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CONTRIBUTIONS
TO THE
BIOLOGY, ANATOMY AND PHYSIOLOGY
OF
OPISTHOPHTHALMUS LATIMANUS & OTHER SCORPIONS

by

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VI. ANATOMICAL OBSERVATIONS.

1. Introduction

Before starting a study of the neuromuscular physiology of a scorpion limb, it was necessary to know something of its muscular and nervous anatomy. Frequently in such cases, it is discovered that anatomists have looked at the problem. Almost as frequently, however, it is also found that the careful work of these people is of little or no use to the physiologist since it is done without reference to any functional considerations. The following brief resumé of the past work on neuromuscular anatomy of the scorpion appendages is a case in point.

Not many workers have described the general anatomy of the scorpion; the appendicular anatomy seems to have suffered even greater neglect. The scorpion leg has had its muscular anatomy described by at least three workers: Börner (1903), Vachon (1949) and Snodgrass (1952). None of these descriptions is very detailed, but within that limitation the accounts agree well with one another. It would appear that there are many more muscles in the leg of a scorpion than in that of a crab or an insect; that there are two segments, the 4th and 6th, which are supplied with flexor muscles but lack extensors, and that two segments, the 6th and 7th contain no muscles at all.

A drawing of the anatomy of the nervous system in the leg without any accompanying description is given by Vachon.(1949) Since the structures supplied by the nerves are not shown, this picture is of little use for physiological studies.

The scorpion pedipalp has been less extensively studied than the legs. It may be remembered from the introduction that there is no opener muscle for the terminal segment of the structure, a fact mentioned in favour of the pedipalp as a muscle preparation. Snodgrass (1948 & 1952) describes the closer system of this claw and makes a suggestion as to the possible opener mechanism. He also considers the possible homologies of the pedipalps and legs without giving any description of the details of pedipalp segments or their muscles. Earlier, Barrows (1925) had followed almost the same course and reached the same conclusions as Snodgrass.

Lastly, McClendon (1904) has given a drawing of the nerves, including those of the pedipalp, in the developing scorpion. Unfortunately no details are mentioned and no assistance could be obtained for this study from the figure.

It will be clear that this information is insufficient to form the basis of a physiological investigation and therefore a fresh anatomical study of the muscles and nerves of the pedipalp of O. latimanus has been made. The study was extended to the anatomy of the legs with the possibility in mind that the structure of these latter might throw some light upon the form and function of the former. As Snodgrass (1948) says: "to understand the nature of the pedipalp chela it will be necessary to study the structure and musculature of the distal segments of an ordinary walking leg."

Later during the study it was decided to use the sting as well as the pedipalp for an experimental preparation. Snodgrass (1952) has dealt very briefly with the musculature of the tail of Centruroides sp. In O. latimanus the tail muscles are not uniform throughout the tail so that is is impossible to describe a "typical" tail segment for this animal as Snodgrass does in his study. The main picture is nevertheless fairly similar in the two animals.

Once again there are drawings of the nerve supply throughout the organ (Vachon, 1949) but there is no reference to what structures the inadequately represented nerves supply.

In the tail, only the muscles of the sting were used experimentally so that details of the last two segments might well prove sufficient here. However, as will be explained later on, there are reasons for dealing with the tail as a whole.

Conventions of Nomenclature adopted in the study.

The name of a segment of almost any arthropod limb, as given by one worker, has been questioned by some other worker. This is certainly true of the arachnid limb. For this reason the limb segments will be described by alphabetical letters only, starting with the most proximal. An exception to this is made in the case of the last two segments of the pedipalp: the second-to-last segment will be called the "hand", while the last segment, that which articulates on the hand, the "finger". These are, of course, segments "E" and "F", since the pedipalp has six segments. The distal part of segment E is elongated to form a finger-shaped process against which segment F is apposed. This distal process will be referred to as EE.

The part of the scorpion body recognised by Snodgrass (1952) as the metasoma is considered as being made up of six "tail" segments. They have been labelled from U to Z, moving distally, segment Z is the sting and consists of the poison bulb and the sting lance.

The following convention has been adopted in the designation of the muscles. The capital letter of the segment whose movement a muscle effects begins each cipher. Then follows a number, designating a particular muscle, and lastly, if the muscle is branched, each branch will also have an index number. Thus $B5^4$ is one of at least four branches of a muscle called 5, which moves segment B by its contraction.

Nerves bear as a small letter the segment in which they appear to arise from the main trunk. Each has also a number. The subsequent divisions of each nerve are left unnumbered until the final terminal fibres are reached. These are each characterised by a numerical superscript (see Fig. 44).

With regard to the description of nerves and muscles, it was felt that a new convention was necessary for this study. Snodgrass (1927) has set forth a descriptive convention which is commonly used. For the following reasons it was felt that this was unsuitable in connection with a study of the scorpion pedipalp. Firstly there are many more muscles in this limb than there appear to be in most other

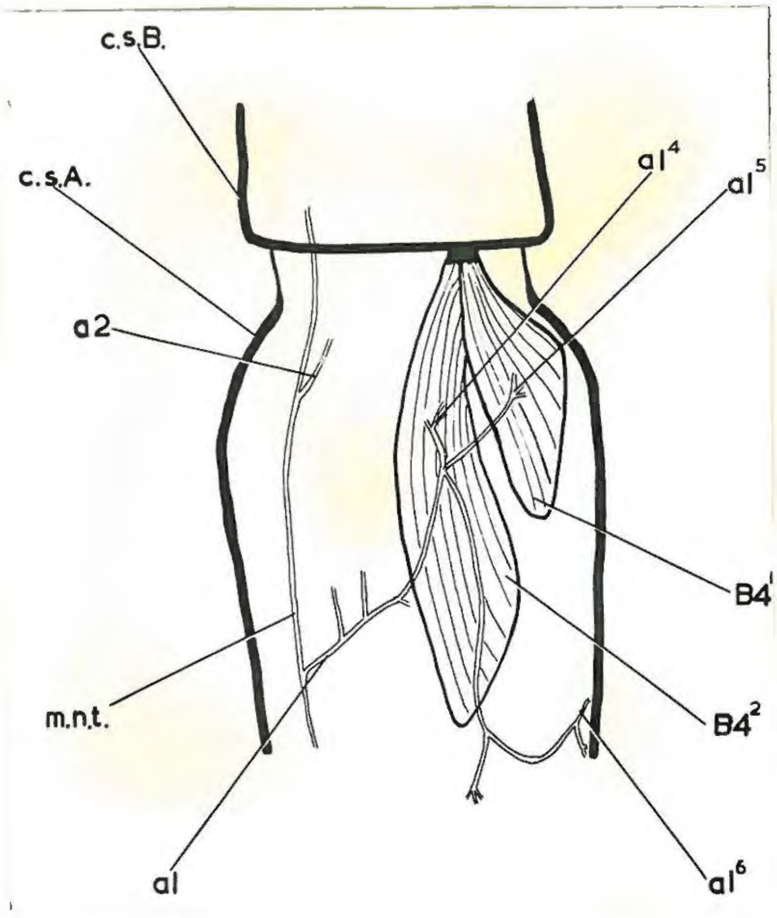


Fig. 44. An illustration of how the convention describing muscles and nerves is used in this study. al., first nerve branch off the main nerve trunk; $\underline{al^4 - al^6}$., branches of nerve al; a2., second nerve branch off the trunk; $\underline{B4^1}$ and $\underline{B4^2}$., two branches of a muscle B4 which moves the segment by its contraction; c.s.A and c.s.B., cuticle of segments A and B respectively; m.n.t., main nerve trunk.

Of a leg or the pedipalp?

arthropod limbs. Snodgrass himself (1952) comments on the "remarkable" number of muscles in the scorpion leg. Since in the claw he mistakes nine, possibly eleven, muscles for one muscle, the problem is even more complex than he realised. If this large number of muscles is to be described with any degree of accuracy, the convention used must be capable of giving a finer definition of origin and insertion of a muscle than is possible with Snodgrass's terminology. Secondly, the limb is not locomotory and, as a result, the orientation of the joints differs from that found in an ambulatory appendage. In the Snodgrass convention the limb is considered as being held fully extended from the body so as to lie perpendicular to the sagittal axis. With an ambulatory limb in this position the free edges of any podomere lie in a plane parallel to the sagittal axis. In the case of the scorpion's pedipalp this is, however, not true. The formation of the joints results in the free edges of particular segments lying in planes which have no particular relation to the sagittal plane of the body. The muscular movements of the segments distal to such joints therefore cannot be described simply in terms of "posterior", "anterior", "dorsal" or "ventral". When the contraction of a muscle moves the segment slightly dorsally and rather towards the body but at the same time has moved it to a position more anterior than its previous position, the decision as to whether this muscle is a "levator", a "flexor" or an "adductor" is a difficult one. A compound terminology is, of course, possible, but would be highly cumbersome. Finally there are, in the scorpion pedipalp, many muscles with a rotator function, a function not common in ambulatory limbs. Their presence, like those of the peculiar joints, raises difficulties in that they do not produce a movement in one plane only.

Partially [illegible]

The convention which has been adopted here depends on regarding the cross-section of each joint of a limb as a circle. This circle is divisible into 360° and the positions of the cardinal points are determined in the following manner. The limb is considered in its resting position and at each joint the point farthest from the ground is noted. This, for each segment, is taken as North (0°). The limb is now imagined as being stretched out sideways at right angles to the body. Some of these North points are no longer mid-dorsal. The surface of the joint may now be imagined as being viewed from a position proximal to the joint. Consider a right hand limb (see Fig. 45). The bearings are measured in a clockwise direction, and therefore when N is mid-dorsal, E (90°) will lie posteriorly. A left hand limb will be read in a counter-clockwise direction, so that 90° will still be posterior. In this way the problem of mirror imaging is resolved and the convention will describe in similar terms the muscles of either side.

