolutionary history of the origin and elaboration of muscular leg extension encompasses much of the functional and morphological diversity in arachnid walking legs. The transpatellar muscles (6, 7) are foremost in this transformational sequence. In their primitive states, the transpatellar muscles are essentially anterior-posterior mirror images (Fig. 14). They arise from the dorsal surface of the femur and the walls of the patella and insert on the proximal rim of the tibia. They traverse two joints, and, therefore, each muscle may be expected to perform at least two functions. The primitive femoropatellar joint consists of a dorsal hinge that permits flexion-extension, and the primitive patellotibial joint has a dorsal monocondylar articulation that undergoes protraction-retraction. Contraction of one or both transpatellar muscles may flex the femoropatellar joint. The anterior muscle (6), which inserts on the anterior rim of the tibia, may assist in protraction of the patellotibial joint. The posterior transpatellar muscle (7) inserts on the posterior rim of the tibia and may act as a retractor. This arrangement characterizes the legs of *Limulus* (Figs 5A, 16), Araneae (Figs 5B, 16), Palpigradi (Fig. 6B), and, with a few modifications, Amblypygi (Fig. 5C), Uropygi (Fig. 5D) and Acari (Fig. 6D, E).

The earliest important deviation from the primitive condition apparently took place in the common ancestors of Opiliones, Scorpiones, Pseudoscorpiones and Solifugae, involving the evolution of a femoropatellar extensor from the posterior transpatellar muscle (7). One of the earlier stages in this transition appears to have been maintained in palpator opilionids (Figs 7A, 16). Muscle 7 arises from a small process that extends above the condyles of the femoropatellar joint, although the muscle retains its primitive insertion on the posterior rim of the tibia and, presumably, its primitive function as a retractor of the patellotibial joint. In contrast to its primitive form, 7 is a large, spindle-shaped muscle lacking a direct connection to the patella. On the other hand, the anterior transpatellar muscle (6) retains the basic elements of both its primitive morphology and function. The dorsal articulation that formed the primitive patellotibial joint is joined by a ventral condyle, and so the slight flexion-extension movements that occur at this joint in *Limulus* and spiders is absent in Opiliones.

The extensor in Opiliones may have been overlooked by previous workers as it is unusually arranged. Appendicular muscles in arthropods and vertebrates are typically situated proximal to their sites of action. One effect of concentrating muscle mass proximally is a reduction in the moment of inertia at the distal end of each joint and a resulting reduction in the energy that a muscle must expend in shifting the mass of the leg. The femoropatellar extensor in Opiliones is situated within the patella, distal to its site of action (Fig. 7). Although this arrangement could be considered suboptimal from a purely mechanical perspective, it is understandable given the apparent evolutionary history of the muscle.

The femoropatellar extensor of palpator opilionids is bifunctional, which can also be partly attributed to its evolutionary history. Contraction tends to cause simultaneous extension at the femoropatellar joint and retraction at the patellotibial joint. When working independently, the muscle cannot cause movement at one joint without promoting movement at the other. The unconstrained double action of this muscle is not known to be in conflict with the proper function of the legs during locomotion; the animal would probably move the joints independently by recruiting the appropriate batteries of antagonists to resist or control the influence of the transpatellar muscle at each joint. In this context laniator opilionids have avoided mechanical complications associated with a bifunctional transpatellar muscle by shifting the insertion of 7 to the dorsal condyle of the patellotibial joint (Fig. 7C) where it eliminates this muscle's influence over movement. Muscle 7 serves only to extend the femoropatellar joint of these opilionids, and the task of retraction at the patellotibial joint is left to another muscle (5) (Fig. 11C).

When comparing the walking legs of palpator opilionids with those of scorpions, ignoring simple differences in proportions in favour of basic organizational features, the similarity of the femoropatellar joints and the musculature associated with them becomes apparent. The insertions and resulting functions of the transpatellar muscles (6, 7) are essentially the same (Fig. 16). Scorpions appear to maintain the basic elements of the patellotibial joint as well, but the entire joint, and everything distal to it, appears to have undergone a 90° rotation so that the primitive posterior face of the joint is directed dorsally. The primitive function of the joint (protraction-retraction) becomes flexion-extension. The posterior transpatellar muscle (7) is appropriately termed a transpatellar extensor in scorpions, because it apparently causes simultaneous extension at the femoropatellar and patellotibial joints. The bifunctional properties of the transpatellar extensor may provide an interesting system for mechanical analysis as it does in opilionids.

