

The comparative functional morphology of the leg joints and muscles of five spiders

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Summary

The leg joints and muscles of five species of spiders with different habits are described. Differences in the structure of the metatarsus-tarsus joint and the trochanter-patella muscles are related to the habits of the animal. The variation of the patella-tibia joint between mono- and bicondylic is described and discussed.

Introduction

Although a lot can be learned about the functions of anatomical features from a study of one species, this is limited to direct observations. When several species with different habits are examined, a comparison between them allows our knowledge of function to be extended by inference and deduction into areas which are not otherwise accessible. It was therefore decided to add to the study of limb joints and musculature made of the eusparassid *Heteropoda venatoria* (L.) (Clarke, 1984) by examining 5 more species, chosen for their diversity of habit.

Methods

The following species were studied: *Avicularia avicularia* (L.) (Theraphosidae), *Dolomedes fimbriatus* (Clerck) (Pisauridae), *Tegenaria saeva* Blackwall (Agelenidae), *Araneus diadematus* Clerck (Araneidae) and *Latrodectus mactans hasselti* Thorell (Theridiidae) (popularly called the Australian red-back spider).

The maximum angles of movement which could be made by the joints were measured on dead animals using a protractor (see Clarke, 1984). Specimens were dissected in 70% alcohol, which does not alter the flexibility of the tissues. Live animals were observed and filmed running, walking, climbing and taking prey, in order to discover the differences (if any) in the ways in which the legs are used by the different species.

Definitions

The term joint will be used to indicate an area of discontinuity in the skeleton used by the animal to move skeletal parts relative to each other. An articulation is an area of contact between stiff skeletal elements, within a joint, which is in some way adapted to allow movement. Should the skeletal components of the articulation become separated, the joint will be said to be disarticulated.

There is some confusion in the meaning of the word hinge when applied to the joints of arthropods. In Clarke (1984) it referred only to joints with 2 articulations, these at each end of a flat region and with

no muscles and little membrane between the 2 articulations. This usage was derived from the phrase "dorsal hinge line" used by Parry (1957). However, another use for the phrase "hinge joint" is common in the study of other arachnid groups (see e.g. Van der Hammen, 1982; Selden, 1981). Here it was used for both mono- and bicondylic joints where the bicondylic joint has no muscles on one side. This terminology is not appropriate for the present study, as it would bracket together such dissimilar structures as the coxa-trochanter and femur-patella joints (see below and Clarke, 1984). Though the term hinge was used in my study on *Heteropoda* I propose to discontinue its use to avoid confusion. I shall now refer to joints with 2 articulations separated by a region formed from flattened, closely apposed podomere edges with no muscles as flat bicondylic joints and the area between the articulations as the unmusclcd (formerly hinge) region.

Results

Habits of the animals

Of the 5 species studied, only *D. fimbriatus* is a nomadic hunter, taking prey by seizing it with the first and second pairs of legs (the third pair may assist if the prey is large) and dragging it to the mouth, where it is bitten. If the prey struggles, it will be held there by the flexed legs. The prey is gripped by the tarsi, and therefore the spider supports itself on the patellae and tibiae. This method of prey capture is also used by *H. venatoria* (Clarke, 1984) and *A. avicularia*. *A. avicularia* spends its life on a sheet web, but this does not play a part in prey detention. *T. saeva* does use its thick silk sheet for prey detention. *T. saeva* keeps away from the struggling animal, lunging forward

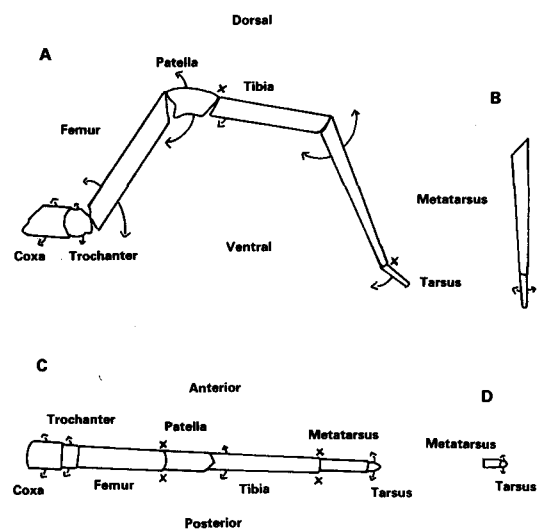


Fig. 1: Range of movement. **A** Posterior view of leg, typical standing posture, *D. fimbriatus*, *A. avicularia*, *T. saeva*; **B** As A, metatarsus-tarsus only, showing difference in posture, *A. diadematus*, *L. hasselti*; **C** As A, dorsal view; **D** As B, dorsal view. Arrows indicate the range of movement of the podomere at its base, assuming the proximal podomere is held still. A cross indicates that no movement can take place in that direction from the position shown.

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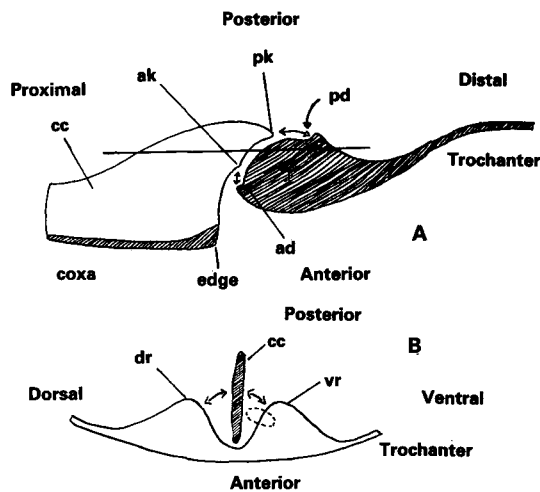


Fig. 2: Diagram of the mechanism of the coxa-trochanter articulation. **A** Antero-posterior movement, dorsal view; **B** Dorso-ventral movement, proximal view. Hatching indicates a cut surface. Arrows indicate paths of movement of the structures at their heads. The section line on A indicates the plane of section of the costa coxalis in B. The dotted area on B indicates the position of the ventral knob. ad = anterior dip, ak = anterior knob, cc = costa coxalis, dr = dorsal raised area, edge = distal edge of coxa, pd = posterior dip, pk = posterior knob, vr = ventral raised area.

repeatedly to bite it, until it is subdued. The spider often does not move its feet when lunging, but swings forward and back as though rocking in a cradle. The first legs are commonly held above the head, out of the way, while lunging.

A. diadematus and *L. mactans hasselti*, though the former lives in a vertical orb web and the latter underneath a horizontal sheet, both detain prey in the same way. Silk is drawn from the spinners by the fourth legs, working alternately, and thrown over the prey until it is completely wrapped.

All these species can climb well, but *A. diadematus* and *L. mactans hasselti* (especially the former) do not walk well. Female adults of *A. diadematus* often trail their hind legs when walking and struggle awkwardly over a glass surface. *D. fimbriatus* and *T. saeva* have no difficulty over glass, though they cannot match the ability of *H. venatoria* to walk upside down on glass.

Angles of movement

The angles of movement made by each joint are shown in Fig. 1. In addition, the coxa-body joint allows some rotation about the long axis of the leg. The metatarsus-tarsus joints of *A. avicularia*, *D. fimbriatus* and *T. saeva* also make this movement.

Joint structures

These will be described species by species, *A. diadematus* first, the others after, where there are differences.

A. diadematus

Coxa-body joint (as Fig. 3, *T. saeva*): As with the other species in this study, the rectangular coxal opening has one, loose ventral articulation with a

finger-like projection of the sternum. The small hollow on the posterior ventral edge of the coxa is separated from the sternum by arthroial membrane. In preserved specimens the sclerotised parts are not in contact and so the joint can be described as disarticulated. Movements are limited by contact of the lateral surfaces of the coxa with the coxae of the legs on each side, by the overhanging carapace on dorsal movement and by the coxal bulge (as in Figs. 4, 5) meeting the sternum on ventral movement.

