

On the relationship between structure and function in the leg joints of *Heteropoda venatoria* (L.) (Araneae: Eusparassidae)

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Summary

The limb joints of *Heteropoda venatoria* (L.) are described and shown to be highly complex. Their adaptations for producing the different ranges of movement seen at each joint are explained. Of particular interest are the two disarticulatable joints and the coxa-trochanter joint which is a structure of formidable complexity.

The leg muscles are described and a new system of nomenclature is proposed.

Introduction

Little attention has been given to the detailed anatomy of articular structures in arthropods, although as exoskeletal jointed limbs are the fundamental characteristic of this taxon, a study of them would be valuable to our understanding of the group. The reason for the lack of interest seems to be the appearance of joints in cleared specimens (see, for example, Couzijn, 1976), which shows articulations consisting of two opposing areas of cuticle, somewhat shapeless and more heavily sclerotised than the rest, offering little scope for study. Yet a few studies, such as that of Bennet-Clark (1975) on the locust 'knee', show that arthropod articulations may be complex and highly adapted. Spiders were chosen for further investigations of joints because the group has been largely ignored by previous investigators of comparative functional morphology.

An examination of articulations alone would take them out of the context of the skeleto-muscular

system in which they function and therefore it was decided to pose the following four questions: What angles of movement can be made by each joint? What are the articular (and other joint) structures which make these movements? What muscles are associated with each joint? What use is made of the different movements in the life of the animal?

Methods

Specimens of the eusparassid *Heteropoda venatoria* (L.), a suitably large animal, were used for this study. The maximum angles of movement of each joint were measured using a 360-degree protractor. Specimens which had just died were placed with the joint in question on the centre of the protractor. The distal podomere was moved until resistance to the movement was encountered and the angle subtended between the podomeres was read off. The author believes this method to be accurate to within five degrees.

Joint structures and muscle configurations were investigated by dissecting specimens preserved in 70% alcohol. After muscles and other soft tissues had been cut away the joints were moved so that the part played by each structure in making the movements could be seen.

Eight-millimetre films of the animals running, walking, jumping and catching their prey were studied carefully frame by frame.

Definition of terms

Within the context of this paper the words 'joint' and 'articulation' have the following meanings. A joint is an area of discontinuity in the skeleton, used by the animal to move the skeletal elements relative to each other. An articulation is an area of contact between the stiff skeletal elements within a joint and is in some way adapted to allow movement. A joint is disarticulated when the components of the articulation become temporarily separated.

Muscle nomenclature

It is with considerable reluctance that I add another system of muscle nomenclature to the sizeable list of those already in use — each author has used a different scheme and none of them is suitable for comparative work.

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Until the 1950s authors used a functionally based system (e.g. Brown, 1939; Dillon, 1952). As there was no evidence as to function, this was not accurate. Parry (1957) therefore used a system of numbers. Although accurate, such a system cannot be used in comparative work, since the discovery of a new muscle in another animal leads to the muscles in a podomere being called, for example, 4, 5, 31, 6. It is also (as Palmgren, 1978, remarks) very difficult to remember. Palmgren's (1978) alternative was a purely anatomical system: e.g. *M. tergo-coxalis anterior profundus*. In animals with few muscles such a system is excellent, but spiders have too many – there are three coxalis muscles, hence the need for descriptors creating very long names.

I use a system in which the shortest unique abbreviation of the origin and insertion is supplemented by a number if there is more than one muscle between those podomeres; e.g. FP2 = second femur-patella muscle, CoTr1 = first coxa-trochanter muscle.

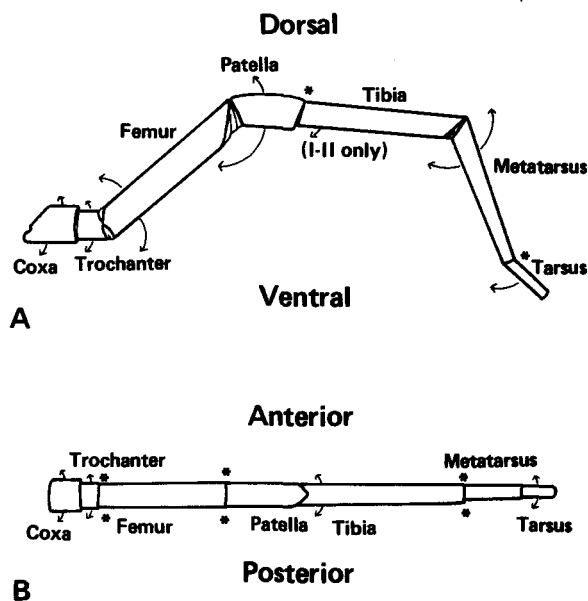


Fig. 1: *Heteropoda venatoria*, leg I, ranges of movement. **A** Posterior view of leg in the usual standing position; **B** As above, dorsal view. Arrows indicate the furthest movement which can be made by the podomeres at their bases if the proximal podomere is held still. Asterisks indicate that no movement can be made in that direction. Length of leg I = 4.2 cm.

Although containing less information than one would like, this system is easy to use, having the advantage of being the same in text and on diagrams, and it has no important disadvantages.

Results

Movements

The ranges of dorso-ventral and antero-posterior movements are shown in Fig. 1. A small rotation about the long axis of the leg occurs as the coxa moves posteriorly on the body. The tarsus is also able to make a small rotation on the metatarsus.

