

## Spider Leg-muscles and the Autotomy Mechanism

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### SUMMARY

Spider leg-muscles have been redescribed and the absence of extensor muscles at two joints confirmed. The possibility that the flexors at these joints act in antagonism to the blood-pressure is discussed. The coxal muscles are inserted on to sclerites in the rim of the trochanter and autotomy occurs at this joint. At autotomy the sclerites are detached from the trochanter and support the articular membrane, which restricts bleeding.

### INTRODUCTION

PETRUNKEVITCH described the leg-muscles of spiders in 1909, correcting earlier and very formalized conceptions and drawing attention to the absence of extensor muscles at several of the joints. Brown (1939) and Ellis (1944) agreed with Petrunkevitch's account, and Ellis considered the role of blood-pressure in extending the joints which lacked extensors, suggesting that certain muscles operated valves to produce a local rise of pressure. Dillon (1952) redescribed the leg musculature: he maintained that extensors were present at all but one, or possibly two, joints and differed in other ways from Petrunkevitch. Snodgrass (1952) modified Dillon's account of the lower leg, omitting details of the coxal muscles. The families of spiders examined by these authors were:

Petrunkevitch: Theraphosidae, Lycosidae, Eusparassidae.

Brown: Agelenidae.

Ellis: Theraphosidae, Agriopidae, Theradiidae, Agelenidae.

Dillon: Theraphosidae, Agriopidae.

Snodgrass: Theraphosidae.

None of the authors who examined more than one family reported any significant differences between them, and as Petrunkevitch, Dillon, and Snodgrass all included the large *Tarantula Eurypelma* sp. (Theraphosidae), the differences in their accounts appear to be those of interpretation and not of systematics.

This paper contains an account of the leg-muscles of the common British house spider *Tegenaria atrica* (Koch: Agelenidae). I have followed Snodgrass (1952) and recent entomological practice in referring to the muscles by number rather than by means of the earlier functional nomenclature which leads to difficulties when function is in doubt or when comparative studies indicate that muscles differing in function are nevertheless homologous. The corresponding muscles in the accounts of Petrunkevitch, Dillon, and Snodgrass have been indicated as far as possible, the abbreviations P, D, and S being

used for this purpose; but a full appreciation of the similarities and differences requires a comparison of the drawings.

A close examination of the coxal muscles has brought to light further facts about the autotomy mechanism of spiders, first described by Bonnet (1930). Unlike crustacea and insects, spiders autotomize their legs at a functional joint and an account is given of the interesting mechanism by which the joint is severed and bleeding restricted.

The musculature has been worked out by ordinary dissection of adult animals under a binocular microscope. Although the account refers specifically to *T. atrica*, I have had the advantage of making a preliminary dissection of a specimen of the much larger *Lycosa ingens* (Blackwall: Lycosidae) from Deserta Grande (Madeira) kindly given to me by Mr. Roderick Fisher. Only minor differences appear to exist between the two species.

#### THE ARTICULATION AND MUSCULATURE OF THE LEGS

The leg-muscles and articulations of *Tegenaria atrica* are shown in figs. 1 and 3. Each part of the limb is shown as though examined by transparency from a lateral face as far as the median vertical plane. The coxa, trochanter, femur, and patella are viewed from both anterior and posterior faces, but the tibia, basitarsus, and telotarsus are seen only from one face as the musculature is symmetrical about the median vertical plane. The coxa is also drawn as seen from above, both from the dorsal surface as far as the median horizontal plane (fig. 3, c) and from this plane down to the ventral surface (fig. 3, d). It is not proposed to repeat in the text what is evident in the diagrams but to discuss the probable functions of the muscles, considering movements about each joint in turn, starting at the distal end of the leg.

*Claw* (fig. 1, d). Like most web-spinning spiders the Agelenidae have three claws, paired dorsal ones and a smaller median one. The paired claws are attached to the thin cuticle at the end of the telotarsus and have considerable freedom of movement. The median claw is an extension of a sclerotized terminal plate (the pretarsus of Snodgrass) and is relatively rigid on the telotarsus. To the extreme dorsal and ventral points of the terminal plate are attached the long median tendons of the median muscle 27 which elevates the claws, and the paired muscles 28 and 29 which depress them.