The position and extent of the insertion of a muscle can easily be described by giving the bearings in degrees over which it extends. In Fig. 45, the insertion of Muscle A1 is from 70-110°. Since this is not an obliquely pulling muscle, the information tells us that, when the limb is stretched sideways, this muscle will pull the segment backwards. It also tells us that the insertion is 40° (i.e. 110 minus 70) wide.

If the muscle is a straight pulling one, its long axis will lie parallel to that of the segment in which it originates. It will make a right angle with the tangent to the mid-point of its insertion. This can be seen diagrammatically, in muscle A1 of Fig. 45. If the muscle pulls obliquely, i.e. it is a rotator muscle, see A2 of Fig.45, the angle made with the tangent may be any angle from 0 to 180°, but of course not 90°, which gives a direct pulling muscle. In this study the angle measured in judging the obliqueness of a muscle was always that which corresponded to k of Fig. 45. Angle q was never used.

Where k is greater than 90° in a right hand limb, the muscle will be pulling in a clockwise direction and this can be spoken of as pulling in a positive direction. Where k is less than 90° in a right hand limb, an anti-clockwise rotation results from the contraction and the muscle is a negative rotator. In the left hand limb, a positive rotator (where k is greater than 90°) would be pulling in an anti-clockwise direction.

As has been explained, this convention of muscle description

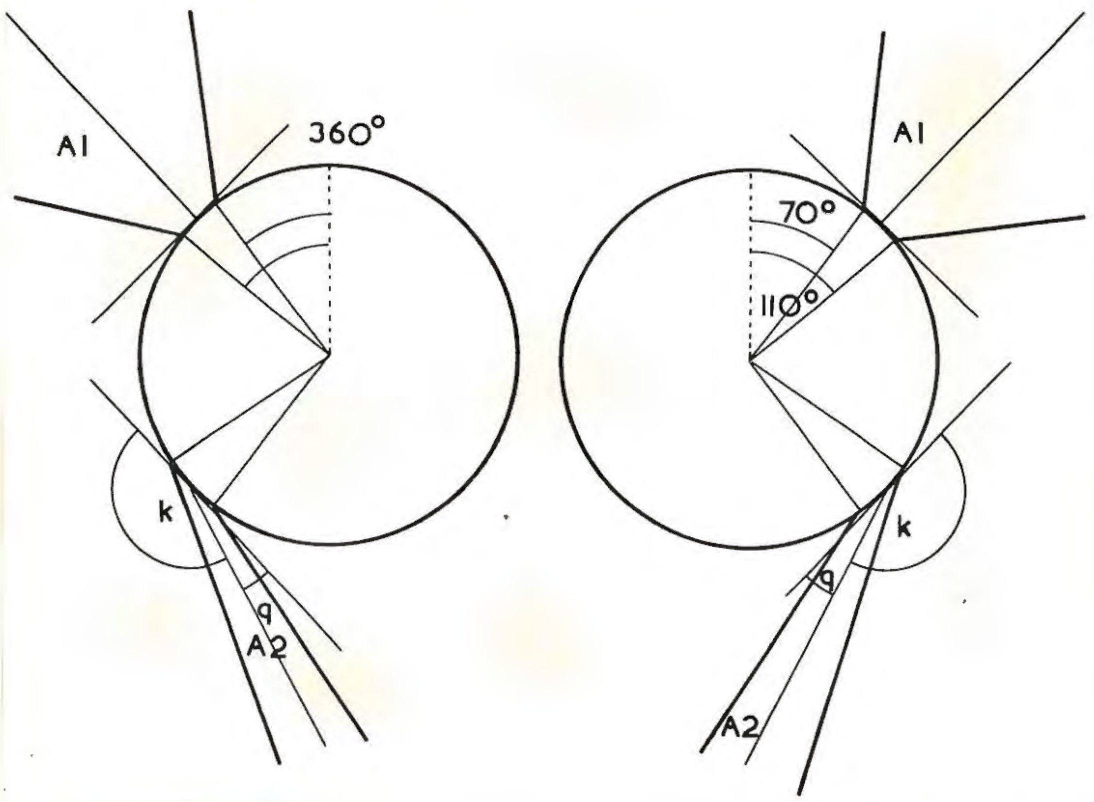


Fig. 45. The convention used for description of a muscle. The two circles represent cross sections through the joints of a limb, left on the left hand side, right on the right hand side. Two muscles, A1 and A2, are represented. The insertion angle for A1 is shown and is 70 - 110° (i.e. 40°); pull angle is shown for A2 and is angle k; angle q is never used.

was evolved for dealing with pedipalp musculature. It is not necessary that the tail segments should be considered under the ~~same~~ same rules. However, it was found, after the claw had been described, that this convention seemed the simplest and clearest for the tail segments as well. Since these are bilaterally symmetrical, it would not matter for most purposes whether 90° or 270° were used in the description; however, as with the right limb, the count is made by looking at the proximal surface of a segment and working clockwise.

pedipalp

In describing the musculature it seems logical to start with the form of the proximal joint of a segment. On this will depend the movements of which the segment is capable. Then will follow a description of the muscles which perform these movements and how the segment which contains them is built to provide suitable areas of attachment. Lastly, where possible, the potential movements, as surmised from the joints and muscles, will be related to the natural movements during the life of the animal.

After this work was completed, it was found that Petrunkevitch (1909) had seen the necessity for a more exact convention for the description of muscles. He therefore put forward a series of new forms for the planes in which structures could lie. Fig. 46 and the accompanying legend indicate clearly how little this convention needs to transform it to the simple, though rather more precise, one used in this study.

Methods.

In the main, anatomical investigations of nerves and muscles were carried out by dissection. The hardness of the exoskeleton and the difficulty of removing it without disturbing nerves and muscles meant that sectioning of material was done mainly for the histological details. Both fresh specimens recently killed in carbon bisulphide and also specimens fixed in 70% alcohol or Bouin were used for these dissections. The best results were, however, obtained from animals killed and left in the laboratory for a day or two, then dissected under 70% alcohol.

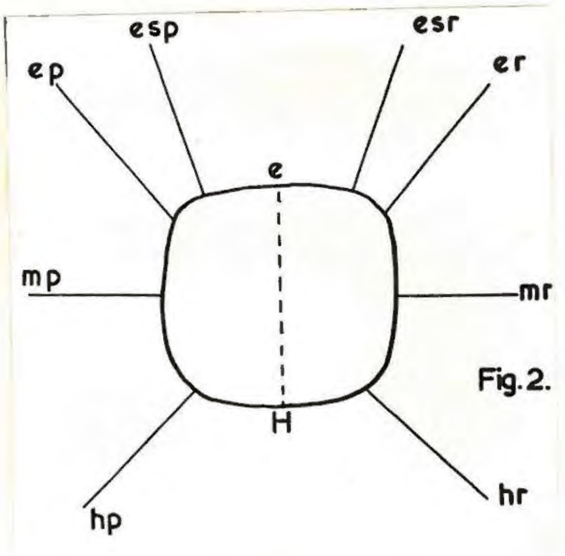


Fig.2.

Fig. 46. Convention suggested by Petrunkevitch (1909) for the description of the muscles of spider limbs. The legend accompanying the original figure is as follows:

"Diagram representing a cross section of the leg of Pholcus phalangoides. EH, the plane of symmetry. It is understood that the observer sees the cross-section in looking from the body of the spider towards the end of the leg. In consequence it is evident from the letters accompanying the diagram that it is a cross section of a right leg. In a left leg the two halves are reversed. ESP, proepisynaxial; ESR, retroepisynaxial; EP, epipro; ER, epiretra; MP, middle pro: MR, Middle retro; HP, hypopro; HR, hyporetro hair."

Staining of dissections was not very successful. The following procedure, however, was furthest from failure. A dilute solution of methylene blue (0.1%) was made with Ringer for fresh dissections, with water for fixed ones. This was blown from a pipette on to the small area under dissection. Left for 10 seconds, the excess stain was then washed away by a pipette full of clean water or Ringer. The distinction in shade of blue of the nerve and that of the muscle and connective tissue is slight but clear enough.

Dissection of the nerves raises a difficulty, namely in fixed material there is little distinction to be seen between a nerve and the blood vessel which normally runs fairly near it; their appearance is more or less the same (both are stained the same shade by methylene blue). In a living or freshly killed animal the distinction __is__ quite clear: the blood can be seen in its vessels. Here, however, dissection is hampered by the splaying and contraction of muscles and nerves which have been cut. In the fixed animal the two apparently indistinguishable structures can in fact be identified as nerve and blood vessel. One of the two is more easily broken, less easily stretched than the other. Comparisons with the fresh material make it clear that the weaker structure is the blood vessel. Hence we have a practical, if somewhat unorthodox, method of distinguishing one structure from the other in the dissection.

In this section no detail will be given of the organisation of the muscle into fibres or the branchings of the nerve once it has reached its "destination", i.e. muscle or general sensory field.