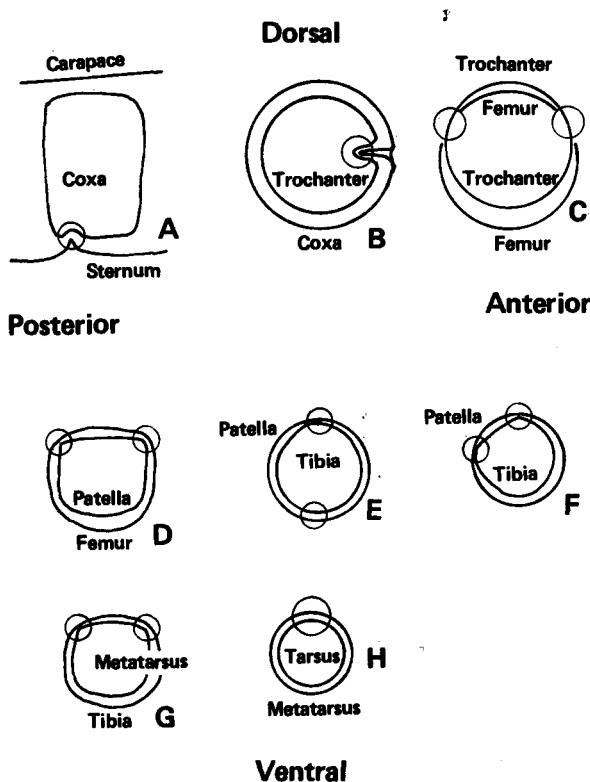


Fig. 2: Diagrammatic cross-sections of the leg joints. Small circles indicate the positions of the articular areas. **A** Coxa-body joint; **B** Coxa-trochanter joint; **C** Trochanter-femur joint; **D** Femur-patella joint; **E** Patella-tibia joint, legs I and II; **F** Patella-tibia joint, legs III and IV; **G** Tibia-metatarsus joint; **H** Metatarsus-tarsus joint.

Articular structures

These were found to be highly complex, and I shall therefore begin, not with the most proximal, but with the simplest.

Trochanter-femur joint

The profile (i.e., a diagrammatic cross-section) of the podomeres at the joint is shown in Fig. 2c. The external appearance of the articulations is shown in Fig. 3. As the femur approaches its most dorsal (elevated) position, its dorsal edge moves under the dorsal edge of the trochanter, which thus comes to rest against the dorsal surface of the femur. The curve of the trochanter edge fits exactly over the femur. In the extreme ventral (depressed) position it is the trochanter edge which moves under the femur. The ventral edge of the femur rests against the trochanter bulge (Fig. 3), covering the lip (Fig. 3) completely.

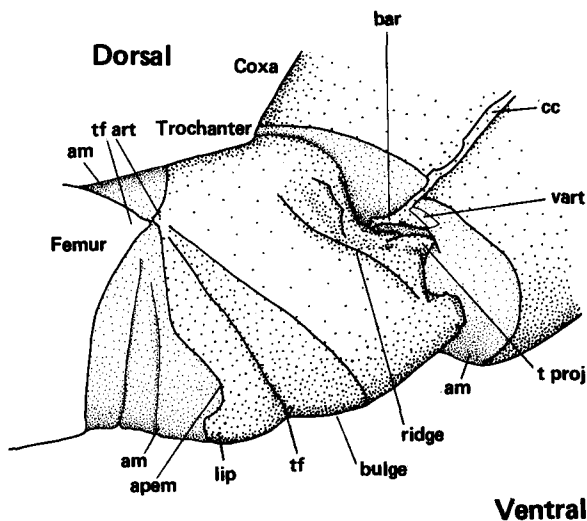


Fig. 3: Anterior view of trochanter. am = arthroial membrane, apem = emargination associated with apodeme of TrP1 muscle, bar = end of costa coxalis, bulge = ventral bulge of trochanter, cc = dark mark on cuticle indicating internal position of costa coxalis, lip = projecting edge of ventral trochanter, tf = dark mark on cuticle indicating internal position of trochanter flange, tf art = anterior trochanter-femur articulation, t proj = ventral projection of trochanter, vart = ventral articulation of coxa. Length of trochanter = 1.75 mm.

Externally the articulation seems to consist of two tiny pegs, one on each podomere, which touch. Internally, the articulation appears as a thick strap of tough, but flexible, material, which, for convenience, I shall refer to as endocuticle. This endocuticle covers the articulation and holds it together, bending as the joint is moved. Movement is limited, not by the flexibility of the endocuticle, but by the following mechanism. The endocuticle of the