The third and particularly the fourth legs of *A. diadematus* vary slightly from the general pattern, in that the sternal projection is stout and rounded at the tip, while the coxal hollow is correspondingly larger and deeper.

Coxa-trochanter joint: There is a single articulation formed by the swollen elaborated anterior edge of the trochanter and the inner end of the costa coxalis. (The costa coxalis is a long ridge of cuticle, projecting like a shelf inwards from the anterior coxal wall (Fig. 8).) The articulation is some distance from the edge of the coxa, and the trochanter is surrounded by an expanse of membrane equal in extent on all sides. A small sclerite lies in the membrane, posteriorly, but plays no direct part in making movements and does not reach the coxal edge. It has the appearance of a stiffened, permanent fold in the membrane.

The anterior articulation is complex, but, though varying in detail between species a basic mechanism can be detected. This will be described before the detailed structures of the articulation, as it will assist in the comprehension of this elaborate object.

Figures 4, 5 and 9 show typical external views of the coxa-trochanter articulation; Figs. 6, 8 and 11 show the

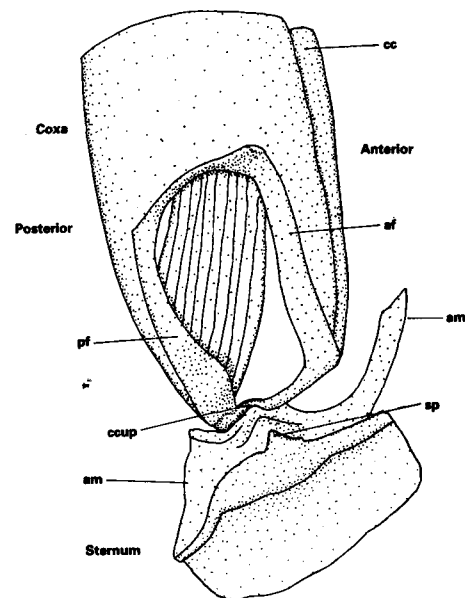


Fig. 3: Coxa-body articulation, *T. saeva*. The articular area of the sternum has been cut away, with the coxa, from the rest of the body. This is a dorsal (i.e. interior) view. The coxa is turned ventrally to show the articular area more clearly. af = anterior flange, am = arthroial membrane, cc = costa coxalis, cup = coxal cup, pf = posterior flange, sp = sternal projection.

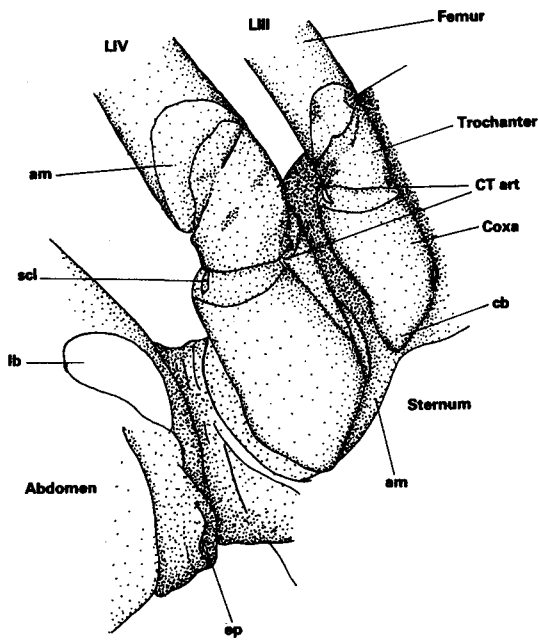


Fig. 4: Coxa-trochanter joint, *L. mactans hasselti*, third and fourth legs, ventro-lateral view. am = arthrodial membrane, cb = coxal bulge, CT art = Coxa-trochanter articulation, ep = epigyne, lb = lung book, scl = sclerite. Length of coxa, fourth leg = 1.75 mm.

internal view. The blade-like nature of the costa coxalis and the curve of the region which actually touches the trochanter can be seen (this is particularly clear in Fig. 8). The part of the trochanter in contact with the costa coxalis is also curved. This curved area of the trochanter is drawn in diagrammatic cross-section in Fig. 2a. The costa coxalis fits snugly over it, and is able to slide back and forth between two areas — (ad and pd on the figure) which appear as dips when the whole structure is dissected. These structures might equally be called small ridges, and their function is to limit the movement when the tip of the costa coxalis or the small projection in the middle of it come to lie against them. This is the mechanism by which antero-posterior movement of the joint is made.

If the costa coxalis is sectioned along the line shown

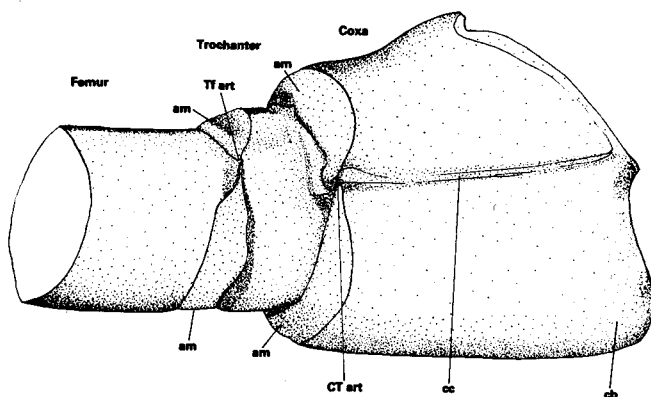


Fig. 5: Coxa-trochanter joint, *D. fimbriatus*, anterior (external) view. am = arthrodial membrane, cb = coxal bulge, cc = position of costa coxalis shown by dark line in cuticle, CT art = Coxa-trochanter articulation, TF art = Trochanter-femur articulation. Length of coxa = 2 mm.

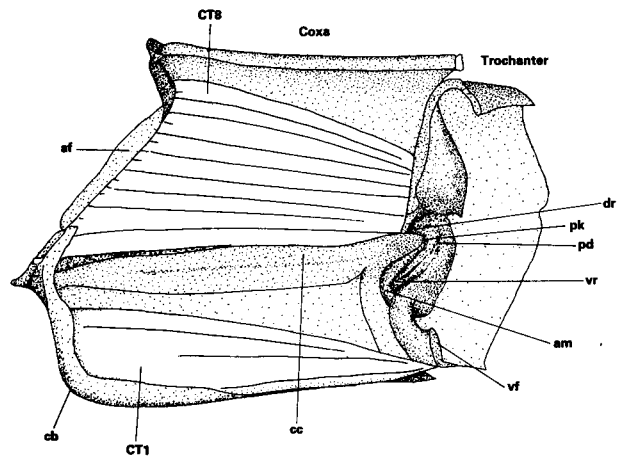


Fig. 6: Coxa-trochanter articulation, *D. fimbriatus*, internal (posterior) view. The posterior wall of the coxa, and most of the muscles have been removed. af = anterior flange, am = arthrodial membrane, cc = costa coxalis, cb = coxa bulge, CT1, CT8 = coxa-trochanter muscles, dr = dorsal raised area, pd = posterior dip, pk = posterior knob, vf = ventral flange (cut), vr = ventral raised area.

in Fig. 2a while the trochanter is kept intact, turned vertically and then rotated through 90°, Fig. 2b is obtained. This shows the two large swollen raised areas of the trochanter edge (dr and vr). The connection of the costa coxalis with the trochanter lies between them, and is such that the costa coxalis is able to move on it like a pole-vaulter's pole in its rest — the base stays in one place but the end moves. This movement is limited when the sides of the costa coxalis meet the sides of the raised trochanter areas. Situated as the articulation is, on the anterior side of the leg with these projections dorsal and ventral, this is the mechanism which produces dorso-ventral movement.