Manton (1958) offered a somewhat different interpretation of the functional morphology of the transpatellar extensor by claiming that this muscle is too small in comparison with the flexors to cause propulsive leg extension. She argued instead that depression of the trochanterofemoral joint causes passive extension at the distal joints and that the role of the transpatellar extensor is merely to position the joints to facilitate this process. Although Alexander (1967) supported Manton's view, this model has never been subjected to critical testing, and there are several reasons for questioning it. The practice of deciding the function of a muscle based on its size alone is questionable at the outset, and even if it were legitimate, the facts do not conform with Manton's conclusions. The transpatellar extensor is not small, occupying the dorsal half of the greatly expanded patella (Fig. 8A); it is certainly no less massive with respect to the flexors than the trochanterofemoral depressor (11) (Fig. 12A). In addition, Manton's model cannot account for the results of kinematic analyses of walking scorpions. Root & Bowerman (1978) have shown that the angular excursions during extension at the femoropatellar and patellotibial joints greatly exceed those that could be accountable by depression at the trochanterofemoral joint. Peculiarities in the rate of extension are not observed in depression, suggesting localized control of extension. Some of the extension not explained by movements at the trochanterofemoral joints may result from passive extension

brought about as the animal is propelled forward by the other legs, but such speculation merely serves to highlight ignorance of this mechanism and the need for further study.

The process of leg extension in pseudoscorpions has received little attention, probably due to the small size of these arachnids which impedes effective functional analysis. The structure of the anterior leg pairs in less derived pseudoscorpions is similar to that found in scorpions (Fig. 8A, C), and the mechanical problems are expected to be as complex. The role of the transpatellar extensor in the posterior legs, and the anterior legs of more derived pseudoscorpions, is less complicated due to modifications at the femoropatellar joint (Fig. 8B). This joint, in most pseudoscorpions, has either lost much of its mobility or has been altered to allow only protraction-retraction through the evolution of a vertical bicondylar articulation. In either case, the transpatellar extensor would be expected to have little influence over movement at the femoropatellar joint and appears to act primarily in extending the patellotibial joint. The mechanical uncoupling of these two joints is analogous in certain respects to the situation found in laniator opilionids (Fig. 7C), but with very different consequences. The transformation in pseudoscorpions results in walking appendages that look and work more like the legs of insects than those of primitive arachnids; an extensor muscle operates a single 'knee' and is positioned proximal to its site of action.

The epitome of arachnid locomotor specialization is found in Solifugae. The ancestors of Solifugae had extensor muscles similar to those found in living scorpions and pseudoscorpions. In fact, the transpatellar flexor (6) is still present and retains the 'scorpionoid' arrangement (Fig. 16). Solifuges appear to be closely related to pseudoscorpions, but there are great differences in the methods of leg extension. Extensor muscles in Solifugae were apparently replaced by elastic sclerites. These are found on the anterior and posterior faces of the patellotibial and tibiotarsal joints (Figs 4E, 8D) and apparently work as 'springs', storing energy during flexion and returning it during extension. Until the present study, solifuges were assumed to use muscular leg extension so that virtually nothing is known about the true mechanism or how it compares with muscular and hydraulic leg extension in terms of mechanics and energetic efficiency.

SUMMARY

In contrast to recent opinions that diversity in the morphology of arachnid walking appendages reflects a diverse ancestry, this study suggests that all terrestrial chelicerates are descended from a common ancestor but fails to resolve completely the phylogenetic relationships of the arachnid orders owing to a high degree of symplesiomorphy in appendicular characters. The primitive arachnid appendage probably contained seven segments and thirteen muscles distal to the coxa. There is evidence, however, that the femur in *Limulus* and most arachnids represents the basifemur and telofemur that either fused many times in the course of evolution or, more likely, failed to differentiate during development in all arachnid lineages excepting the Ricinulei, Solifugae and certain Acari.

The primitive arachnid appendage was characterized by the absence of extensor muscles, which indicates that hydraulic leg extension was the primitive mode of propulsion. Extensors appear to have evolved at the femoropatellar joint in one arachnid lineage through the modification of a transpatellar muscle. Presence of the extensor is regarded as a synapomorphy of Opiliones, Scorpiones, Pseudoscorpiones and Solifugae. A modification of the patellotibial joint resulted in the reorientation of the extensor so that it serves to extend both the femoropatellar and patellotibial joints simultaneously. This modification is considered synapomorphic for Scorpiones, Pseudoscorpiones and Solifugae. The extensor muscle is specialized further in Pseudoscorpiones but is replaced in Solifugae by elastic sclerites. Although the ultimate causes of the transformations described above are likely to remain unknown, the resulting morphological and functional diversity provides a source of characters for use in phylogenetic analysis and for investigations into the relationship of form and function.

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