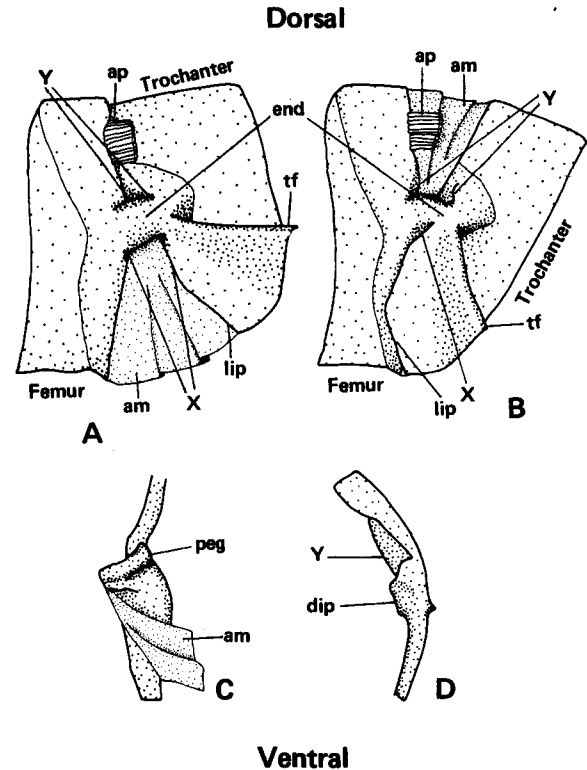


Fig. 4: Trochanter-femur articulation. **A** Internal view, nearing full extension, the surrounding cuticle cut away; **B** As above, flexed; **C** Trochanter peg, the femur and endocuticle removed, looking as though down the femur; **D** Femur socket, separated from trochanter and membrane, seen as though down the trochanter. am = arthroial membrane, ap = cut apodemes (TrF1 and CoF1), dip = femur socket, end = endocuticular strap, lip = projecting ventral edge of trochanter, peg = trochanter peg, tf = trochanter flange (cut), Y-Y = areas of trochanter and femur which meet to limit dorsal movement, X-X = as above, ventral movement. Articular area approx. = 0.05 mm.

articulations is much thicker than that lining the cuticle as a whole. In consequence it bulges into the lumen and the sides of these bulges of endocuticle limit movement (see Fig. 4). When the femur moves dorsally the femur edge, as stated earlier, moves under the trochanter edge and there it comes into contact with the dorsal side of the endocuticular bulge. This stops further movement. On ventral movement the trochanter edge moves under the femur, where it meets the ventral side of the endocuticular bulge.

When the two podomeres are separated the trochanter is found to have a small rounded peg and the femur a shallow rounded dip on their respective edges (Fig. 4c, d). Rejoining the podomeres suggests that the peg rolls around the socket as the joint moves. The arthrodistal membrane does not appear to play any part in the articulation, which is held together by the endocuticle surrounding it.

Patella-tibia joint

The principal articulation of this joint is situated in the dorsal mid-line (Fig. 2e, f). The articulation and its mechanism are similar to one of the trochanter-femur articulations, and it is the difference in orientation, rather than in structure, which allows it to produce antero-posterior instead of dorso-ventral movements.

The tibial edge moves inside the patella on both anterior and posterior movements and comes to rest on the endocuticular bulge surrounding the peg-like projection of the patella articular area. This peg fits into a dish-like socket on the tibia. The patella-tibia joints of the first and second legs can also make a small dorso-ventral movement. This seems to be limited by the ventral edge of the tibial dish meeting the ventral part of the patella peg.

On the ventral edges of the two podomeres there is a rudimentary articulation (Fig. 2e). A projection from the tibia fits into a small socket on the edge of the patella when the joint is at its most ventral (flexed) position (Fig. 5). Otherwise the two podomeres are separated by membrane.

The third and fourth legs have a different second articulation (Fig. 2f). This is a close permanent contact between the two podomeres, situated on the posterior face of the leg (dorsal to the patella slit,—

Fig. 5). Between the main dorsal articulation and this smaller simpler posterior one, the podomeres are flat and the membrane narrow; this is effectively a hinge joint. Dorso-ventral movements are not made by the third and fourth legs.

Femur-patella and tibia-metatarsus joints

These two joints are similar in all essentials. Dorsally the podomeres are flattened and have only a little membrane between them. Laterally and ventrally, on the other hand, there is ample membrane, regularly folded. Laterally the podomere edges are straight, particularly in the distal podomere. Ventrally the proximal podomere is extensively emarginated in a shape which allows it to fit exactly against the ventral side of the distal podomere, on extreme ventral (flexor) movement. This feature is particularly prominent in the femur. These are hinge joints with two articulations, one at each end of the dorsal hinge line (Fig. 2d, g). A peg and socket structure is discernible, but the greater part of the articular structures are concerned with limiting the movement. The socket is long and shallow (like a piece of guttering) and the long shallow peg fits into it.

Dorsally the femur rises above the patella (Fig. 6). There is a small raised area of cuticle on the dorsal surface of the patella near the articulation and this comes into contact with the raised area of the femur

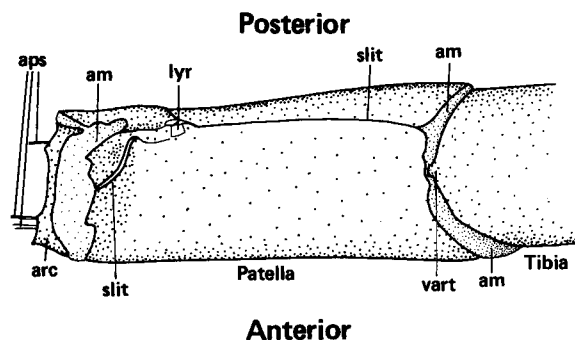


Fig. 5: Ventral view of patella, leg I. am = arthrodial membrane, aps = apodemes of TrP muscles, arc = arcuate sclerite, lyr = lyriform organs, slit = membranous slit, vart = ventral patella-tibia articulation. Length of patella = 4.25 mm.

on extreme dorsal (levator) movement, limiting its extent. On extreme flexor movement the lateral edge of the patella meets the shallowly thickened endocuticle of the femur edge (Fig. 7). In so far as can be seen (the endocuticular thickenings of the patella obscure part of the action), the peg rolls around the socket between the two extreme positions.

The tibia-metatarsus joint is similar, but less extreme in the shapes of the various parts, and has less ventral and more dorsal movement than the femur-patella joint (Fig. 1).

Coxa-trochanter joint

This is a complex structure. The trochanter is smaller in diameter than the coxa and is separated from it by arthroial membrane. The membrane is approximately equal in extent all around the trochanter. The single anterior articulation (Fig. 2b) is formed between a projection of the coxa and the thickened edge of the trochanter. The projection is not a simple 'finger' of cuticle, however, but the end of a shelf-like internal growth of the anterior coxal wall, usually referred to as the costa coxalis (Fig. 3). This is situated longitudinally in the podo-

mere, and tapers distally to proximally, being deepest at the articulation.