The dotted area indicates the position, in some species, of a small ventrally directed knob-like

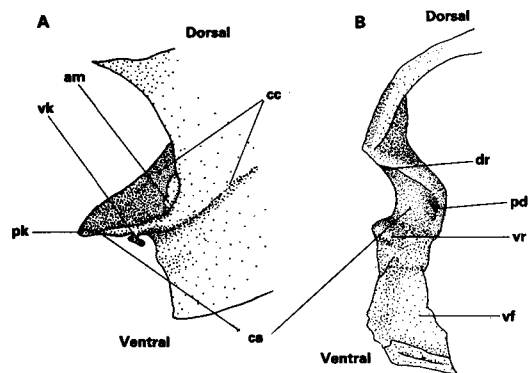


Fig. 7: Coxa-trochanter articulation, *D. fimbriatus*. This is the articulation in Fig. 6 pulled apart. The coxa has been turned over, so that the relationship between the posterior knob and the ventral knob is clear. The trochanter is turned a little so that the raised areas are obvious. **A** Coxal articular area, separated from trochanter, turned into antero-distal view; **B** Trochanter articular area, separated from coxa, turned into antero-proximal view. am = arthrodial membrane, ca = curved areas which "ride" over each other, cc = costa coxalis, dr = dorsal raised area, pd = posterior dip, pk = posterior knob (fits posterior dip), vf = ventral flange, vk = ventral knob, vr = ventral raised area.

projection of the costa coxalis, which slides over the outside ventral raised area in some situations. This lies outside the plane of the diagram (above the page).

A. diadematus deviates from this pattern in that dorsal movement is stopped, not by a swollen projection but by a pad of endocuticle lying between the costa coxalis and the trochanter (Fig. 8a: end). This is compressed on dorsal movement; when squeezed to the limit, movement stops.

In a small species, such as *A. diadematus*, it is difficult to be certain on this point but the antero-posterior movement appears to be made by rolling (like a tyre on a road), rather than by sliding (like a skater on ice) which is usual in the larger species.

Trochanter-femur joint: This joint is much the same in all species studied: a full description is found in Clarke (1984).

Femur-patella joint: This joint also shows little variation and is described fully in Clarke (1984).

Patella-tibia joint: This is a remarkable joint, showing more variation between the different legs of the same animal, than it does between species. A stout dorsal articulation consisting of a patellar peg projecting in a ventral direction into a tibial socket and held together by endocuticle is always present in all species. In the first and second legs it is the only articulation present. Anterior, posterior and a small ventral movement are made by the projection sliding in

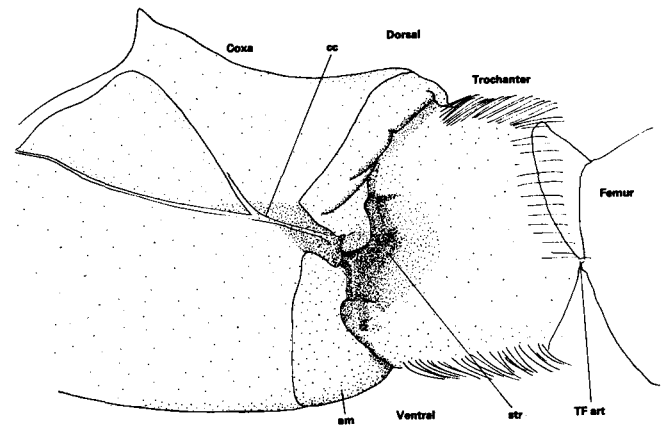


Fig. 9: Coxa-trochanter joint, *A. avicularia*, anterior view. am = arthrodial membrane, cc = dark mark showing position of costa coxalis, str = swollen raised articular area of trochanter, TF art = Trochanter-femur articulation. Length of trochanter = 1 mm.

the socket until the side of the bulge which supports the projection meets the edge of the socket (as in Fig. 13b, *A. avicularia*). The orientation of the articulation, with the tibial socket "hooked" around the ventral end of the patella peg (as in Fig. 14, *A. avicularia*) and the overhang of the patella dorsally, makes dorsal movement impossible. A small projection is present on the ventral edge of the tibia in the first and second legs: *H. venatoria*, however, is the only species studied in which a corresponding socket is found on the patella.

The third and fourth legs have a different articular structure. A stout dorsal articulation similar in form to that of the first legs, is present, forming the dorsal articulation of a flat bicondylic joint. The more ventral articulation (as in Fig. 15, *D. fimbriatus*) is smaller and simpler than the dorsal, consisting of the two thickened closely opposed podomere edges. This articulation is dorsal to the posterior patellar slit, which itself varies in structure between the first and fourth legs (Fig. 16).

Tibia-metatarsus joint (as in Fig. 19, *D. fimbriatus*): This flat bicondylic joint with the unmuscled edges dorsally and articulations laterally varies little between species, and its mechanism is very like that of the

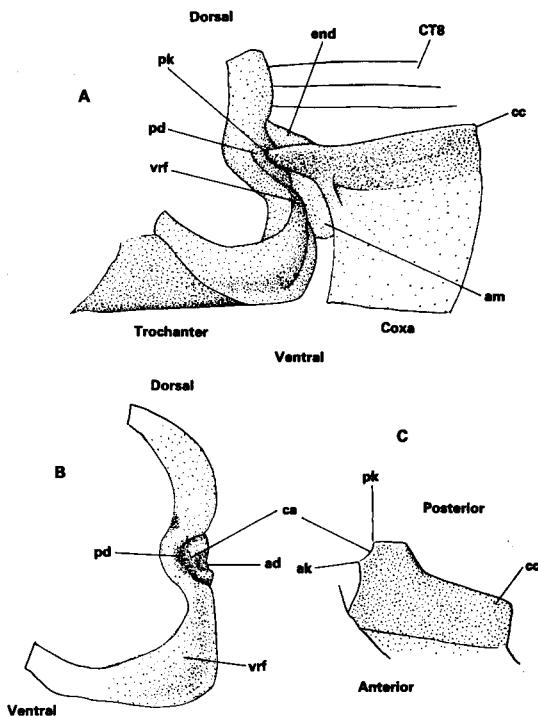


Fig. 8: Coxa-trochanter articulation, *A. diadematus*. The articulation shown in A is taken apart in B and C. **A** Internal (posterior) view of articulation; **B** Trochanter, anterior half of proximal edge; **C** Articular end of costa coxalis, ventral view. ad = anterior dip, ak = anterior knob (fits into anterior dip), ca = curved areas which "ride" over each other, cc = costa coxalis, end = pad of endocuticle, CT8 = coxa-trochanter muscle, pd = posterior dip, pk = posterior knob (fits into posterior dip), vrf = ventral raised area and flange. Width of trochanter = 0.5 mm.

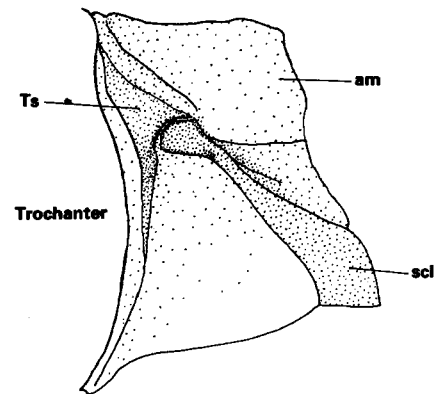


Fig. 10: Coxa-trochanter joint, *A. avicularia*, junction of sclerite with trochanter edge, postero-distal (external) view. am = arthrodial membrane, scl = sclerite (cut), Ts = sclerite at trochanter edge.