The "destination" of a nerve or the "function" of a muscle has __not__ been tested in most cases. If the result of a contraction of a certain muscle were not clear, several simple techniques were used to investigate the matter. For instance, the whole of the origin was freed with the chitinous piece on to which it was attached. This was pulled in the normal line of pull of the muscle. The resulting movement at the attached end of the muscle was noticed. Electrical stimulation of such muscles was not particularly satisfactory as they are normally small and it proved very difficult to fix the stimulating electrodes into the muscle without damaging it. Where nerves were concerned, the question of function arose more frequently. Distinction between motor and sensory nerves was normally clear; the former enter one or more muscle bundles, the latter run from the base of sensory hairs such as trichobothria or from the region around the arthrodial membrane. Suitable stimulation of the motor nerves caused muscular contraction while no such result could be obtained from any of the fibres predicted as sensory fibres prior to the testing. The connection to the brain was, of course, severed before the stimulation in either case.

The tail and leg muscles were found to be fairly regular in number, position and size. The nerves supplying them were, consequently, also regular from animal to animal. The pedipalp muscles were more variable. The sexual dimorphism of the species has been discussed above (p.112). The muscular irregularities, however, occur not only between the sexes, but between animals of the same sex and even between limbs of opposite sides of the same specimen. As a consequence of this irregularity there is little hope of getting a picture of the nervous anatomy which would fit all specimens of O. latimanus. In the main, the differences in various dissections seem to lie in how far proximally each branch separates from the main nerve. Where the muscle differences are of position and size, this is to be expected. A general picture has been obtained by splitting branches back as far as possible in each dissection and using the most proximal point at which the branch could be obtained as the true point of separation.

2. Gross Myology of the Pedipalp.

For clarity of description and subsequent reference a drawing (Fig. 47) of the entire pedipalp from several views is given.

As has already been explained, the description of the myology will be treated systematically starting with the most proximal podomere, A, and its muscles which are within the prosoma. In every case a table is provided of all the relevant muscles together with their angles of insertion and their pull angles. These are in each case further summarised in circular diagrammatic form, while drawings of the different muscles in their strict anatomical relations and, in certain cases, of the exoskeleton showing the precise positions of their origins are provided.

The Prosomal-A Joint. (Figs. 48 and 49)

Muscle	Insertion angles	Pull angles	Comments.
A 1	90 - 30	50	Origin on epistomal sclerotisation. A short stout muscle with branch joining A 2.
A 2	35 - 55	90	Origin on carapace, two branches; origin of muscle B 2 on insertion of A 2.
A 3^1	95 - 110	90	Origin on anterior edge of carapace
A 3^2		90	Origin on lateral curve of carapace.
A 4	125 - 150	95	Origin on dorsal carapace between origins of two A 2 muscles.
A 5^1	155 - 140	110	Origin on tendon between auxil~~l~~iary hardening and endoskeleton.
A 5^2		100	Origin on auxil~~l~~iary hardening
A 5^3		120	Origin on epistomial sclerotisation.
A 6	255 - 290	90	Origin intucked on medial basal exoskeleton of A segment.

The Anatomy of the Prosomal - A Joint.

This is a mono-condylic joint. A has a small sclerotised rod (Fig. 48a) which runs proximally into the body from a point at about 340° on the proximal ring of segment A. It lies with a pull angle of about 30° from the A segment and articulates with the

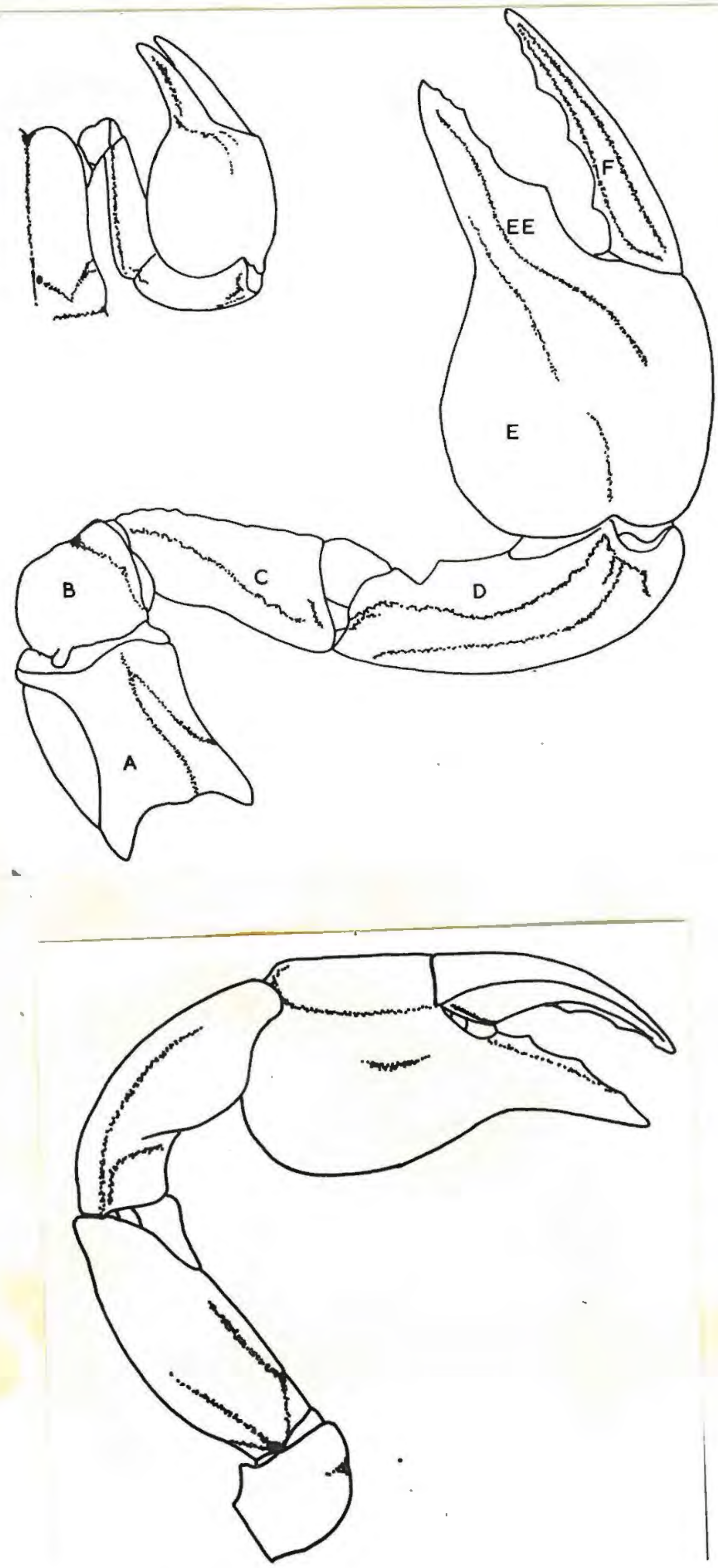


Fig. 47. Entire pedipalp of O. latimanus. Centre, dorsal view with pedipalp slightly extended; top, same in resting or folded position; bottom, undersurface of slightly extended limb.

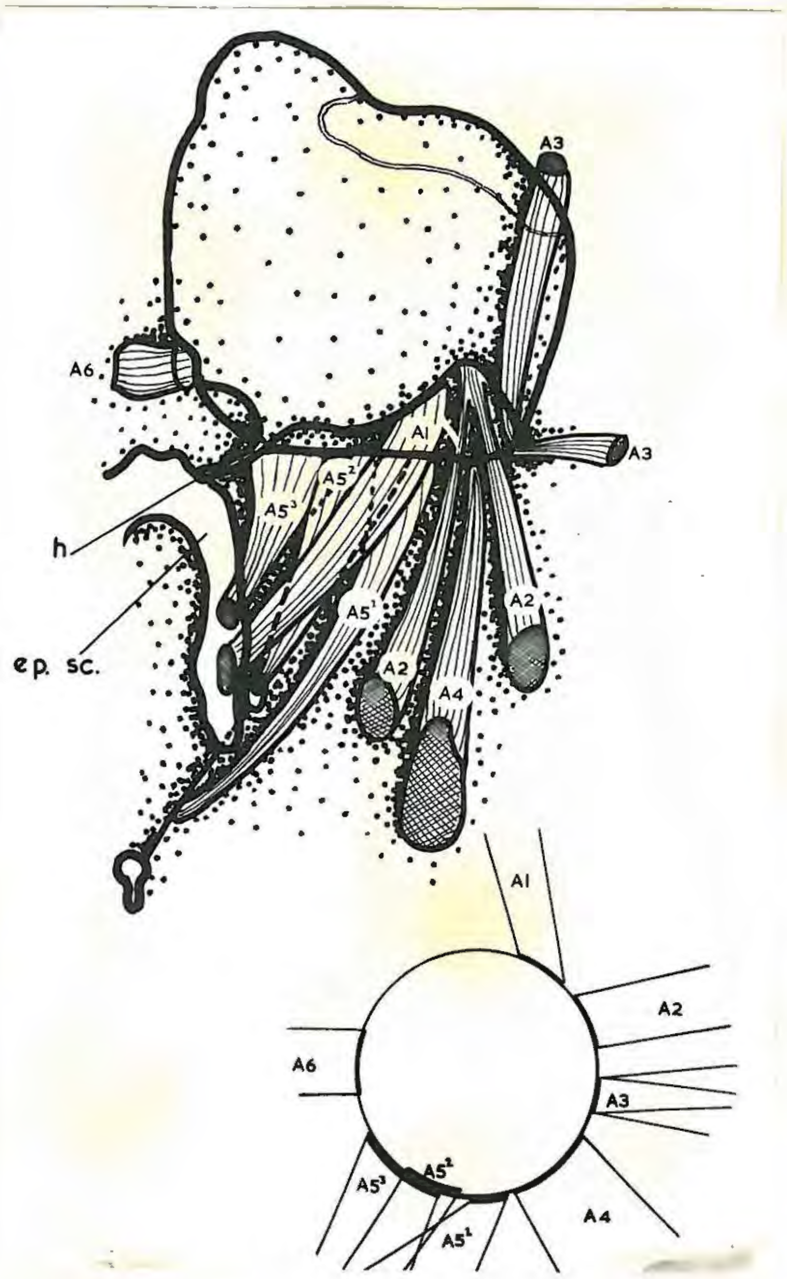


Fig. 48. Muscles moving segment A.
(a) Upper figure. Sketch showing the muscles in situ; <u>h.</u> is the rod which articulates segment A on to the epistomial sclerotisation <u>ep sc</u>.
(b) Lower figure. Ring diagram of insertions and pull angles of A muscles.