The articulation is formed from the innermost portion of the distal end of the costa coxalis (Figs. 3, 8). This is curved (Fig. 9a) and thus fits over the curved, thickened edge of the trochanter (Fig. 9b). This close fit enables the coxa to slide over the trochanter, the orientation being such that antero-posterior movement of the joint is produced.

Posterior movement is limited when the tip of the costa coxalis slides into a small dip on the side of the trochanter thickening (Fig. 9). The limiting mechanism of anterior movement cannot be seen clearly as the bulge of the trochanter (Fig. 3) conceals the joint when in the anterior position. The secondary (ventral) articular projection of the coxa slides over the ventral trochanter projection (Figs. 3, 8, 9) in anterior and ventral movement, but is not in contact with it during more dorsal movements.

Dorso-ventral movement occurs when the coxal projection rocks on the trochanter in a plane perpendicular to the sliding antero-posterior movements. The extent of this rocking is limited when the sides of the costa coxalis meet the steep straight sides of

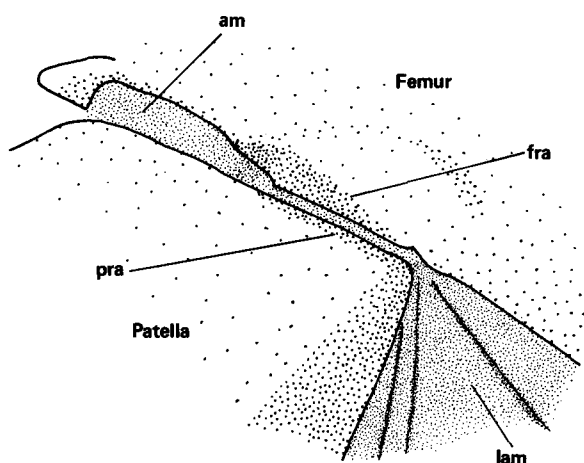


Fig. 6: Oblique dorsal view of femur-patella joint. Only one articulation can be seen clearly from this angle. am = arthroial membrane, fra = femur raised area, lam = lateral arthroial membrane, pra = patella raised area. Width of femur approx. = 2 mm.

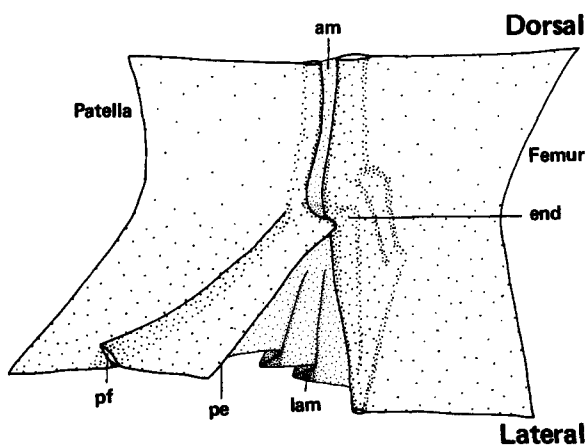


Fig. 7: Internal view of one femur-patella articulation. am = arthroial membrane, end = endocuticular bulge, lam = lateral arthroial membrane, pe = straight stiff edge of patella, pf = lateral patella flange (cut). From cut dorsal edge of femur to articulation approx. = 0.5 mm.

the sliding area (Fig. 9b). The angle and smoothness of the sides of the bulges allows an exact fit with the flat sides of the costa coxalis.

The articulation is bound together internally by thick flexible endocuticle. Some sclerites were observed in the trochanter which seem to be similar in structure and function to those described by Parry (1957) and Bauer (1972), i.e. they are part of the autotomy mechanism of the joint. No detailed study was made of them.

Metatarsus-tarsus joint

This joint is usually found to be disarticulated in preserved specimens. It disarticulates without hindrance, and in this state moves freely in all directions to the limits of the arthrodial membrane, which is thicker here than at the other joints.

Unlike the other joints, the articular structures lie entirely outside the arthrodial membrane. Dorsally the metatarsus has a large projection of flexible

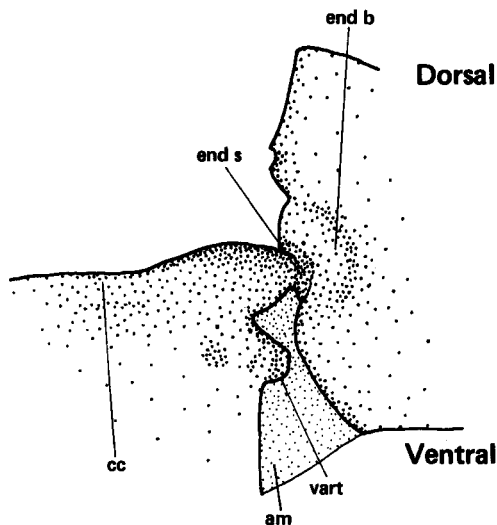


Fig. 8: Coxa-trochanter joint, internal view. Most of the trochanter and coxa are removed. am = arthrodial membrane, cc = costa coxalis, end b = endocuticle covering bulge of trochanter which surrounds articulation, end s = strap of endocuticle holding articulation together, vart = ventral articulation of coxa.

cuticle. This is pointed at the end and bends downwards, forming a hook (Fig. 10a). This projection articulates with a dorsal raised area on the tarsus. The side of this swelling facing the metatarsal projection