Muscle 27 (median) = M. extensor unguium (P) = M. levator pretarsi (D) = 21 (S—fig. 25)

Muscles 28 and 29 (paired) = M. flexor unguium (P) = M. depressor pretarsi (D) = 22 (S—fig. 25)

I agree with Snodgrass that muscles 28 and 29 do not have the origins in the basitarsus figured by Petrunkevitch and Dillon.

*Basitarsus-telotarsus joint* (fig. 1, d). There are no muscles directly associated with this joint, a condition commonly found at joints subdividing the tarsus of insects. Nevertheless, the joint plays a part in leg movement and owing to the disposition of the long tendon of muscles 28 and 29, contraction of these

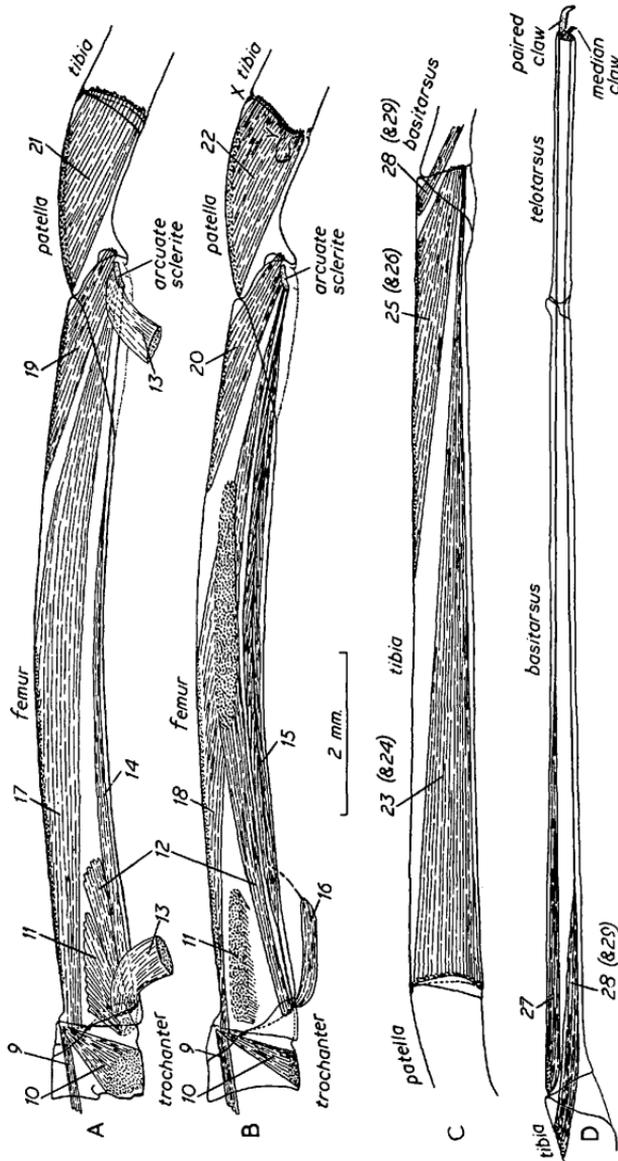


FIG. 1. Leg-muscles of *Tegenaria atrica*. A, trochanter, femur, and patella seen from the anterior face. B, the same, from posterior face. C and D, tibia, basitarsus, and telotarsus seen from the anterior face. Apart from the patella-tibia articulation, the view from the posterior face is similar, but note that the claw tendons are median.

depresses the telotarsus as well as the claws. Contraction of muscle 27 appears to have little effect. There is no articular condyle at the joint which consequently is a universal one.

*Tibia-basitarsus joint* (fig. 1, c). The articulation is along a dorsal hinge-line, so the possibility of muscular elevation of the basitarsus is excluded. Laterally and ventrally the articular membrane is extensive, folding up during depression and becoming extended and slightly convex during elevation. Depression is due to two pairs of muscles 23 and 24, and 25 and 26. Although muscles 28 and 29 originate at the distal end of the tibia, they do so close to the hinge line, and have no significant effect at this joint.