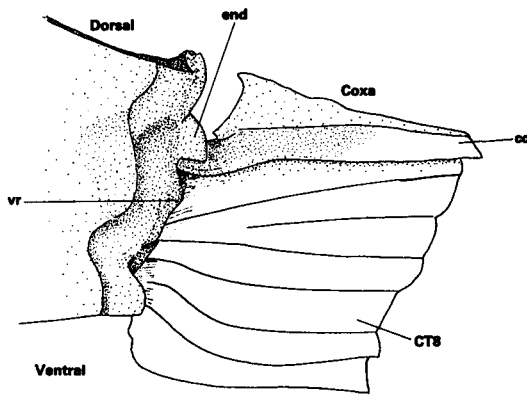


Fig. 11: Coxa-trochanter articulation, *A. avicularia*, internal (posterior) view. cc = costa coxalis, CT8 = coxa-trochanter muscle, end = pad of endocuticle, vr = ventral raised area.

femur-patella joint (see Clarke, 1984). In *A. diadematus* however, a third articulation is found between the unmsclcd edges. This consists of a simple, flattened peg fitting tightly into a socket. Its range of movement, when cut away from the rest of the joint, is the same as that of the intact joint. No definite function could be found for this structure, though it is difficult to disarticulate and may, therefore, help to hold the joint together.

Metatarsus-tarsus joint (Fig. 20, cf. Fig. 21, *L. mactans hasselti*): There is great variation between species in structure and possible ranges of movement at this joint (Fig. 1).

In *A. diadematus* the joint has a small range of movement, and there is little membrane between the

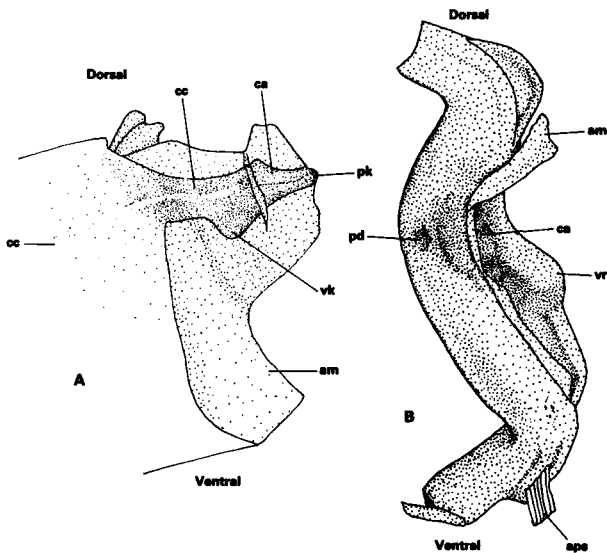


Fig. 12: Coxa-trochanter articulation, *A. avicularia*. This is the articulation in Fig. 11 taken apart. The coxa has been turned over to show the external view. The trochanter has been turned slightly to give a better view of the articular surface. **A** Articular end of costa coxalis, seen antero-distally; **B** Articular part of anterior proximal trochanter edge, seen distally (i.e. looking down the trochanter). am = arthrodistal membrane, aps = apodemes of CT1, ca = curved articular area, cc = costa coxalis, pd = posterior dip, pk = posterior knob, vk = ventral knob, vr = ventral raised area.

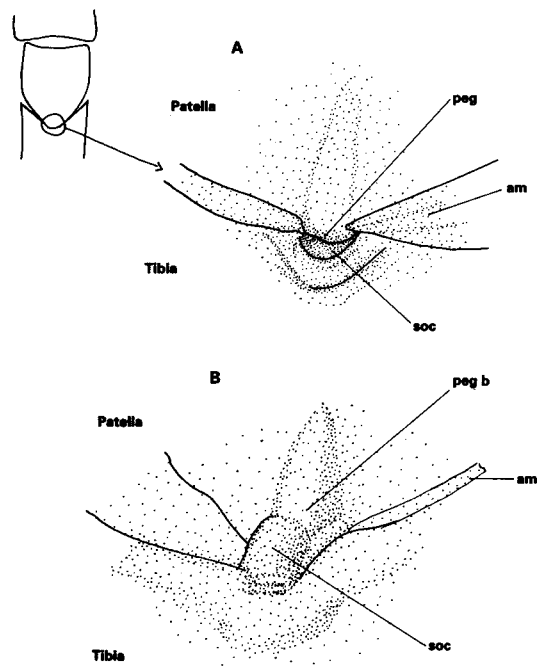


Fig. 13: Patella-tibia articulation, *A. avicularia*. **A** External (dorsal) view of dorsal articulation; **B** Ditto, internal (ventral) view. am = arthrodistal membrane, peg = patellar peg, peg b = bulging cuticle which supports peg, soc = tibial socket.

two podomeres. Dorsally the metatarsal edge is rounded and projects a little, meeting the slightly curved edge of the tarsus. Laterally, the metatarsal edge is emarginated and the emargination is occupied by a projection of the tarsus. Ventrally the metatarsal edge is large, stout and projecting, almost engulfing the tarsal edge (Fig. 20). The two podomeres are connected by arthrodistal membrane, which, though narrow, allows the small antero-posterior and dorso-ventral movements which occur.

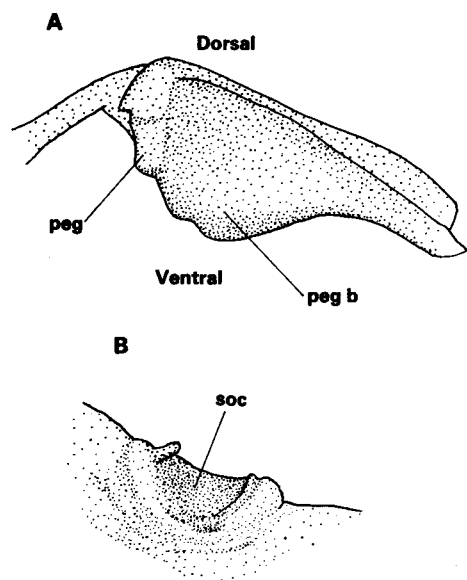


Fig. 14: Patella-tibia articulation, *A. avicularia*. **A** Patella articulation, disarticulated, seen distally (i.e. as though from along the tibia); **B** Tibial socket, disarticulated, seen dorsally. peg = patellar peg, peg b = bulging cuticle which supports peg, soc = tibial socket.

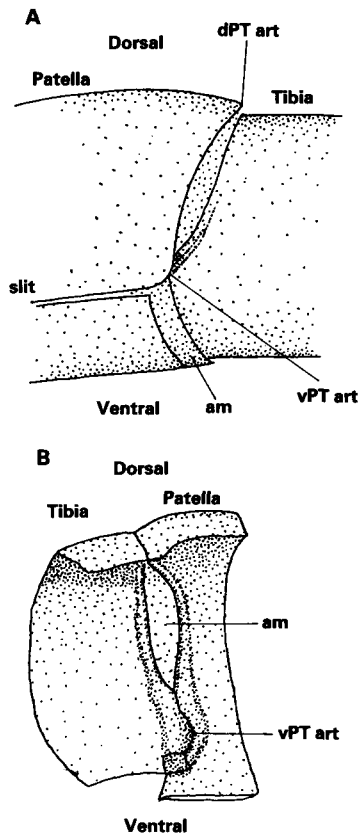


Fig. 15: Right patella-tibia articulation, *D. fimbriatus*, leg IV. **A** External, posterior view; **B** Internal (anterior) view. The anterior parts of the podomeres have been removed, together with the muscles. am = arthrodistal membrane, dPT art = dorsal patella-tibia articulation, vPT art = ventral patella-tibia articulation.

Latrodectus mactans hasselti

L. mactans hasselti is very similar to *A. diadematus* in its joint structures. The following differences were found.

The sternum-coxa articulation of the third and fourth legs does not have a stouter projection and hollow than the first and second legs. There is no third articulation in the tibia-metatarsus joint. The posterior patellar slit is as short as in *A. diadematus* but broader.