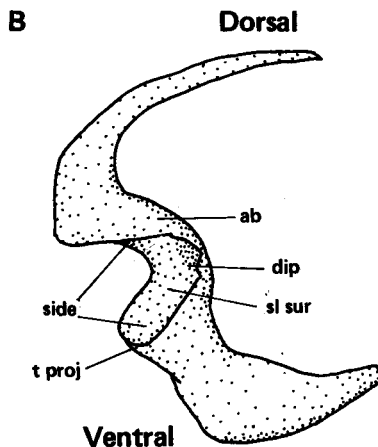
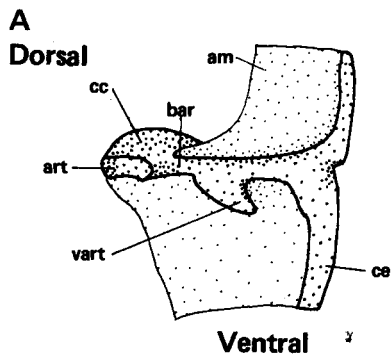


Fig. 9: Coxa-trochanter joint, disarticulated, external view. **A** Coxa articulation with trochanter removed, viewed as though looking down the trochanter towards the coxa; **B** Trochanter articulation with the coxa, with coxa and posterior part of trochanter removed, seen obliquely as though from coxa. ab = articular bulge of trochanter, am = arthrodial membrane, art = area of costa coxalis that fits over sliding surface of trochanter, bar = end of costa coxalis, cc = costa coxalis, ce = anterior coxa edge, dip = dip into which tip of coxa articulation slides, side = sides of articular curve which meets sides of costa coxalis, sl sur = sliding surface, t proj = ventral projection of trochanter, vart = ventral articulation of coxa. Width of trochanter approx. = 1.5 mm.

is smooth, and hollowed into a curve. If the joint is moved dorsally it articulates, the metatarsal projection making contact with the tarsal hollow and curling into it, i.e. the projection bends around the curve of the hollow. The hook is large enough to prevent the projection from 'missing' the hollow and slipping over the top when metatarsus and tarsus first meet.

The metatarsal projection turns in the tarsal hollow to allow antero-posterior movements. The lateral sides of the tarsal swelling meet the dorsal edges of the lateral metatarsal projections (Fig. 10a), thereby limiting the extent of the antero-posterior movements. The metatarsal projection may also slide to and fro along the length of the hollow, whose orientation is such that a rotation about the long axis of the leg is produced. This movement is also limited by contact between the lateral sides of the tarsal swelling and the edges of the lateral metatarsal projections.

Coxa-body joint

Remarkably, this joint is loosely articulated. A small projection from the sternum is separated by an expanse of thick membrane from an equally small hollow on the posterior side of the ventral edge of the coxa (Fig. 2a).

It is not clear whether these sclerotised areas ever meet. No other articular structure is present, the coxa being separated by membrane from the carapace and pleuron. Movement is limited by the legs on either side (or by the abdomen and palps in the fourth and first legs respectively), by contact between the sternum and coxal bulge (Fig. 13) ventrally and by the carapace dorsally.

Other cuticular structures

A number of non-articular structures are associated with the joints and muscles.

Several joints have inwardly projecting ridges of cuticle situated on one or other of the podomeres. The most prominent are the anterior and posterior edges of the coxa (Fig. 12) and those of the proximal tibia.

These ridges have muscles attached to them on both sides. The dorsal and lateral edges of the proximal patella and metatarsus have similar projec-

tions (Fig. 7) and these regions of the podomeres are more resistant to deformation than the 'ordinary' cuticle in the centres of the podomeres. These ridges are of minor importance as muscle attachments, the major area of insertion being the cuticle around them. The projection of the trochanter ventrally between the articulations with the femur (Fig. 3) is, however, both undeformable and has a large muscle attachment (TrF1 and TrF2).

Apodomes do not usually arise directly from the sclerotised edges of podomeres, but from the arthrodial membrane, e.g. the apodeme of TrP1 shown in Fig. 11a. The sclerotised plate seen here at the

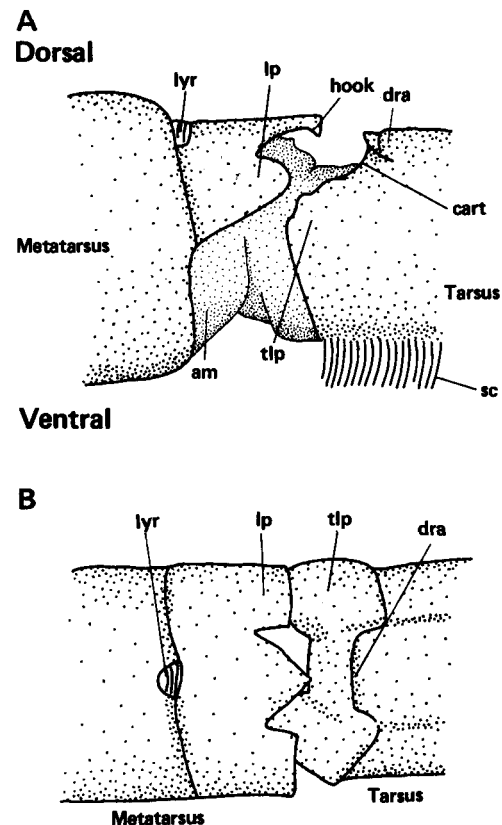


Fig. 10: Metatarsus-tarsus joint. **A** Lateral view; **B** Dorsal view. am = arthrodial membrane, cart = curved articular area, dra = dorsal raised area, hook = hook, lp = lateral projection of metatarsus, lyr = lyriform organ, sc = scopula, tlp = lateral projection of tarsus. Width of metatarsus approx. = 0.6 mm.