Muscles 23 and 24 (paired) = *M. flexor metatarsi longus* (paired) (P)  
 = *M. flexor tarsi anticus* and *posticus* (D)  
 = 19 and 20 (S—fig. 25)

Muscles 25 and 26 (paired) = *M. flexor metatarsi bilobatus* (paired) (P)  
 = *M. flexor tarsi major* and *minor* (D)  
 = 17 and 18 (S—fig. 25)

Petrunkevitch figures some fibres of the paired muscles 23 and 24 as originating laterally at the anterior end of the patella: this has not been confirmed by Dillon, Snodgrass, or myself. I have, however, found a small slip of muscle 23 (the anterior one) which extends proximally a short way into the patella where it appears to terminate on a nerve-fibre and may be proprioceptive in function. This unusual arrangement will be dealt with in a later paper.

*Patella-tibia joint* (fig 1, A, B). There is a single dorsal condyle at *X* and the joint is free to move in a horizontal plane only, being capable of more retraction than protraction. This movement is due to the two muscles 21 and 22 which lie wholly within the patella. The posterior rim of the patella is indented as shown at *Y* in fig. 1, B, and the extent of the articular membrane in this region varies in the different legs, being least in the hinder two legs (shown in fig. 1, B) and more extensive in the anterior two legs. Movement at the joint causes marked distortion in the indented region of the patella rim and it is thus significant that at the head of the indentation lie two lyriform organs (with their axes at right angles) which Pringle (1955) has shown to be proprioceptors.

Muscles 21 and 22 (paired) = *M. promotor* and *retractor tibiae* (P)  
 = *M. promotor* and *remotor tibiae* (D)  
 = 14 and 15 (S—fig. 25)

In addition to this pair the other authors have described other muscles in the patella, the presence of which I do not confirm. Petrunkevitch figures a *M. flexor tibiae* originating dorsally at the proximal end of the patella and inserting by a tendon ventrally at the proximal end of the tibia, which he says is 'to all appearances functionless'. Snodgrass figures a ventral muscle (his muscle 16, fig. 25) with an undescribed origin and anteroventral insertion. Dillon figures *M. depressor tibiae anticus* and *posticus* originating dorsally at

the distal end of the femur and inserting ventrally, at the proximal end of the tibia in the Theraphosidae, and on the side of the patella in the Agriopidae. Having examined many serial sections of the femuro-patella joint I am sure that this muscle does not exist in *Tegenaria*. I also do not confirm that Dillon's M. promotor tibiae (my muscle 21) has the complex form that he illustrates.

*Femur-patella joint* (fig. 1, A, B). The articulation is along a dorsal hinge-line with condyles at each end, so the possibility of elevator muscles is precluded (as at the tibia-basitarsus joint). Owing to the swept-back form of the distal rim of the femur, there is a very large area of articular membrane laterally and ventrally. This becomes folded when the joint is flexed (fig. 2)

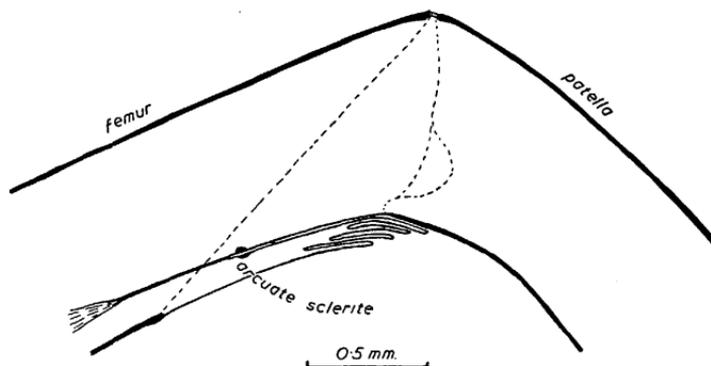


FIG. 2. *Tegenaria atrica*: vertical median section through the flexed femur-patella joint, showing the folded articular membrane. Note that the arcuate sclerite is formed as a thickening and sclerotization of a permanent (crescent-shaped) fold of the membrane.

and slightly convex when the joint is fully extended. Mid-ventrally near the patella there is a semicircular invagination of this membrane the rim of which is sclerotized to form an arcuate sclerite, convex proximally (see figs. 1 and 2). This sclerite is referred to by Ellis as the chitinous plate, and by Dillon as the myophoric lamella.

The muscles originating within the femur and producing depression (flexion) are:

Muscles 17 and 18 (paired) originating along the mid-dorsal line over the proximal half of the femur and inserted on to the arcuate sclerite.

Muscles 19 and 20 (paired) originating along the mid-dorsal line over the distal quarter of the femur and inserted on to the sclerite and the rim of the patella.