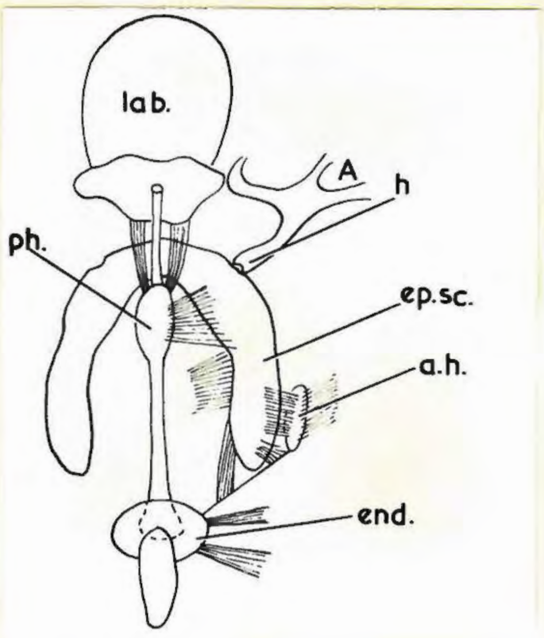


Fig. 49. The epistomial sclerotisation and associated structures and muscles in O. latimanus
A. Coxa of pedipalp carrying articulation h with epistomial sclerotisation; ax.h. auxilliary hardening; end., endoskeletal sclerotisation; lab., labrum; ph., sucking pharynx.

epistomial sclerotisation, forming the pivot for movement of A on the body. This epistomial sclerotisation (Figs. 48 and 49) is a peculiar Y-shaped endoskeletal structure which is strung on to the carapace by a pair of dorsal muscles and on to the endoskeleton proper by the curious arrangement of an auxiliary hardening and its associated "tendon". The auxiliary hardening is itself linked by muscles to the coxae of the legs III and IV, which thus anchor the epistomial sclerotisation. The last-mentioned bears, as well as the segment A pivot, the origins of muscles of the proximal segments of the pedipalps and chelicerae and also those for the sucking pharynx. It is therefore roughly homologous in function with the insect tentorium. The functional features of the epistomial sclerotisation have been given in greater detail than is necessary for comprehension of the pedipalp attachment because the structure appears to be an example of how the arachnids may avoid using sclerotisations by having a large number of muscles acting as struts. Apart from the tendon-like strand running from the auxiliary hardening to the true endoskeleton, the epistomial sclerotisation is supported entirely by muscles whose outermost attachment is either to the carapace directly or to the immobile coxae of the legs.

The actual articulation of the A rod on to the epistomial sclerotisation is in the form of a ball and socket joint, the socket being at the anterior end of the sclerotisation and the two being fairly tightly tied together. Potentially, therefore, an almost universal bearing type of articulation has been achieved at the prosoma-A joint.

Functional Relations of the Muscles to the Prosoma-A Joint.

The A segment is lifted, i.e. carried through the 360° plane, by the A1 and A2 muscles. In addition, the former produces a strong negative (anti-clockwise) rotation. This dorsal lifting is restricted by the presence of the chelicerae above the pedipalp base. The opposing movement, effected mainly by A5, is also restricted but in this case by the gnathobasic parts of legs I and II. Muscle A5 consists of three branches with widely different origins so that the pull of any individual branch can be different from that of the others or any other. The overall rotator effect, however, is a positive twist.

It has just been pointed out that the lifting and depressing of A are limited so that part of any powerful pull of the A1 and A2 or A4 and A5 muscles must be wasted, though the rotator effect could be used in twisting the whole segment. A different effect can, however, be achieved when dorsally inserting muscles pull against ventrally inserting muscles which have the opposite rotator sign. If A1 and A5 contract equally together depression and elevation will cancel each other out, as will be the actual rotation of A. The resulting effect will be that segment A is pulled towards the mouth and, at the point where the sclerotised articulation prevents further movement, A will swing over on its pivot towards the mouth.

This movement has, however, a stronger component: that of A6. This A6 muscle, stretching across the base of the labrum, is common to both A segments. It would seem fairly effective in drawing the two A segments together. It is the "rostral muscle" of McClendon (1904) or the "labral muscle" (Snodgrass, 1948).

used in feeding

Opposing this A6 action is that of the two A3 branches as well as the combination of A2 and A4. As with A2, $A3^1$ contracting alone produces a depressor as well as a lateral effect.

The A-B Joint. (Figs. 50 and 51)

Muscle	Insertion L.	Pull L.	Comments.
B1	10 - 35	60	two branched, B1 has origin on proximal part of dorsal ridge, $B1^1$ prox. part of A.
B2	55 - 80	90	three branches, all with origins on proximal ring of A, dorsal edge.
$B3^1$	100 -140	75	origin on anterior part of carapace, not deeply separated from $B3^2$
$B3^2$		115	
$B3^3$		150	
B4	160-185	70	proximal part of A ring has B4 origin
$B5^1$	230 - 245	70	origin on ventral part of A
$B5^2$		90	origin on "dorsal ridge" of A
$B6^1$	270 - 340	30	Origin on ventral wall of A
$B6^2$		50	Origin on ventral wall of A, proximal to origin of $B6^1$
$B6^3$		90	Origin on medial distal ledge whose outer surface bears A6 origin
$B6^4$		90	origin on "dorsal ridge" of A.

The Anatomy of the A-B Joint.

In this joint there is no special sclerotised articulation, a characteristic not normally found in arthropod limb joints. But for the limitations imposed by the arthrodial membrane and the internal tissues of the limb itself, B would be able to rotate completely on A. At about 305° there is a peg of hard chitin which at first was thought to function as a point of specific articulation, but in fact it merely carries the insertion of the large B6 muscles, having no sclerotised contact with segment A. At 90° the arthrodial membrane is especially wide, the distal edge of A at this point being cut back so that the movement of B in the 270-90° plane has a very large degree of freedom, especially towards 90°.

Functional Relations of the Muscles to the A-B Joint.

B6 is the largest and heaviest of the muscles effecting movement of B segment. This muscle is so deeply branched that it is