junction with the membrane is less usual, although a much larger one, usually called the arcuate sclerite, is found at the junction of the femur-patella muscle apodemes and the membrane (Fig. 5). This structure is similar to that described by Parry (1957) in *Tegenaria*. The edges of the podomeres are frequently emarginated opposite the attachments of large

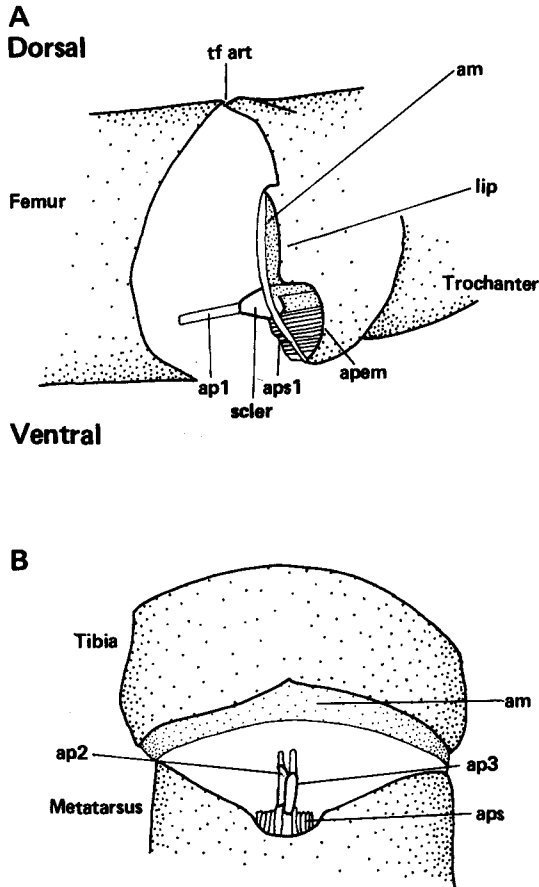


Fig. 11: Apodemes. **A** Femur-trochanter joint, ventral view, with most of the arthrodial membrane removed; **B** Tibia-metatarsus joint, as above. am = arthrodial membrane, apem = emargination, ap1 = apodeme of TrP1, aps1 = apodemes of TrP2 and TrP3, ap2 = apodeme of TiM1 and TiM3, ap3 = apodeme of TiM2 and TiM4, aps = apodemes of TiM5 and TiM6, lip = projecting edge of trochanter, scler = sclerotised plate at junction of ap1 and membrane, tf art = posterior trochanter-femur articulation. Width of trochanter approx. = 1.75 mm, width of tibia approx. = 1 mm.

apodemes. Some muscles join the podomere edges by many small apodemes (e.g. CoTr1) which usually join the membrane for a very short distance.

A small oblique sclerite which is found in the membrane between the dorsal coxa and posterior trochanter and which has the appearance of a sclerotised fold of membrane does not make contact with the trochanter. The significance of this is made clear in the discussion. The membranous folds found in the trochanter-femur, femur-patella and tibia-metatarsus membranes also have the appearance of permanent structures, like those on the skin of an Indian rhinoceros.

The most remarkable non-articular structure is the posterior patella slit (Fig. 5). This is a membranous slit in the sclerotised patella, reaching from the distal edge to an area with two lyriform organs. The slit breaks up into two indistinct channels in their vicinity, but reforms and continues to the proximal edge of the patella.

Movements as used by the animal

All the movements may be used when walking and climbing. There is no readily discernible set pattern; rather the animal seems to use its joints as it likes, just as we might bend down at the waist or with our knees.

In general the legs are moved forwards and backwards by the coxa-body joint assisted by the coxa-trochanter and patella-tibia joints, which may also move alone. The distance between body and foot is increased and decreased by the trochanter-femur, femur-patella and tibia-metatarsus joints. The trochanter-femur and coxa-trochanter joints lower the foot if required.

The extreme ventral movements of the femur-patella and tibia-metatarsus joints are not used in walking, but they are used for prey capture. This is done by clasping the prey between the tarsi of the first and second legs (the third legs may also participate) and pulling the prey to the mouth. When the prey reaches the mouth the femur-patella and tibia-metatarsus joints are fully flexed.

The muscles

The majority of the leg muscles are shown in Figs. 13 and 14. The extrinsic muscles are not illustrated

but are listed below. In addition the following intrinsic muscles are not illustrated: FP1 has an anterior pair, FP2; FP4, the anterior pair of FP3, is not shown; FP5 inserts on the ventral edge of the patella and has no pair; PTi1 has a larger anterior pair, PTi3; PTi1 is absent in the third and fourth legs (which have a posterior hinge joint); TiM1 has an anterior pair, TiM2, as has TiM3 (TiM4); TiM1 and TiM3 share an apodeme, as do TiM2 and TiM4 (Fig. 11b).

The extrinsic leg muscles are as follows:

- CaCo1 – the most anterior. Origin: carapace, near the edge. Insertion: anterior ventral coxal edge (Fig. 12).
- CaCo2 – posterior to CaCo1. Origin: 2 bundles, one on the carapace near the edge, the other on the foveal plate. Insertion: anterior dorsal coxal edge.
- CaCo3 – the most posterior. Origin: spans the full width of one side of the carapace and includes the foveal plate. Insertion: posterior dorsal coxal edge.