Muscle 13 originating on the antero-ventral proximal rim of the femur and inserted on to the anterior half of the sclerite.

In addition to the above muscles there is a muscle complex composed of

muscles 14, 15, and 16 which originates on the ventral rim of the trochanter and is inserted through two tendons on the arcuate sclerite, thus having a depressor action at both trochanter-femur and femur-patella joints. The more anterior muscle 14 is almost distinct from the rest of the complex, but does receive a few fibres (not shown in fig. 1) from the more posterior muscle 15. Muscle 15 originates on a tendon from the trochanter and the fibres insert along the length of another tendon which runs to the arcuate sclerite. A distinct fibre group, muscle 16, originates on the trochanter lip and inserts on the same tendon as the fibres of muscle 15.

Muscles 17 and 18 (paired) = *M. flexor patellae bilobatus* (paired) (P)  
 = *M. flexor patellae robustus* (single) (D)  
 = 9 and 10 (S—fig. 25)

Muscles 19 and 20 (paired) = *M. flexor patellae bilobatus* (paired) (P)  
 = *M. flexor patellae major* (anterior) and  
*minor* (posterior) (D)  
 It is not figured by Snodgrass.

Muscle 13 is considered by Petrunkevitch to be part of the *M. flexor patellae longus* to which he gives a double origin. It may correspond to Dillon's *M. flexor patellae brevis*. It is not figured by Snodgrass.

Muscles 14, 15, and 16. These are represented by Petrunkevitch as a single muscle, his *M. flexor patella longus*. They probably correspond to the distinct muscles named by Dillon *M. extensor femoris proximalis*, *princeps*, and *communis* respectively. They also appear to correspond to the two lateral and one ventral muscle figured by Snodgrass (his muscles 11, 12, and 13, fig. 25).

*Trochanter-femur joint* (fig. 1, A, B). This is the only dicondylic joint, the condyles being lateral so that movement is limited to the vertical plane. Depression is due to muscles 11 and 12 lying in the femur and elevation to muscle 10 in the trochanter and to a smaller muscle (9) originating in the coxa.

Muscles 11 and 12 = *M. extensor femoris posticus* (D)

They are not figured by Petrunkevitch. Snodgrass figures a single muscle (his muscle 8, fig. 25) which is inserted dorsally along the anterior half of the femur and most nearly corresponds to my muscle 11.

Muscle 10 = *M. flexor femoris bilobatus* (paired) (P)  
 = *M. flexor femoris bilobatus* and *dubius* (D)  
 = 7 (S—fig. 25)

Muscle 9 = *M. flexor femoris longus* (P)  
 = *M. gracilis* (D)  
 = 6 (S—fig. 25)

Both Dillon and Snodgrass figure a slip of this muscle originating on the anterior rim of the trochanter, which I do not confirm.

*Coxa-trochanter joint* (fig. 3, A-D). This involves the only ball-and-socket

joint in the leg, the socket being formed in the anterior rim of the trochanter (fig. 1, A, C); and the 'ball' being the enlarged end of a long horizontal apodeme which projects into the coxa along the mid-lateral line on the anterior face. There is no other condyle and the joint is free in the vertical and horizontal plane. Fitting closely into a groove in the rim of the trochanter are five slender sclerites (fig. 3, *a-e*), while a sixth sclerite runs obliquely across the articular membrane on the posterior face of the joint (fig. 3, B, E, *f*). All the eight coxal

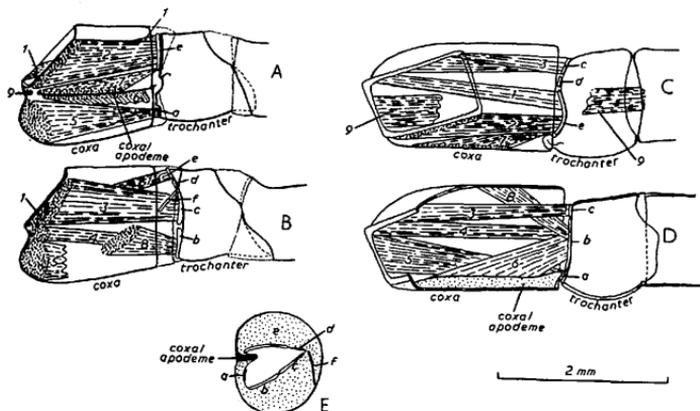


FIG. 3. *Tegenaria atrica*: muscles of the coxa and trochanter. A and B, anterior and posterior faces respectively. C, dorsal view extending down to the level of the coxal apodeme, which, for clarity, is not drawn but lies just below muscle 7. D, view extending down from the level of the coxal apodeme to the ventral surface. E, distal end of the coxa immediately after autotomy.