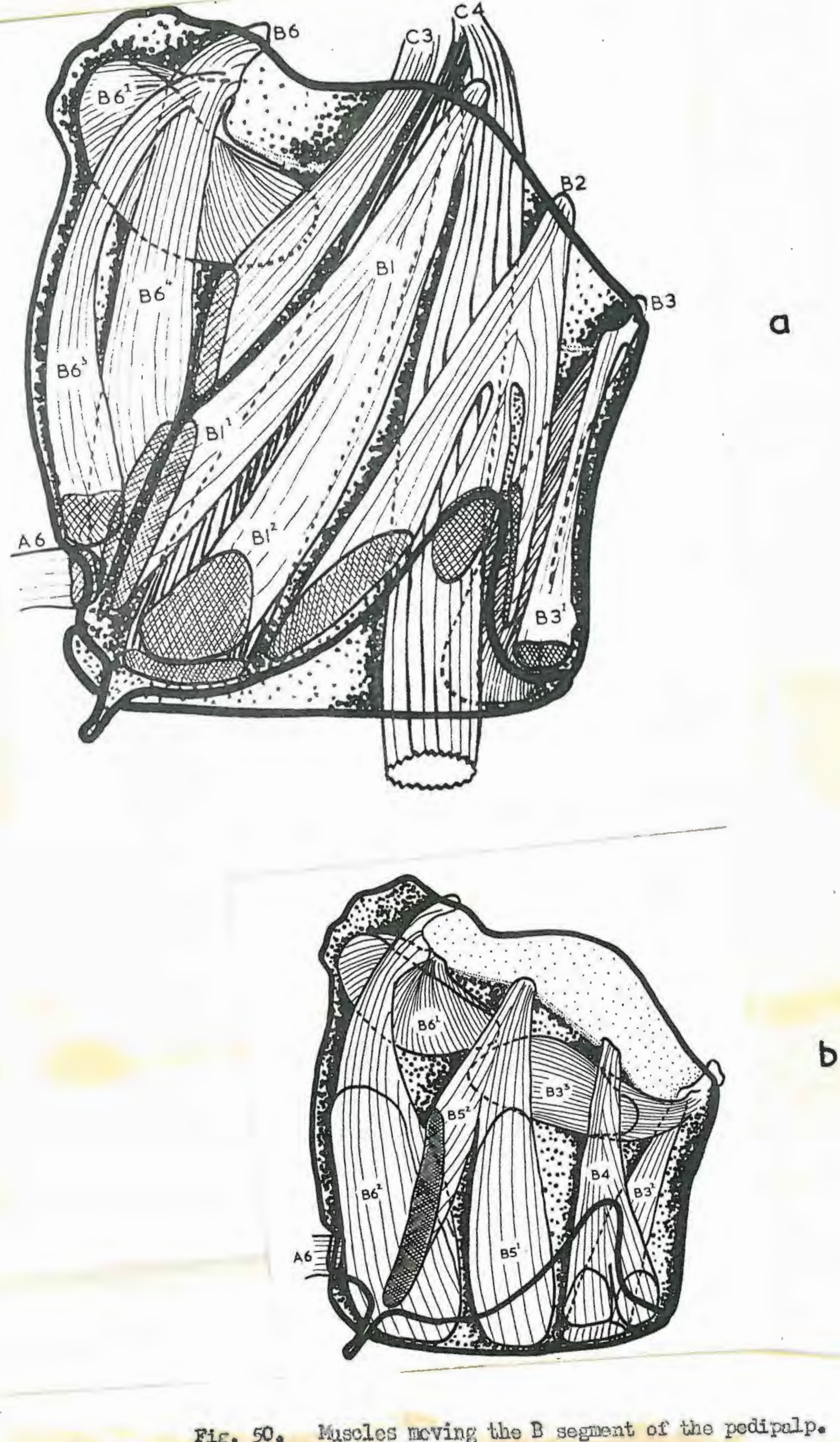


Fig. 50. Muscles moving the B segment of the pedipalp.
(a) More dorsal muscles.
(b) More ventral muscles.

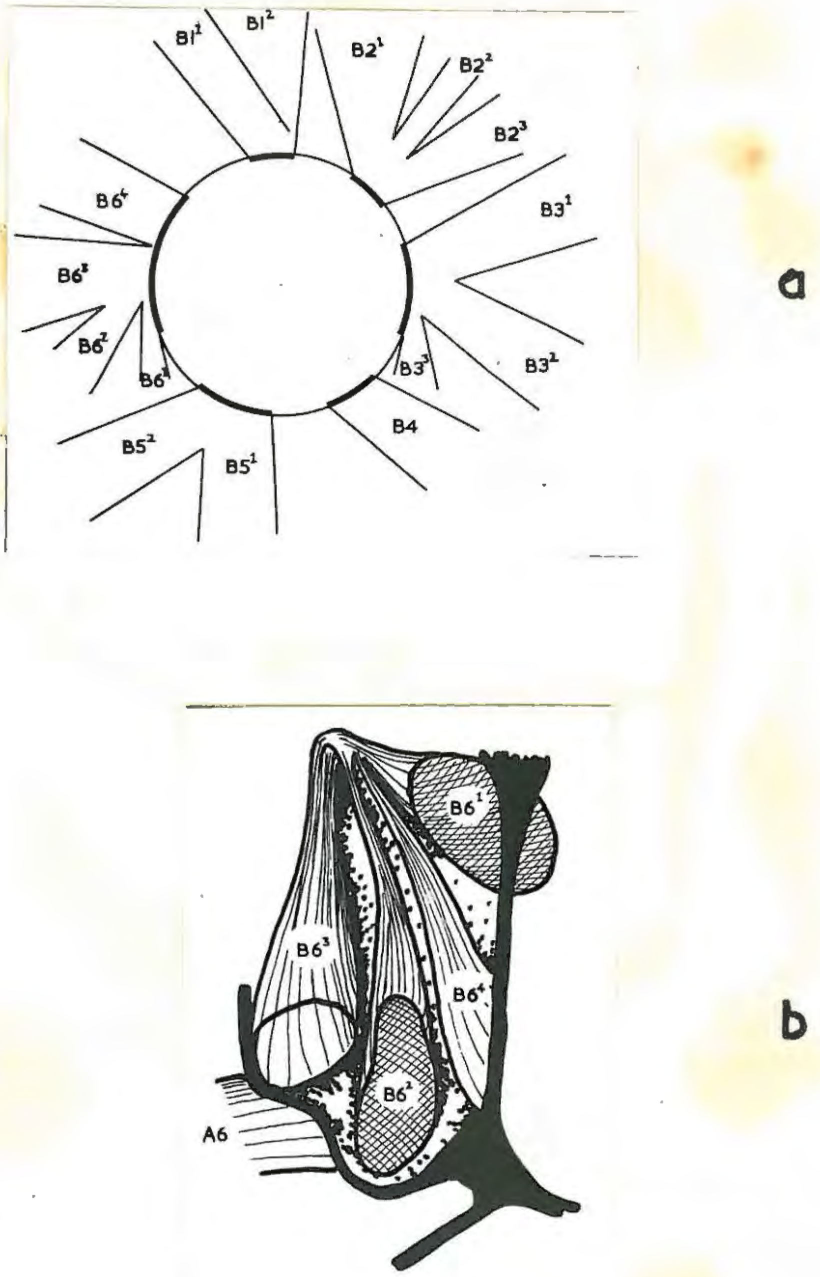


Fig. 51. (a) Ring diagram of the B muscles.
(b) The B6 muscle complex.

probable that some investigators might consider each branch a separate muscle. The branches do in fact give a fairly wide viariation in pull angle though they share a common insertion. The two predominant muscles are the two direct pulling ones, B6^3 and B6^4, so that a combined contraction of all the B6 branches will pull B through the 280° plane, rotating it slightly in an anti-clockwise direction. This movement either brings B more anteriorly or closer in to the mouth region, depending on its initial position.

Antagonistic to the B6 muscle are the three B3 branches. None of these is as powerful as any of the B6 branches. Not only is the combined effect of the B3 branches antagonistic to that of B6, but the strong negative rotator effect achieved through B6^1 and B6^2 has its specific antagonist, the positive twist of B3^3.

The effect that B3 has of moving B through the 270 - 90° plane is assisted by the combined contraction of B2 and B4. These are mainly concerned with elevating and depressing the segment but since they have antagonistic rotator effects, when they pull together both their lift/depress and their rotator actions are cancelled and the B segment is moved either more posteriorly or away from the mouth region, depending on B's initial position.

B2 also lifts B, not directly dorsally but through the 200 - 10° plane. Its rotator component is negative, due mainly to one branch of B2. In its lifting action on B, B2 is assisted by the two branched muscle B1. Once again there is a rotator action also involved; in this case, a negative one. This means that if B1 contracts simultaneously with any depressor of B which has a positive rotator effect, e.g. B5, the action achieved by the B6 muscle, viz. that towards 270°, will be augmented.

Antagonistic to the B1 and B2 muscles are B4 and B5. B4 has already been mentioned in connection with its rotator effect; it also has a component moving B through the 180° plane, as have the two B5 branches. When these two muscles contract together, the antagonistic rotator effects cancel each other out and a simple depressor action is achieved.

From this consideration of the B muscles, it is quite clear that by the contraction of single muscles or by combination of various muscles or branches, movement through almost any plane or rotation in either direction is possible for the B segment. It may be noticed that the most obviously powerful movements are those through 270° plane, i.e. either anterior or towards the mouth, and it will become clear that these are the most frequently used actions of B on A.

The B-C Joint. (Fig. 52)

Muscle.	Insertion L.	Pull L.	Comments.
C1	340-355	177	No clear evidence of tendon on either end.
C2	70-135	90	Three branched
C3	135-140	90	Origin on dorsal ridge of A (Fig.50a)
$C4^1$	140-145	90	Common tendon through B, $C4^1$ origin on endosternum,
$C4^2$		90	$C4^2$ at base of A. (Fig.50a)

The Anatomy of the B-C Joint.

The joint of C with B is a strictly di-condylic joint with the condyles at 10° and 160°. Both of these are the common arthropod type, each being formed by two sclerotised nodules tied together so tightly by their ligaments that one can only just rock on the other. The presence of these two pivots restricts the possible movement of C on B to flexion and extension in the horizontal plane. There is a fairly broad arthrodial membrane from 160° - 10° but that from 10-160° is very narrow, a point which will be discussed later.

Functional Relations of Muscles to the B-C Joint.

The relations shown in the ring diagram, Fig. 52b, require explanation. Muscles C^2 to C^6 insert directly on to C at the B-C joint. Muscle C^1 inserts about halfway along the podomere. The muscle complex D3 is also shown, but its form will be discussed later.