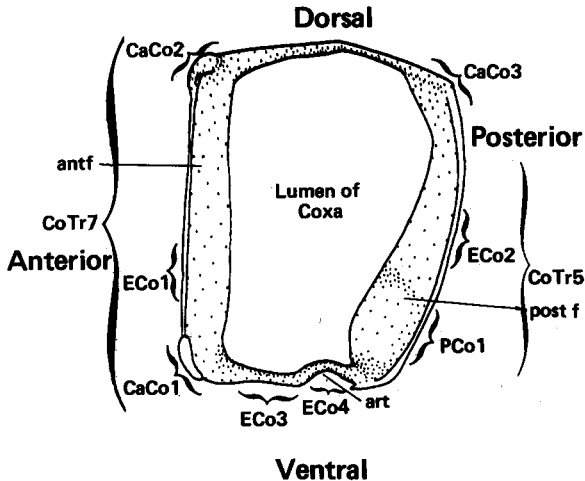


Fig. 12: Proximal opening of coxa, showing flanges and areas of muscle attachment. The muscles have been removed. Small inner brackets indicate muscles inserted on this (proximal) surface of the flanges. Two large outer brackets indicate that the muscle originates on the distal surface. antf = anterior flange, art = articulation, postf = posterior flange. Width of coxa approx. = 1.5 mm.

- PCo1 – small and posterior to the CaCo muscles. Origin: pleural sclerite, immediately under carapace edge. Insertion: posterior edge of coxa, via an apodeme.
- ECo1 – Origin: dorsal surface of endosternite. Insertion: anterior coxal flange (see Fig. 12).

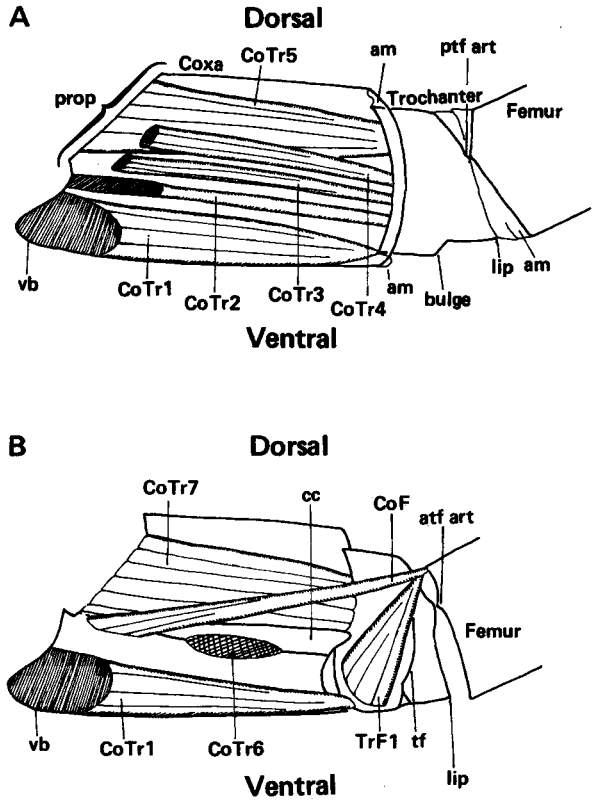


Fig. 13: Diagrams of coxal muscles. **A** Posterior muscles, shown as though the posterior wall of the coxa were transparent; **B** Anterior muscles, seen after the posterior half of the leg has been removed. Hatching indicates the area of origin on the coxal wall. CoTr6 originates in the cross-hatched area and inserts on the posterior trochanter edge under CoTr3 and CoTr4. am = arthrodial membrane, atf art = anterior trochanter-femur articulation, cc = costa coxalis, lip = projecting ventral edge of trochanter, prop = proximal opening of coxa (see Fig. 12), ptf art = posterior trochanter-femur articulation, tf = trochanter flange, vb = ventral bulge of coxa. Length of coxa dorsally = 3 mm.

- ECo2 — Origin: posterior to ECo1. Insertion: posterior coxal flange.
- ECo3 — Origin: ventral surface of endostemite. Insertion: anterior ventral edge of coxa.
- ECo4 — Origin: as ECo3. Insertion: posterior ventral edge of coxa.