muscles are inserted on to these sclerites and not on to the trochanter itself: their function will be discussed below. Muscle 9, which passes through the joint to insert on the femur, has already been described. No attempt has been made to analyse the functions of the coxal muscles and it is unlikely that they act singly. Petrunkevitch gives a very simplified account of the coxal musculature describing only four muscles (*M. flexor*, *extensor*, *promotor*, and *retractor trochanteris*). Similarly Snodgrass refers to only five major groups of fibres, two being dorsal and three ventral, which he does not figure in any detail. Dillon figures nine muscles besides the one inserted on to the femur (my muscle 9), seven of which are approximately related to those shown in my fig. 3 as follows:

- Muscle 2 = *M. levator trochanteris posticus* (D)
- Muscle 3 = *M. remotor trochanteris dorsalis* (D)
- Muscle 4 = *M. depressor trochanteris obliquus* (D)
- Muscle 5 = *M. depressor trochanteris ventralis* (D)
- Muscle 6 = *M. depressor trochanteris medius* (D)

Muscle 7 = *M. levator trochanteris anticus* (D)

Muscle 8 = *M. remotor trochanteris ventralis* (D)

I have not confirmed Dillon's *M. promotor trochanteris major* and *minor*; nor does he show my muscle 1.

#### NON-MUSCULAR EXTENSION

I agree with Petrunkevitch (1909) and Ellis (1944) that no elevator muscles occur at the femur-patella or tibia-basitarsal joints: as the articulation is along a dorsal hinge-line such muscles are out of the question. Dillon (1952) agrees that there are no elevators at the femur-patella joint, but suggests that his *M. depressor* and *levator pretarsi* (my muscles 28 and 29, fig. 1, D) may act as elevators of the tibia-basitarsal joint. This would only be possible if the articulation were not dorsal, and Dillon in fact figures it as slightly below the dorsal line. I have not confirmed this in the Mygalimorph *Grammostola* sp. (closely related to his *Eurypelma* sp.): here there is a fully dorsal hinge-line, as in *Tegenaria*.

It is easy to confirm Ellis's (1944) observations that an increase in hydrostatic pressure in the leg causes elevation at the two joints where elevator muscles are lacking. This can be shown by gently pressing the femur or tibia of a limb either attached to or removed from the body; or by injecting fluid into an animal's body, when all eight legs become fully extended. Ellis suggested tentatively that normal extension might be due to a *local* rise of pressure, the arcuate sclerite (fig. 1, A, B) being raised by a special levator muscle so as to press against the main leg-artery and divert blood into lateral branches in the region of the articular membrane. There are several objections to this idea, at least as applied to *Tegenaria*: (a) it cannot explain extension at the tibia-basitarsus joint, where there is no arcuate sclerite; (b) at the level of the arcuate sclerite in the femur-patella joint the artery is so disposed in relation to the main leg nerve that it is difficult to see how one could be constricted without the other; (c) muscles 19 and 20 (fig. 1, A, B), corresponding to Ellis's levator muscle, are inserted partly on to the sclerite and partly on to the rim of the patella, being favourably placed to produce a flexion force when the joint has already been considerably flexed by the longer muscles inserted on to the sclerite (muscles 14, 15, 16, 17, and 18, fig. 1, A, B).

It is proposed to consider the extensor mechanism of these joints in more detail in a later paper, but two alternatives to Ellis's suggestion may be briefly referred to. Firstly, extension might be due to indirect muscles, as in the insect wing mechanism. In fact extension can be produced by a compression force acting along the hinge line of the joints, but no muscles are suitably placed to produce such forces naturally. Secondly, the flexors might act in antagonism to the blood-pressure of the leg so that extension occurred when the flexors were inhibited. This is consistent with Ellis's observation that dehydrated spiders and those deprived of some blood cannot fully extend their limbs. The rate of extension would be determined by the rate of relaxation of the flexors, subject to a maximum rate determined by the hydro-

dynamics of the system. A possible objection to this idea is that the locomotor demands made upon the circulatory system might not always be consistent with the respiratory demands, though it will be noted that during rapid movement an increase in blood pressure would be expected for *both* respiratory and locomotor reasons. If this explanation proved to be the true one, it would be of evolutionary interest in view of the likelihood that arthropod limbs evolved as turgid appendages (Pryor, 1951), a condition still exhibited in such animals as the Onychophora.