The main extensor muscle is the short stout C6 but C5 provides additional extension. This C6 is interesting in that it

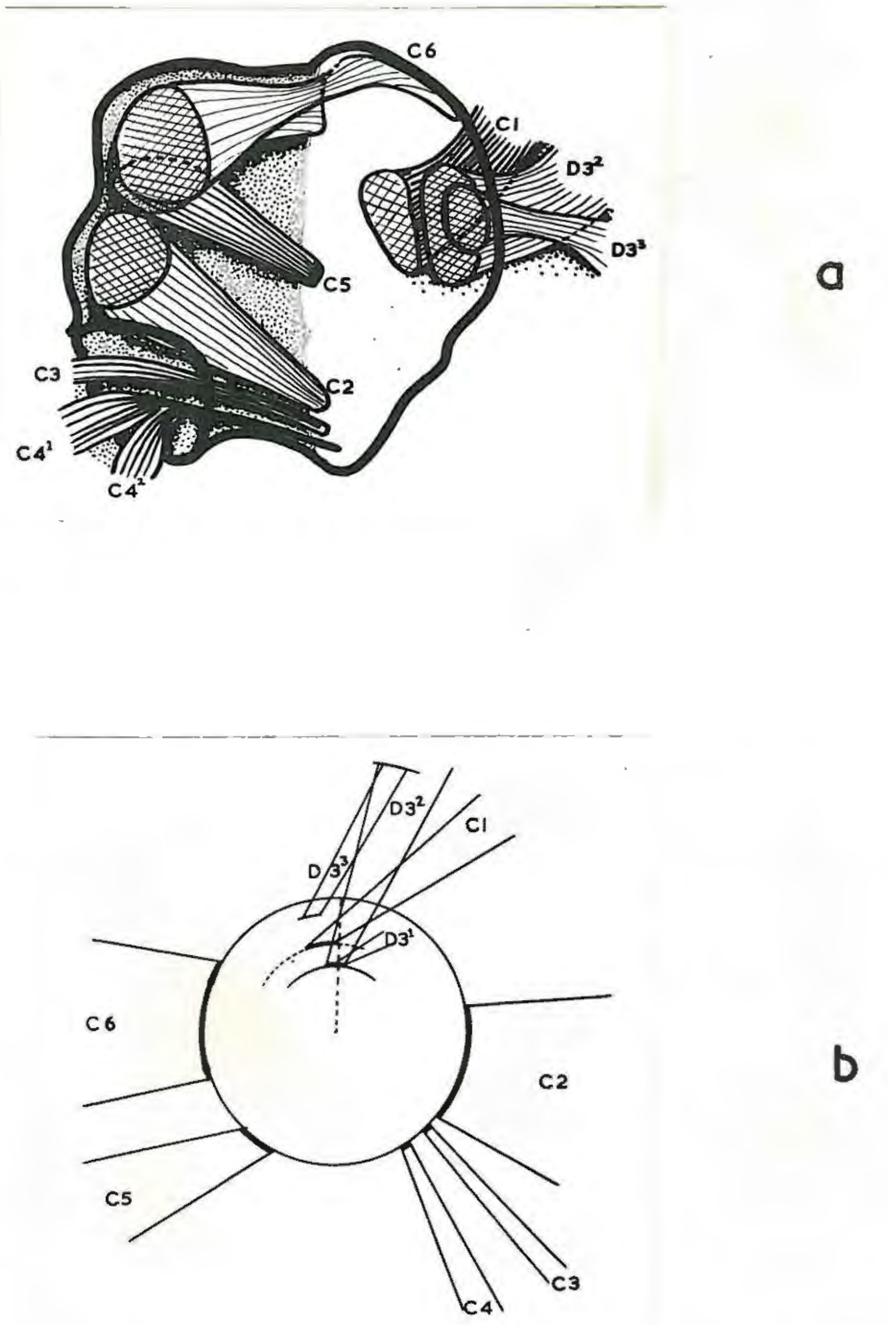


Fig. 52. (a) C and certain D muscles of the pedipalp.
(b) Ring diagram of these muscles.

is the first muscle to be described where, although a rotator component is evident in the angle of the pull, no rotator action is allowed by the joint formation. This phenomenon, which seems wasteful of muscular effort, will be met many times again. Its possible significance and explanation will be discussed later (p. 211). It will also be noticed that the insertion of C5 is very close to the ventral pivot and well separated from its coextensor, C6. This ventral insertion appears further to decrease the extensor efficiency of C5 for C6 is clearly operating in mechanically optimal conditions. This second instance of apparent waste on the part of C5 will also be referred to later (p. 211).

The C1 muscle is peculiar in that it stretches from the distal end of one segment into the proximal end of the next. Normally muscles have either an origin on the proximal end of one segment and an insertion on the proximal end of the next, or else an origin on the distal end of one segment and insertion on the proximal end of the segment after next. This peculiarity of C1 will also be discussed later (p. 211). The muscle would, from its line of pull, rotate the C segment in a positive direction. However, as was explained earlier, the form of the B-C joint prevents this and the insertion of C1 is such that its contraction aids the extension movement of C6.

An extensor effect is also achieved by part of the complex of D3 muscles but this seems better described in the next section, together with the effect of D3 on the C-D joint.

Opposing the extension caused by muscles C1, C5, and C6, is a flexion by C2, C3 and C4.

Anatomical Features of B Associated with Operation of B-C Joint.

Segment B is a short one. The muscle origins all occur across the dorsal and antero-lateral surface. All of this area is especially hard, a fact reflected externally by numbers of small rounded tubercles knobles. There are two distinct areas of muscle origin: a dorsal and distal area for C1 and D3 and a more proximal area for C2, C5 and C6. The bulges reflecting the origins of the two major antagonists, C2 and C6, are quite distinct.

C-D Joint (Fig. 53)

Muscle	Insertion L.	Pull L.	Comments.
D1	300-30	135	4 well-developed branches, one very short and separate.
D2	185-240	50	Two clear branches, probably separate muscles.
$D3^1$	260-290	60	Tendon at distal end only
$D3^2$		110	Apparent tendon at either end. Origin on B, distal 340°
$D3^3$	290-295	[illegible]	Acts on segment C, origin on B

The Anatomy of the C-D Joint.

The joint is the first in which there is a line-pivot. This is a straight line along which the abutting surfaces of C and D are held together so tightly that the whole acts as does the hinge of a door. The cross section of the joint therefore appears as the greater segment of a circle as has been indicated by the pivot line, pl. in fig. 53b. This arrangement results in movement being possible in one plane only, though this is not as strictly true as it is in the case of the di-condylic joint B-C. The line-pivot runs from 40 - 135°, so that the permitted movement runs through the anterior horizontal plane, i.e. directly through 270°. That part of the joint, from 135 - 40°, which does not constitute the pivot, consists of a soft wide arthrodial membrane. At either end of this, i.e. at the points nearest one or other end of the pivot, the membrane is crossed by a sclerite, whose nature and probable function will be discussed later (p. 203).

Functional Relations of the Muscles to the C-D Joint.

Here again the form of the ring diagram requires explanation as far as the muscle complex D3 is concerned. Reference should be made both to Fig. 52b and 53b. Muscle $D3^1$ originates in C and inserts upon D at the C-D joint. Muscles $D3^2$ and $D3^3$ arise together from a single origin in B, but while the former passes directly through C to insert upon D at the C-D joint, the latter inserts in C and its action is therefore upon segment C, not segment D. However, the muscles have so clearly a single origin that it seemed more reasonable to regard them as branches of a single unit.

The single line-pivot acts as does a door-hinge: from one side it can only be pulled, from the other only pushed. Since muscles can only pull and since the D1 and D2 muscles are definitely flexors, it is not surprising that segment C contains no musclar extensor. From the nature of the joint this is impossible. A muscular extensor could only act on the C-D joint by having an origin in the distal part of D and an insertion on the proximal part of C. No such muscles have been found.

The muscles have their insertions extending around almost the whole arc of the joint, excluding, of course, the pivot-line. The largest flexor is D1 which has a rotator effect in addition to its flexion. This rotation has an antagonist in the other large flexor, D2, so that its effect can be cancelled and the flexor effect summed when both contract together. In freshly killed animals, when D is extended to a limited extent, some slight rotation of the joint is possible, but it is difficult to detect any such movement in the live animal.

The remaining muscle, D3, constitutes a complex of three branches, each producing a different effect by its contr~~ibu~~action. $D3^1$ appears to flex D on to C, while $D3^2$ is the main muscle responsible for this flexion. $D3^3$, in addition to C1, C5 and C6, extends segment C from B. When $D3^2$ and $D3^3$ are contracted, D is flexed on to C, while C is extended from B. In the case of $D3^3$ a possible rotator action can once more be seen from the pull line, but cannot be put into effect because of the nature of the B-C joint.

A description of possible extension mechanisms will be given with the consideration of the E-F joint, and the problem of extension of D seems best left till then.

Anatomical Features of C Associated with Operation of ~~B-C~~ C-D Joint.

There are no marked specialisations of podomere C in relation to the muscle attachments.

The D-E Joint (Figs. 54 and 55)

Muscle	Insertion L.	Pull L.	Comments.
E1	31-47	150	Three branches, most proximal with long tendon.
E2	118-147	50	Two branches, more proximal of which has long thick tendon.
E3	167-177	20	
E4	173-186	90	
E5	185-194	117	
E6	207-217	160	Inserts on a thick tendon
E7	230-257	45	
E8	222-299	35	Many parts to this muscle but no clear branches.

The Anatomy of the D-E Joint.