Dolomedes fimbriatus

There are four notable differences in joint structure between *A. diadematus* and *D. fimbriatus*.

Coxa-trochanter joint (Figs. 5-7): *D. fimbriatus* is large enough for one to see clearly that the costa coxalis slides over the trochanter in antero-posterior movement (see Fig. 2a). Dorsal movement, like ventral, is limited when the side of the costa coxalis, rocking on the trochanter, meets a raised area (Fig. 6). The articulation is held together by endocuticle, but this does not extend to form a pad dorsally (as in *A. diadematus*).

Besides limiting ventral movement, the stout ventral raised area (Fig. 6) has another function. There is a small projection from the costa coxalis (Fig. 7a: vk) which, though not usually in contact with the trochanter, meets and slides over the external surface of the raised area on ventral movement. The purpose of

this is not clear, though the size of this projection seems to be in direct proportion to the amount of anterior movement. *D. fimbriatus* has little anterior movement at this joint.

Patellar slit (Fig. 15): The posterior patellar slit is quite different from that of *A. diadematus* and *L. mactans hasselti*, but closely resembles that of *A. avicularia* (Fig. 18).

Tibia-metatarsus joint (Fig. 19): *D. fimbriatus*, like *A. diadematus*, possesses a third articulation within the unmscled area of the joint.

Metatarsus-tarsus joint (Fig. 22): This joint is quite different from that of *A. diadematus* or *L. hasselti* and allows a wide range of movement (Fig. 1), including a rotation about the long axis of the leg. In common with the metatarsus-tarsus joint of *T. saeva*, *A. avicularia* and *H. venatoria* (Clarke, 1984) the sclerotised parts of the articulation are not in contact in dead specimens (i.e. the joint is disarticulated). The wide ventral movement is made in this state.

When articulated (i.e. when the dorsal metatarsal projection is in contact with the tarsal raised area) antero-posterior and rotational movements are made. Both are limited by contact between the lateral surfaces of the tarsal raised area and the dorso-lateral sides of the metatarsus. The smooth curved proximal face of the tarsal raised area slides over the curved edge of the metatarsal projection. The metatarsal articular area extends internally (i.e. under the membrane and into

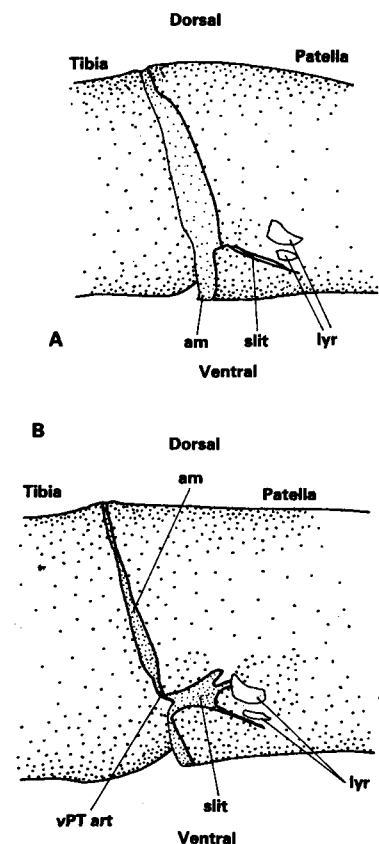


Fig. 16: Left patella-tibia joint, *A. diadematus*, posterior (external) view. **A** Leg I; **B** Leg IV. am = arthrodistal membrane, lyr = lyriform organs, slit = posterior patellar slit, vPT art = ventral patella-tibia articulation. Width of patella, leg IV = 1 mm.

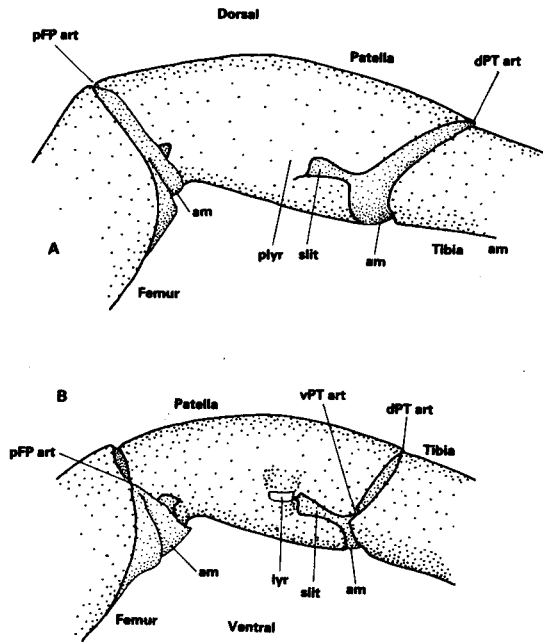


Fig. 17: Right patella-tibia joint, *T. saeva*, posterior (external) view. **A** Leg I; **B** Leg IV. am = arthroial membrane, dPT art = dorsal patella-tibia articulation, lyr = lyriform organ, pFP art = posterior femur-patella articulation, plyr = position of lyriform organs (not visible), slit = posterior patellar slit, vPT art = ventral patella-tibia articulation. Length of dorsal side of patella = 2 mm.

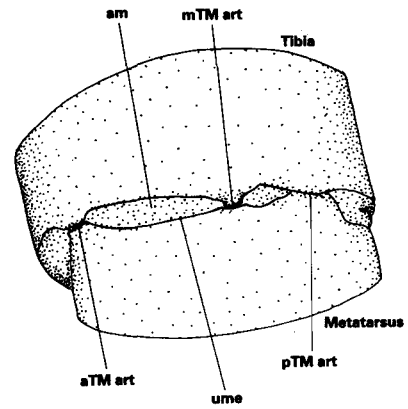


Fig. 19: Tibia-metatarsus joint, *D. fimbriatus*, dorsal view. am = arthroial membrane, aTM art = anterior tibia-metatarsus articulation, mTM art = middle tibia-metatarsus articulation, pTM art = posterior tibia-metatarsus articulation, ume = unmusled edge.

edge (described by Parry, 1957 and Bauer, 1972) very easily.

Patella-tibia joint (Fig. 17): The posterior patellar slit is different in form from that of the other species studied.

Tibia-metatarsus joint: This does not possess a third articulation on the unmusled edge.

Metatarsus-tarsus joint: This is very like that of *D. fimbriatus*.

Avicularia avicularia

This animal — much larger and only distantly related to the other species in this study, differs from them in several respects.

Coxa-body joint: This is like the other species, except that the coxal edge lacks the anterior and posterior flanges which usually support it.

Coxa-trochanter joint (Figs. 9-12): The anterior edge of the trochanter is straight, not curved as in the other species studied, and so forms sharply angled “corners” with its dorsal and ventral edges (Fig. 9). The ventral flange is absent, as is the dorsal raised area. Dorsal movement is limited, as in *A. diadematus*, by a pad of endocuticle. The ventral knob projection on the costa

the lumen of the podomere), in the form of two projections (Fig. 22c). Small projections from the tarsal raised area slide over these, but their function is not clear. It may be to limit dorsal movement by preventing the tarsus from riding up and over the metatarsus.

Tegenaria saeva

T. saeva is much like *D. fimbriatus* in its joints, but there are a few differences.

Coxa-trochanter joint: The structure and mechanism are very like those of *D. fimbriatus*, but the ventral knob projection from the costa coxalis is very small and the ventral trochanter raised area is less developed. Very little anterior movement is made.