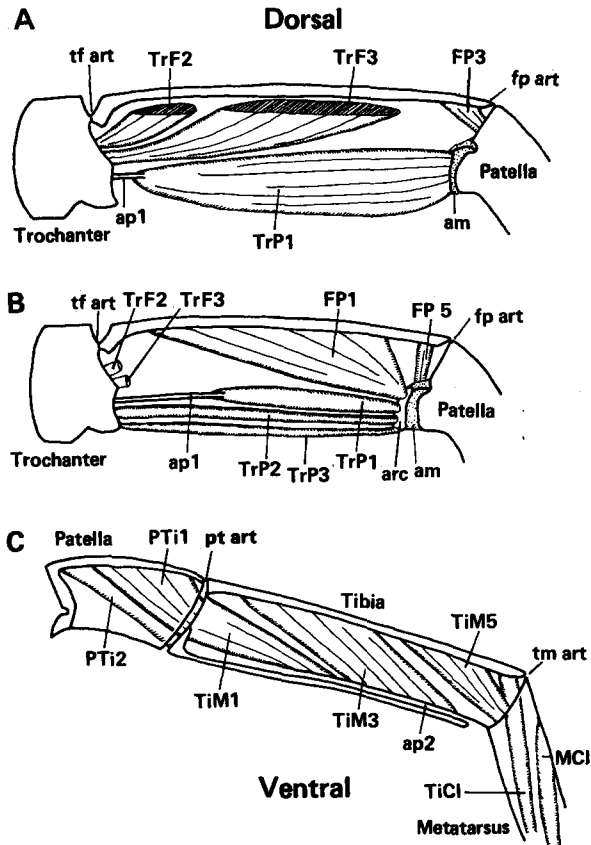


Fig. 14: Diagrams of distal leg muscles. **A** Muscles of femur, seen as though the posterior femur wall were transparent; **B** As above, with TrF2, TrF3 and most of TrP1 removed; **C** Muscles of patella and tibia of leg I, seen as though the posterior cuticle were transparent. PTi1 and TiM1 insert and originate on the proximal and distal sides respectively of a flange on the proximal edge of the tibia. am = arthrodistal membrane, ap1 = apodeme of TrP1, ap2 = apodeme of TiM1 and TiM3, arc = arcuate sclerite, fp art = posterior femur-patella articulation, pt art = dorsal patella-tibia articulation, tf art = posterior trochanter-femur articulation, tm art = posterior tibia-metatarsus articulation. Length of femur = 10.75 mm, length of patella = 4 mm, length of tibia = 10 mm.

Discussion

There are no problems associated with the methods used in this study except that of the effect of alcohol upon the flexibility of the tissues. This effect does not appear to be serious at the concentrations used (70%), since the joints were able to make the same range of movements as observed in fresh specimens.

There is no published description of the muscles of *Heteropoda* and therefore no attempt will be made to match the naming scheme used here with those of previous authors. The muscular pattern of *Heteropoda* follows the same basic design found in other spiders (see Palmgren, 1978; Parry, 1957).

A little work has been done upon the joints of other species of spiders, and this, taken in conjunction with the results described here, allows some comments to be made. Manton (1977) states that, in spiders, no conspicuous levator-depressor (dorso-ventral) movement is made by the coxa-trochanter joint but that its principal movement is a rotation about the proximal-distal (i.e. long) axis of the leg. She also states that this movement is found at the patella-tibia joint, implying in a diagram that it is the only movement of the latter. This is a direct contradiction to the evidence presented here. The coxa-trochanter joint could not be made to rotate about the long axis of the leg, and there is no way in which the oblique sclerite could, as she suggests, assist such a movement. It would rather hinder it. Similarly the hinge found in the patella-tibia joint of the third and fourth legs prevents a rotation about the long axis, and no rotation could be observed in the first and second legs.

Heteropoda is not aberrant, for other authors have found the same directions and magnitudes of movement at these two joints (see Parry, 1957, on *Tegenaria*, Frank, 1957, on *Zygiella* and Ehlers, 1939, on a wide variety of species). Manton does not say which species she studied, but figures *Ciniflo*. *Ciniflo* clearly needs further investigation. It does, however, appear that the coxa-body joint of *Heteropoda* rotates about the long axis and that this rotation is countered, so as to keep the foot flat on the ground, by the metatarsus-tarsus joint as described by Manton.

The posterior patella slit, said by Manton to assist

the rotational movement, must have some other function. Its shape and proximity to lyriform organs (which are cuticular sense organs responding to compression (Seyfarth, 1978)), suggest that it may act as a torsion gauge. The edges of a long slit in a cylinder move when that cylinder is twisted. Such movements could be detected by the lyriform organs. The torsion may be amplified by the slit, enabling it to be detected before it reaches dangerous levels.

A large body of theory can hardly be raised from a study of seven joints in one animal, but, nevertheless, these results do contradict some ideas now current. For example, Wainwright *et al.* (1978) suggest that a joint will be either rigid, move in one direction only, or be quite free and move in all six possible planes of movement. Rigid joints will not be found in animals, where rigidity is obtained by a fusion of the skeletal tissues and a consequent loss of any structure resembling a joint.

The coxa-trochanter joint shows that two directions of movement are possible at a joint. Wainwright *et al.* (1978) also hold that the directions of movement do not determine the design of a joint, but only the numbers of actuators and stops. This obliges us to consider what features make up the design of a joint and to ask what this description of *Heteropoda* suggests is important.

First, the articulations clearly consist of surfaces which move over each other (actuators) and other surfaces whose contact prevents movement (stops). Secondly, there is arthroal membrane (obviously an actuator without which no movement could take place) and the attendant emarginations in the podomeres, some of which are also stops (e.g. the trochanter-femur joint). Muscles are clearly actuators, while flanges often act as stops (in addition to strengthening the podomeres and providing surfaces for muscle attachments).

In *Heteropoda* the joints consist of nothing but actuators and stops, whose size, shape and position are intrinsically related to the magnitude and direction of the movements. Curiously, no structures obviously adapted to bear heavy loads are present. It may be that loads are sufficiently light for the strength of the cuticle, so that no special structures are needed, or this problem may be complicated by the high hydrostatic pressures found in spiders during movement (Parry & Brown, 1959). That loads are not

important in the joint design is suggested by the disarticulated state of the coxa-body joint.

The disarticulatable joints are a most remarkable feature. In the case of the metatarsus-tarsus joint, it seems as if the movements have 'outrun' the structure. While articulated, antero-posterior, rotational and a little dorso-ventral movement can be made, but for a large ventral movement (used when prey is pulled to the mouth), the articulation cannot cope, and the movement has to be made without it. Disarticulation here is the result of complexity.

The coxa-body joint, by contrast, whilst making the same three movements, seems simply to have no need of a firm articulation. The surrounding structures (other legs, abdomen, or palps, sternum and carapace) provide stops; the rudimentary articular structures provide the axis of movement.

The joint structures of *Heteropoda* have been shown to be finely tailored to perform their functions of moving the legs, and their study to give rise to much thought and speculation on the nature of articulations. Further studies, particularly comparative ones, could yield more answers and, no doubt, more questions in this complex area of study.

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