The movement at the D-E joint is responsible for putting the claw in such a position that the flexion of F can be effective in grasping at prey or an enemy. As might be expected from the need for great freedom at this articulation, the D-E joint is universal or what Dillon (1952) would call non-condylic. The amount of twist is limited only by the degree of stretch possible in the encircling arthrodial membrane or in the muscles antagonistic to those producing the movement. At the same time, bending in the vertical plane is limited by sclerotisations; not those of a normal condylic joint but two hard, overlapping flaps projecting distally between 300-40° and 160-230°. (Fig. 55c). If the E segment is bent more than a few degrees from its normal position either in the ventral or dorsal direction, it touches against one or other of these flaps and no further movements can take place in that direction. As far as the E-F joint is concerned, these limitations placed on the movement of E by the form of the D-E joint are quite logical. Since F moves on E through the vertical plane it is unnecessary to have this movement in the D-E joint as well. Since

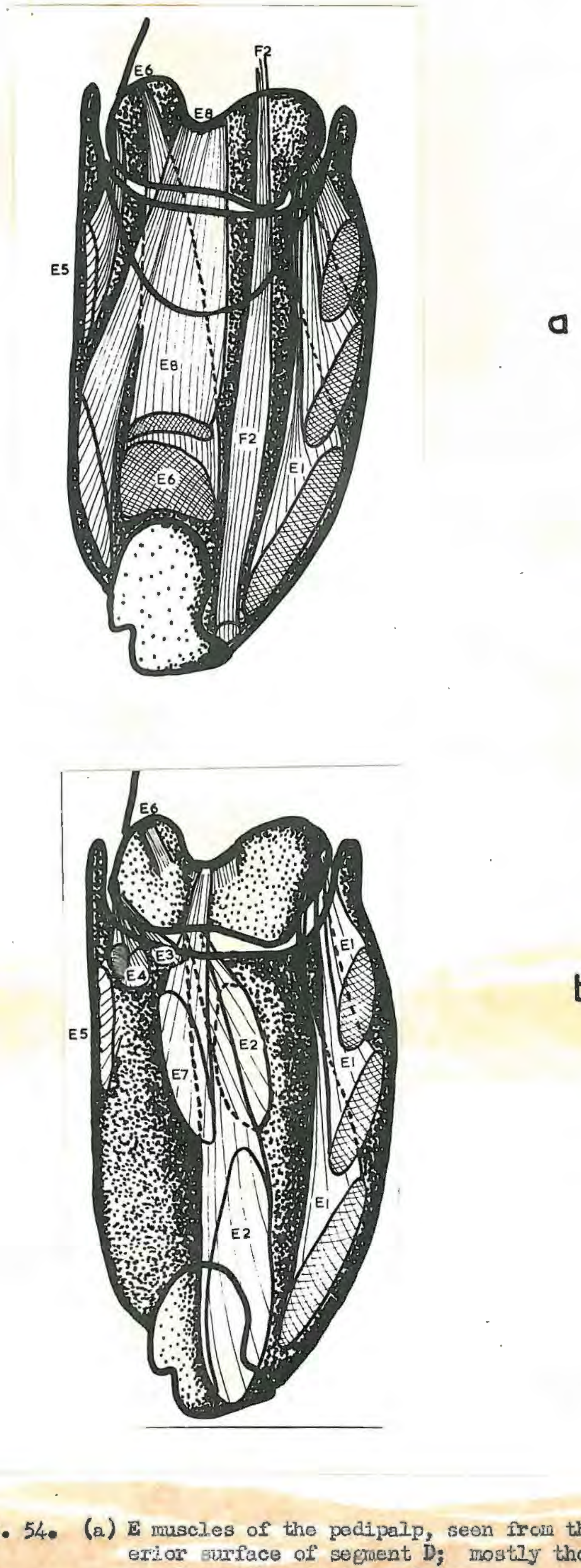


Fig. 54. (a) E muscles of the pedipalp, seen from the anterior surface of segment D; mostly those muscles with anterior origins.
(b) The same but showing mostly those muscles with posterior origins.

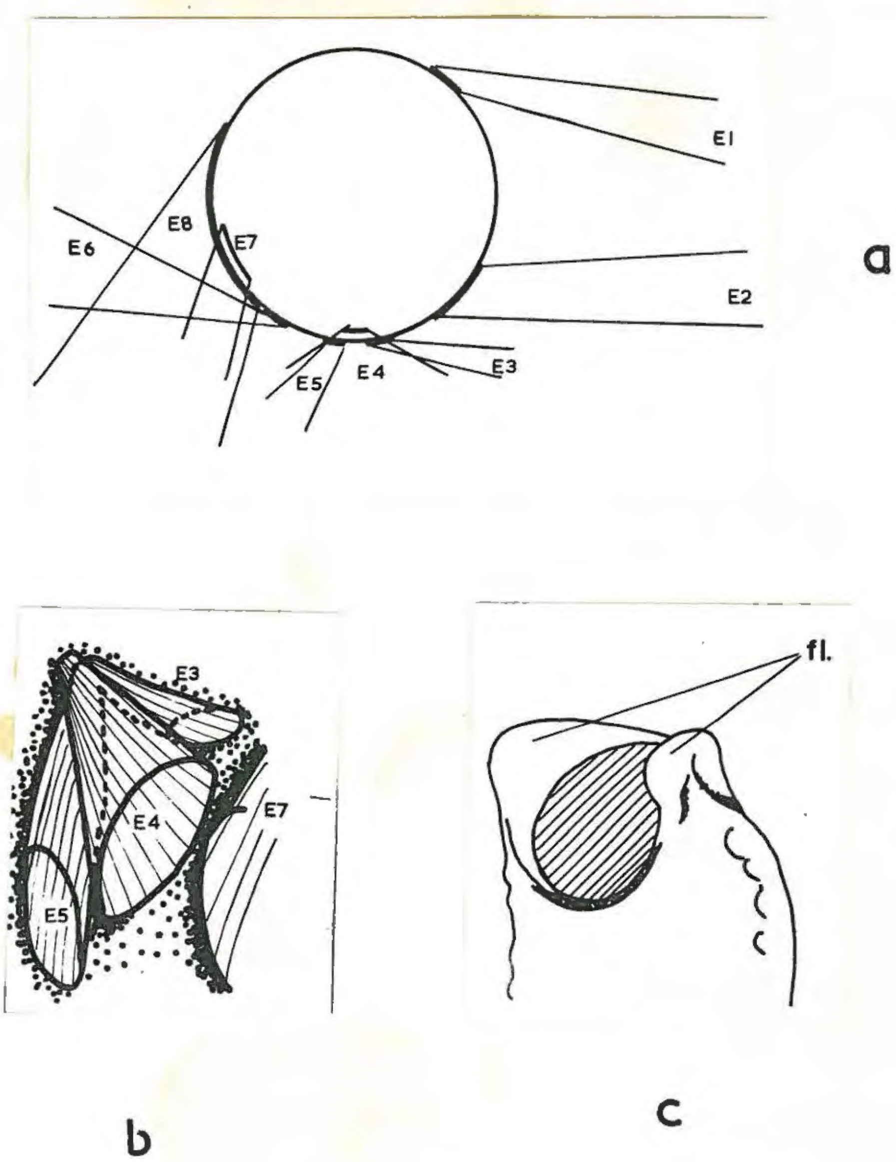


Fig. 55. (a) Ring diagram of E muscles of the pedipalp.
(b) Complex of muscles E3, E4 and E5.
(c) Structure of the distal end of the D podomere, showing flange, fl.; cross hatching indicates the cavity of the podomere.

it is probably easier to control action in this vertical plane when muscular movement is limited to one joint only, that is E-F, it is desirable that there be no possibility of this movement resulting in "give" at the D-E joint as well.

D-E can thus be described as a universal rotator joint with additional movement permissible through the horizontal plane.

Functional Relations of the Muscles to the D-E Joint.

As might be expected from the description of the anatomy of the joint,the muscles effecting the D-E joint are all to some extent rotators, with extension and flexion a rather secondary function. E8 is one of the largest flexors, inserted at the position optimal for this. It gives in addition a strong negative rotation from the fibres that take origin along the ventral and ventro-lateral parts of D (Fig. 54a). This rotation is assisted by E7 whose insertion is just distal to that of E8. Since the origin of E7 lies at about 160° and the muscle is fairly short, its flexor action is powerful. The last flexor, E6, has the antagonistic rotator effect, giving a strong positive twist.

Extension depends on two muscles only, E1 and E2. Alone, neither is very effective since insertion is, in either case, far from the position of optimal efficiency for an extensor muscle. Since the component of their antagonistic rotator effects lies in a pure extensor pull-line, it is presumed that E1 and E2 do normally contract together to extend E. Alone E1 gives a positive twist,while E2 alone would give a negative one.

Three small muscles, E3, E4 and E5, would all serve to pull E ventrally if the D-E relations would permit this. As it is,E3 gives a very acute negative rotator effect while E5 is less strongly a positive rotator. The functioning of E4 is obscure. Its fan9shaped form and straight line of pull suggest that it draws E in a ventral direction. However, this movement can be only very slight because of the nature of the joint, and it therefore seems probable that E4 comes into operation only when the main movement is being produced by some muscle that is less restricted in its action and a slight ventral movement is necessary to make the whole effective.

Anatomical Features of D Associated with Operation of the D-E Joint.

The most prominent anatomical feature concerned with giving area of origin to the E muscles is the great bulge on the anterior proximal face of D. This provides for the entire origin of E6 and also the more direct pulling fibres of E8. In some species of scorpion, e.g. Hadogenes, it is this bulge that is enlarged to produce a great hook (Fig. 56). It would not be surprising to find that in some aspect of the behaviour of such scorpions, this movement of positive rotation and flexion of the hand has become exaggerated and the enlarged E6 muscle which is housed in their hook has evolved with the behaviour.

A hard ridge running from 350° distal to 10° proximal carries the origin of the three large branches of E1 and, at its proximal end where it cuts in to the joint and forms a platform, it supports F2, the auxiliary flexor of the claw. This platform also houses part of the origin of the largest branch of E1. Running from 180° distal to 160° proximal is a second prominent ridge and on this the most acute rotator fibres of E8 as well as muscle E5 take origin. In the case of E3 and those E8 fibres which have not yet been accounted for, the actual edge of the segment is used for an attachment area; the distal arc 160° - 175° for E3, the proximal sloping area from 160-270° for E8.

The third hard ridge runs from 160° distal to 160° proximal and carries the origin of the main part of the two E2 branches. The last muscle in segment D, E7, uses both this ridge and the one mentioned immediately before for its origin.