The joint disarticulates very readily — more so than in any of the other species studied — as the trochanter splits away from the ring of sclerites on its proximal

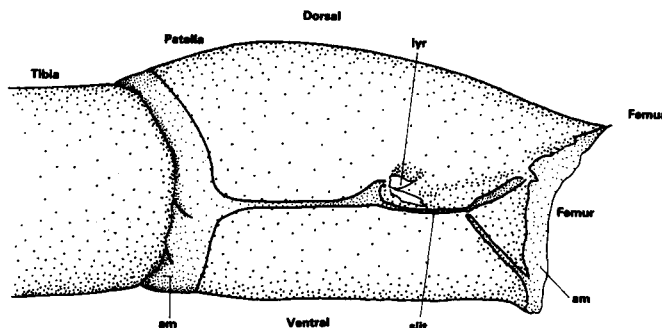


Fig. 18: Posterior patellar slit, *A. avicularia*, ventro-lateral view. am = arthroial membrane, lyr = lyriform organs, slit = posterior patellar slit. Length of patella = 2 mm.

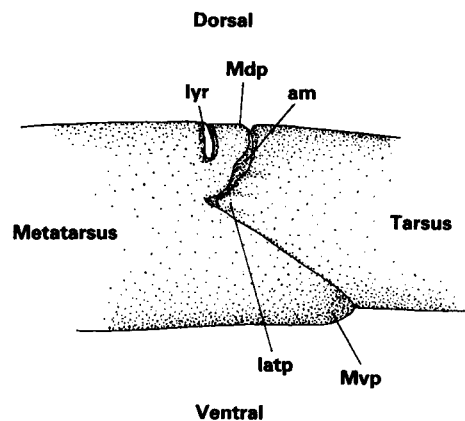


Fig. 20: Metatarsus-tarsus joint, *A. diadematus*, lateral (external) view. am = arthroial membrane, latp = lateral tarsal projection, lyr = lyriform organ, Mdp = dorsal metatarsal projection, Mvp = ventral metatarsal projection.

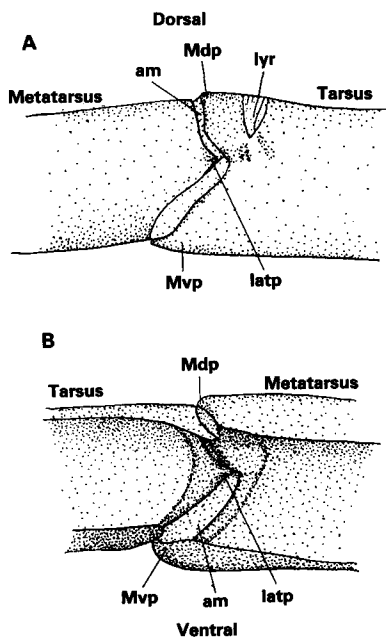


Fig. 21: Metatarsus-tarsus joint, *L. mactans hasselti*. **A** Lateral external view; **B** Lateral internal view. am = arthrodial membrane, latp = lateral tarsal projection, lyr = lyriform organ, Mdp = dorsal metatarsal projection, Mvp = ventral metatarsal projection.

coxalis is large, and *A. avicularia* has a larger anterior movement than *D. fimbriatus* or *T. saeva*.

All species studied have a sclerite posteriorly in the coxa-trochanter membrane, but in *A. avicularia* this is a particularly stout structure and is hinged to the sclerites at the posterior trochanter edge (Fig. 10).

Trochanter-femur joint: The articulations of this bicondylic joint are similar to the other species in structure but differ in position. In *A. avicularia* the articulations are found in the middle of the anterior and posterior surfaces of the joint (Fig. 9), whereas usually the articulations are situated more dorsally (Fig. 5, *D. fimbriatus*).

Patella-tibia joint: The third and fourth pairs of legs are like the first and second: no second articulation is present though there is a small projection from the tibia in the region of the posterior slit.

Metatarsus-tarsus joint (Fig. 23): This is a large complex structure. The tarsal raised area slides freely over the metatarsal articular surface. Movement stops when the sides of the tarsal raised area meet the sides of the lateral metatarsal projections. Ventral movements are made by disarticulating the joint and stopped when the ventral edges of the podomeres meet.

Musculature

Reading through the published accounts of spider leg muscles (ignoring those using cleared specimens, a totally unreliable method) one notices two things. Firstly that there is a basic pattern in the musculature, and secondly, how difficult it is to homologue the muscles from one paper to another. Even when the problems caused by each author using his own naming scheme are overcome, a residual area of confusion remains. This study, the first to compare the intrinsic

leg muscles of several different species (see Palmgren, 1978 for the extrinsic muscles), shows that this confusion has a basis in fact for none of the species studied has a musculature identical to that of any of the others.

The basic musculature is shown in Figs. 24-28. The following variations occur:

Coxa-trochanter muscles (Fig. 24): These vary more in size than in structure. However, CT2 is very variable in origin. In *A. avicularia* it originates along the entire length of the posterior coxal wall, in *D. fimbriatus* from the distal coxal wall only, and in *L. mactans hasselti* from the dorsal part of the coxal bulge. The posterior coxal muscle (CT3-5, Fig. 24a) comprises 3 discrete muscles in *D. fimbriatus* but they are fused in *L. mactans hasselti* and *T. saeva*. CT3 and CT4 are fused in *A. avicularia*, which has 2 extra muscles. One originates on the ventral side of the costa coxalis and inserts on the trochanter edge between the insertion of CT1 and the articulation. The other originates on the ventral anterior proximal coxal wall, just under the end of the costa coxalis. These two muscles were also found by Ruhland & Rathmayer (1978) in *Dugesiella* and by Dillon (1952) in *Eurypelma* and seem to be a

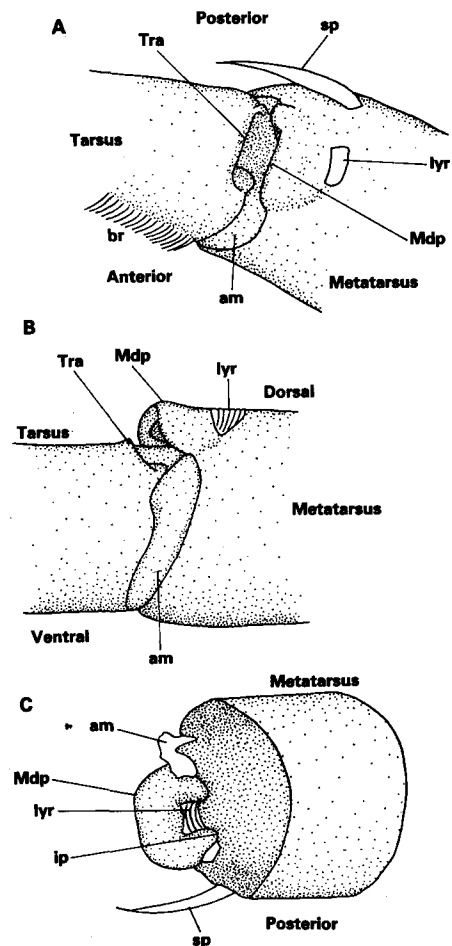


Fig. 22: Metatarsus-tarsus joint, *D. fimbriatus*. **A** Dorsal external view; **B** Lateral external view; **C** Ventral internal view, metatarsus, separated from tarsus to show inside of dorsal metatarsal projection. am = arthrodial membrane, br = bristles, ip = internal projections, lyr = lyriform organs, Mdp = dorsal metatarsal projection, sp = spine, Tra = tarsal raised area.

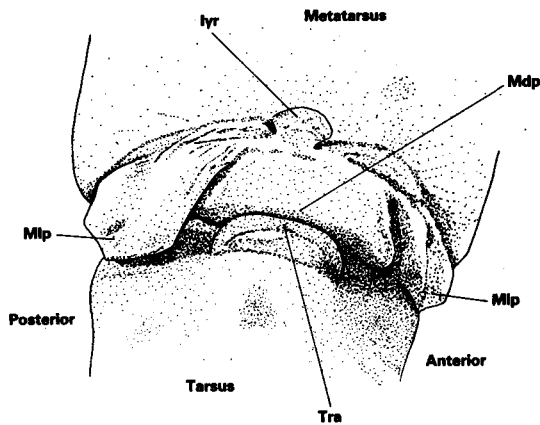


Fig. 23: Metatarsus-tarsus joint, *A. avicularia*, dorsal (external) view. lyr = lyriform organ, Mdp = dorsal metatarsal projection, Mlp = lateral metatarsal projection, Tra = tarsal raised area.

widespread feature of the Orthognatha.