#### THE AUTOTOMY MECHANISM

'Autotomie' was defined by Frédéricq (1883) as 'mutilation par voie réflexe comme moyen de défense chez les animaux'. Usage has since widened the term to embrace all cases of fracture of limbs and other structures at a specific point where structural adaptations associated with the fracture mechanism and reduction of bleeding are found to occur. It seems undesirable to withhold the term 'autotomy' until a precise reflex has been demonstrated or to employ a complicated nomenclature for other cases, e.g. autospasy, autotilly, autophagy (Wood, F. D. and H. E., 1932).

It is generally accepted that spiders' legs readily fracture between coxa and trochanter, but only when an external force is applied to the distal part of the leg by contact with the ground or web, or by being held in the mouth appendages (Wood, 1926; Bonnet, 1930). It occurs when the animal is trapped by one leg, and also some hours after a leg has been injured. No one has confirmed the presence of the upward-pointing chitinous 'knife' at the proximal end of the trochanter, which, according to Friedrich (1906), cuts through muscle 9 and the coxa-trochanter articular membrane when muscle 10 (his *Beuger des femur*, which he shows running dorso-ventrally) contracts. Wood (1926) examined the legs of arachnids, Opiliones, and Amblypyges and concluded that there was no special adaptation for autotomizing the legs, but that fracture occurred, as a result of external forces, at the weakest joint which was the coxa-trochanteral in arachnids, the trochanter-femural in Opiliones, and the patella-tibial in Amblypyges. She did not explain why the weakest joint was in a relatively thick part of the leg and not nearer the distal end. In scorpions the legs did not easily fracture and there was no specific locus of severance.

Bonnet (1930), working on the pisaurid spider *Dolomedes plantarius*, says that all the coxal muscles except muscle 9 are inserted on to the articular membrane of the coxa-trochanter joint and that when the limb fractures these muscles pull the membrane inward towards the coxa. He also describes a chitinous ring, in two parts, which detaches from the trochanter with the articular membrane and borders the opening.

I have shown above (see fig. 3, A-D) that in *Tegenaria* the coxal muscles are all inserted on to a ring of sclerites which fit into a groove in the proximal rim of the trochanter. The joint fractures between these sclerites and the trochanter, and the coxal muscles then pull the articular membrane proximally

while at the same time the sclerites converge on one another (fig. 3, E) so that a comparatively small hole is left in which the blood rapidly clots and which after a day or two is sealed by a brown plate. The fact that the leg fractures (though the membrane is not withdrawn to the same extent) when the animal is narcotized or freshly killed indicates that active contraction of the coxal muscles is not essential in causing the actual fracture. However, when an external force is applied to the end of the leg the opposing passive resistance of the coxal muscles must set up a strain where the sclerites are attached to the trochanter, and thus cause the fracture to occur there. The function of the oblique sclerite (fig. 3, B, E, f) is not clear: possibly this also causes a local strain at its tip between sclerites *c* and *d*, and thus contributes to the fracturing process.

The autotomy mechanism described by Bonnet and myself differs in principle from that found among insects and Crustacea. Among insects the phasmids are particularly liable to autotomy and here (Bordage, 1905) the fracture occurs at the level of the junction of trochanter and femur which are fixed relative to one another; and a double diaphragm occurs at that point and limits the bleeding. In decapod crustacea (Wood, F. D. and H. E., 1932) a plane of weakness occurs near the proximal end of the ischium (not at the joint) and there is a diaphragm just proximal to this point. In neither insects nor Crustacea do any muscles or tendons cross the plane of fracture, and there is nothing remarkable in this since the fracture does not occur at a functional joint. In spiders only one small muscle (muscle 9) crosses the fracture plane despite the fracture plane being at a *functional* joint. This is achieved by the insertion of the coxal muscles, not on to the trochanter itself but on to the sclerites which separate from the trochanter when fracture occurs, thus enabling the articular membrane to function as a diaphragm which reduces bleeding.

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