Trochanter-femur and femur-patella muscles: These are much the same in all the spiders examined. *A. avicularia* is unusual in having a pair for FP3, which is a single muscle in the other species.

Trochanter-patella muscles: Considerable variation is found in this group of muscles. Basically, the trochanter-patella muscles originate on the anterior ventral trochanter edge and insert on the arcuate sclerite (this is a sclerotised plate in the membrane near the ventral patella edge (Fig. 26)).

Two distinct patterns are detectable: a large and

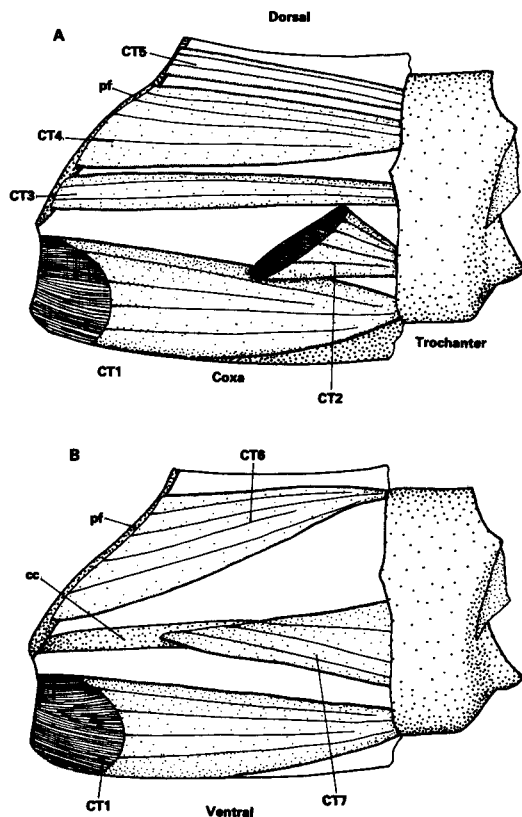


Fig. 24: Diagram of coxa-trochanter muscles, *D. fimbriatus*, posterior view. **A** Posterior-most layer of muscles, seen with wall of coxa removed; **B** As **A**, but with CT3-5 removed. cc = costa coxalis, CT1-7 = coxa-trochanter muscles, pf = posterior flange.

apparently powerful muscle complex found in *A. avicularia* and *D. fimbriatus* (and *H. venatoria*, see Clarke, 1984) and a much smaller, simpler arrangement found in *T. saeva*, *A. diadematus* and *L. mactans hasselti*. These arrangements are so different that no homologies can be found between them. The shape of the arcuate sclerite varies with the muscle structure (Fig. 27).

Patella-tibia muscles: These muscles vary more between the different legs of one animal, than between species. Three muscles are present in the first and second legs, but only two in the third and fourth legs; PT1 is not present and no muscles attach to the posterior edge of the tibia. This is also true of the fourth leg of *A. avicularia*, although a flat bicondylic joint is not present here.

Tibia-metatarsus muscles (Fig. 28): These show little variety beyond a difference in relative size. The dorsal proximal posterior muscle (TiM1) is very large in *L. mactans hasselti*, where its origin occupies not only the tibial flange but also the posterior tibial wall. In *A. avicularia* and *L. mactans hasselti* the two muscles which each attach to the long apodemes are large and merge into each other, whereas in the other species they are separate. In *A. avicularia*, these long apodemes are attached to a plate in the membrane similar to the arcuate sclerite.

Metatarsus muscles (Fig. 28): These vary only in size between the species studied.

Discussion

The methods used in this study do not, of themselves, give rise to any problems. However, there is always a difficulty in interpreting dissections of arthropod muscles. Arthropod muscles are not sheathed, and only space separates the fibres of different muscles. The origins or insertions are not always distinct, in that the origins of two muscles arising from the surface of a podomere may “run into” each other. The insertions may also be continuous, along the edge of a podomere or apodeme. In such a case it is only comparisons with other species which suggest that two muscles may be present. In other cases

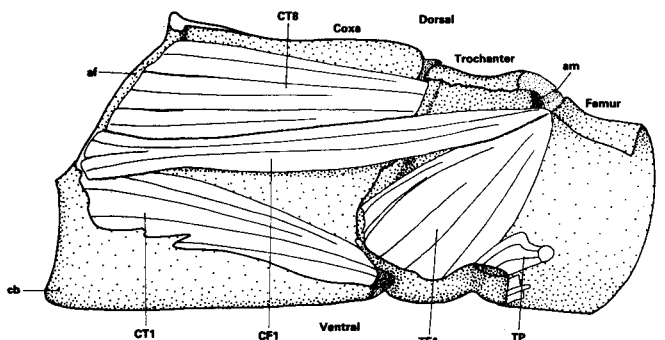


Fig. 25: Coxa-femur muscles, *D. fimbriatus*, posterior view. The posterior parts of the coxa, trochanter and femur, with most of their associated musculature, have been removed. af = anterior flange, am = arthrodial membrane, cb = coxal bulge, CF1 = coxa-femur muscle, CT1 & 8 = coxa-trochanter muscles, TF1 = trochanter-femur muscle, TP = trochanter-patella muscles, cut.

(where either the origin or insertion is not completely continuous) the interpretation — one muscle or two — is subjective, and this leads to difficulties when comparing the descriptions of different authors.

Subjective interpretations also occasionally cause problems with skeletal structures. Palmgren (1981) describes the coxa-body joint of *D. fimbriatus* as having two articulations: a posterior one (also described here, p. 38) and a looser anterior articulation. The anterior coxal edge comes very close to the sternal edge when anterior and ventral movements are made together, and the coxa may rest on the sternal edge. I would not describe this contact as an articulation, for no special skeletal structures are present to limit or assist movement.

As was expected when this study began, animals following different habits have different structures, and this allows the functions of some of the structures to be deduced.

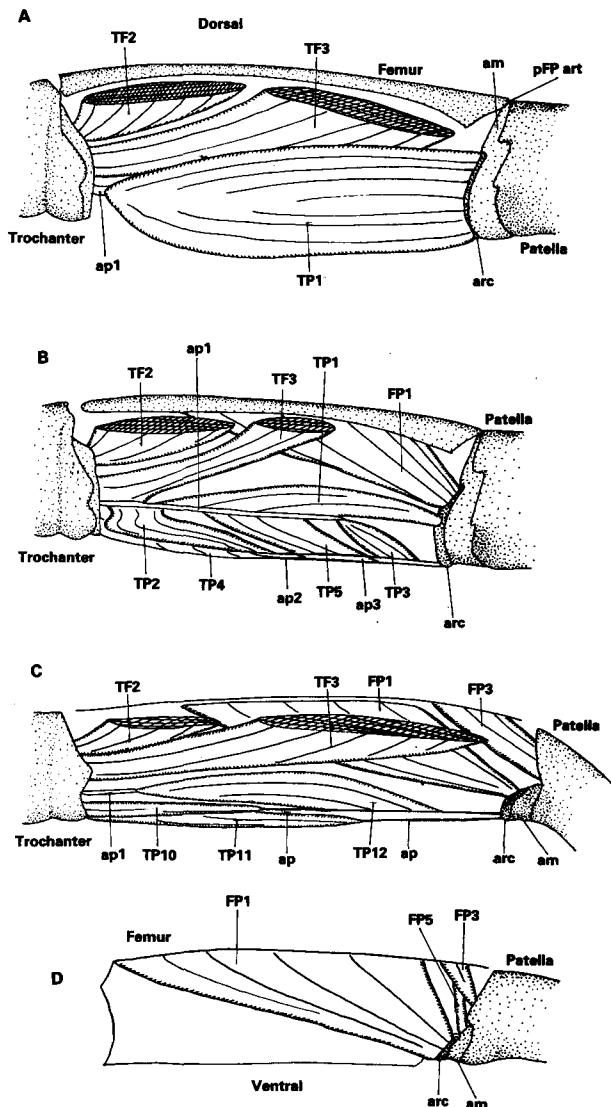


Fig. 26: Femur muscles (diagrammatic). **A** *D. fimbriatus*, postero-ventral view, with posterior wall of femur removed; **B** As A, with most of TP1 removed; **C** As A, *T. saeva*; **D** As C, with TP muscles removed. am = arthrodistal membrane, arc = arcuate sclerite, ap1-3 = apodemes, FP1-5 = femur-patella muscles, pFP art = posterior femur-patella articulation, TF2-3 = trochanter-femur muscles, TP1-12 = trochanter-patella muscles.

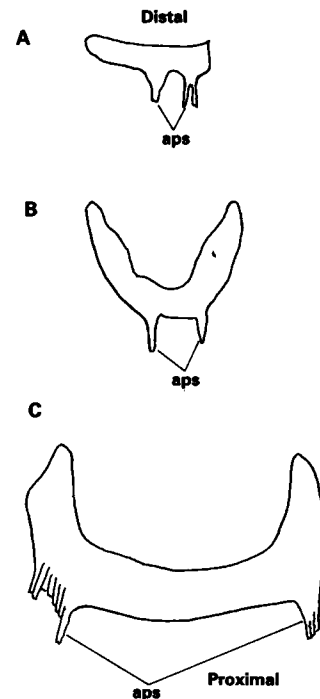


Fig. 27: Arcuate sclerite, removed from the animal, seen ventrally. **A** *L. mactans hasselti*; **B** *T. saeva*; **C** *A. avicularia*. aps = apodemes.

The difference in relative size of the trochanter-patella muscles correlates with differences in prey capture. *A. avicularia*, *D. fimbriatus* and *H. venatoria* (Clarke, 1984) use the grasping method of prey capture (which involves a simultaneous and forceful depression of the trochanter-patella muscles) and have a large complex of TP muscles. The species which do not hold prey with their legs, *A. diadematus*, *L. mactans hasselti* and *T. saeva*, have fewer, smaller TP muscles.

Though the trochanter-patella muscles vary greatly in size and form, the joints which they operate do not, having the same articular structures and ranges of movement in all the species studied. Conversely, the muscles operating the metatarsus-tarsus joint vary only a little in size between species, and not at all in form. The articulation and range of possible movement does vary greatly.

Though the trochanter-femur and femur-patella joints are moved by other muscles besides the TP complex, and the metatarsus-claw muscles have other functions besides moving the metatarsus-tarsus joint, this does indicate that the form of articulations and the configuration of muscles and the range of movement should not be thought of as essentially inter-dependent.

Another illustration of this point is provided by the muscles of the patella-tibia joint. The muscle which attaches to the posterior patella edge (PTi1) where the joint has only a dorsal articulation, is absent when two articulations are present. However, it is also absent in the fourth leg of *A. avicularia*, although only one articulation is present.

Posterior movement is made by both the single (monocondylar) and flat bicondylar patella-tibia joints. In the former case it is presumably made by the muscle PTi1, but in the latter the means are uncertain. The movement may be passive, or it may be made by the

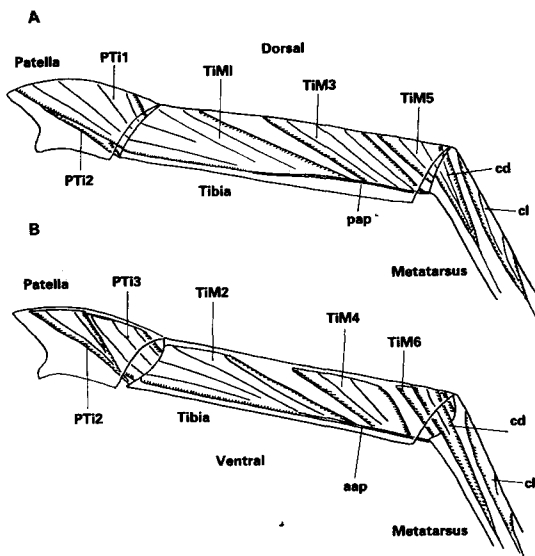


Fig. 28: Patella, tibia and metatarsus muscles (diagrammatic), posterior view. **A** Posterior muscles, seen as though cuticle were transparent; **B** Anterior muscles. Posterior muscles have been removed. aap = anterior apodeme, cd = claw depressor, cl = claw levator, pap = posterior apodeme, PTi1-3 = patella-tibia muscles, TiM1-6 = tibia-metatarsus muscles.

type of hydrostatic "pocket" extension described by Frank (1957). Frank proposed that the ample arthrodistal membrane found ventrally in the femur-patella and tibia-metatarsus joints (these are flat bicondylar joints) forms pockets which, when filled with blood under pressure, push upon the patella or metatarsus and so extend the joint. The pocket, being as far away from the articulations as possible, gains the maximum leverage for the hydrostatic pressure. Ample membrane is also present anteriorly at the patella-tibia joint and may be used to exert hydrostatic pressure at this joint.

The patella-tibia joint shows that a monocondylic joint can become bicondylic quite easily. It seems probable from this study (but not certain) that the monocondylic joint is the original condition, since the dorsal articulation is always more strongly developed in the bicondylar joints. The lack of the muscle PTi1 in the fourth leg of *A. avicularia* and the absence of a flat bicondylar joint probably represents a half-way stage between the mono- and flat bicondylar joint, but gives no indication of which of those two conditions is the original.

The variation in movement and structure at the metatarsus-tarsus joint is associated with life on a thread web. *A. diadematus* and *L. mactans hasselti* both climb on a scaffolding of single silk threads, gripped by the claws at the limb tip. For this a mobile, relatively unmusclad joint (such as that of *D. fimbriatus*) is a disadvantage. When the web vibrates the foot would be thrown around relative to the metatarsus. The situation may be likened to that of a skater, whose ankle needs the support of a rigid boot. This being so, why is there any movement at the joint at all? The probable answer is given by Walcott & Van der Kloot (1959). They found that the lyriform organ always found on the dorsal side of the metatarsus near the joint (see Figs.

20-23) is receptive to air-borne vibrations, and is more sensitive when the tarsus is intact. The small movements allowed by the joint are necessary to amplify the vibrations. If this hypothesis is correct, it is similar to the situation in the mammalian ear, where the three small bones of the middle ear were formerly the articulation of the reptilian jaw with the skull.

It was proposed (Clarke, 1984) that the long thin slit in the posterior side of the patella of *H. venatoria* is also an amplifier, feeding torsion stresses to the lyriform organs associated with the slit before these stresses become dangerous. The differences in form found in this study do not affect this hypothesis, since a short fat slit in a tube also moves when that tube is twisted, a movement which amplifies the stress. The reason for the variation in form is not known, but it is clearly associated with the food capture method. The graspers *A. avicularia*, *D. fimbriatus* and *H. venatoria* have long thin slits, the silk throwers *A. diadematus* and *L. mactans hasselti* have short fat slits. The lunger, *T. saeva*, comes in between.

As was hoped, the functions of some structures — in particular, the trochanter-patella muscles — have been deduced by comparison and more has been learned about joint structures in arthropods. It has been shown that joint configurations are not as rigid as is often supposed and that articular structures and muscular configurations enjoy a degree of independence.

Acknowledgements

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