The E-F Join/t. (Figs. 57, 58 and 59)

Muscle.	Insertion L.	Pull L.	Comments.
F1			Single, very large origin fills much of "bulge" of hand
F2			Origin in D, long tendon passes through E to insert on F
F3			2 branches, $F3^1$ with origin on outer face of hand, $F3^2$ on inner face.
F4			-
F5			-
F6			-
F7			-
F8			-
F9			Origin with F8, proximal to straight part of E-F joint
F10			2 branched
F11			-
F12			Short and stout.

The Anatomy of the E-F Joint.

As in the case of the C-D joint, E-F has a single line-pivot. This stretches from 160° across to 230° so that the cross section of the joint is represented as a larger segment of the circle than in the C-D joint. The cross-section of the E-F join/t is in fact more nearly the shape of an isosceles triangle with the line-pivot as base. The two abutting surfaces of the segments are tied together even more closely than are those of the C-D joint. In consequence of this tight bond there is no possibility of movement in any plane other than that through 10° and 190°. Again there are two sclerites stretching across the corners of the arthrodial membrane. As explained in the description of the C-D joint, this type of articulation allows either a functional flexor or an extensor muscle in its proximal segment: not both. In the case of E-F, the muscles moving the F segment are immediately adjacent to the immobile finger EE; the line-pivot is remote from EE. With this arrangement, the contraction of any muscles in the hand can only serve to flex the segment F towards EE.

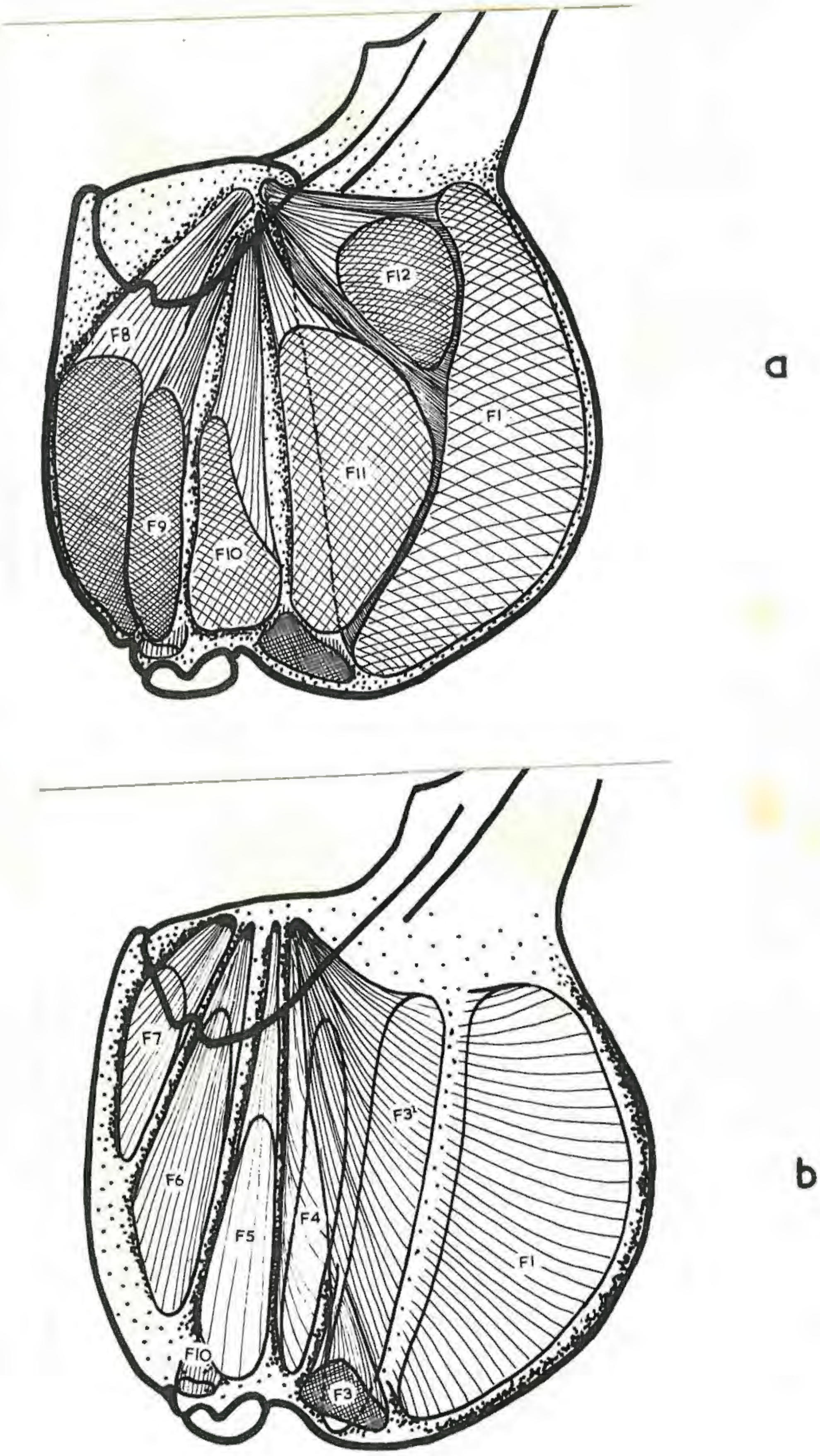


Fig. 57. F muscles, closers of the pedipalp claw.
(a) Those muscles with origin on the internal or anterior surface of the hand.
(b) Those muscles with origin on the external surface.

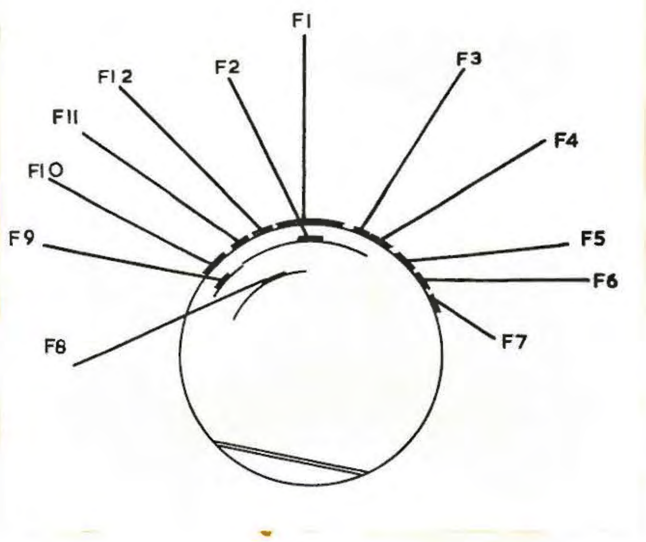


Fig. 58. Ring diagram of the F muscles of the pedipalp

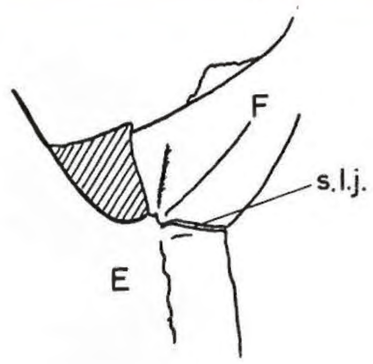


Fig. 59. Detail of the structure of the E-F joint of <u>O. latimanus</u> as seen from the outer, or posterior, surface; <u>s.j.l.</u>, straight line joint; the arthrodial membrane is cross hatched.

Functional Relations of Muscles to the E-F Joint.

If the nature of E-F will allow neither muscular extensors nor the activity of rotators, a single flexor muscle might be expected. The fruit of such an expectation can be seen in published descriptions of the muscles in segment E. Thus Snodgrass (1952) writes: "the hand of the chela .... is filled with a great mass of fibres all attached on the ventral process of the base of the moveable finger." In the case of O. latimanus at least eleven muscles appear distinct in origin and insertion. Discussion as to whether these really are distinct muscles or only branches of a single large diffuse muscle seems rather pointless. But if an accurate account is to be given of the action of this muscle complex, it is easier to regard the major branchings as true muscles; more especially as these are further divided and subdivided.

Determination of the angles of insertion is very difficult in this joint since all muscles insert over a short arc; furthermore, these insertions spread distally from the proximal rim of the F segment. No insertion occurs between 90 and 270° and it is only the "process of the moveable finger" that gives attachment to any muscles at all. Each of the muscles present in E flexes F on to EE and thus closes the claw. In addition, F2, a muscle which originates in segment D, passes between the muscles in E as a long, slender tendon to insert on F as an auxiliary flexor (Fig. 54a).

3. Functional Problems in the Musculature of the Pedipalps.

Two problems which were raised earlier seem best discussed in connection with the functional anatomy of this E-F joint. The first is the mechanics of extension without muscles: the second that the insertion which would appear to be optimal for a particular movement is not invariably found.

Extension without Muscles.

The problem of the mechanism of extension is the simpler, in that it has been recognised before. Snodgrass (1952) calls attention to the phenomenon in the scorpion claw, though not in the C-D joint or leg. In the case of the legs of spiders, the issue has been a controversial matter ever since it was raised in 1909 by Petrunkevitch. It seems reasonable to examine the attack made upon this question by the workers on spider anatomy and to see how this could apply in the case of the scorpion.

The most recent paper on the subject (Dillon, 1952) suggests that the problem is spurious, that arachnid~~s~~ muscles are many, complicated and liable to be missed in dissection and that, in the case of the spider leg, the extensor muscle or muscles have just been overlooked by previous investigators. ~~The basis of this contention will be discussed below (p.) but it is necessary to point out here that~~ Such an explanation is invalid in the case of the scorpion. Firstly, there is no evidence for the existence of any muscles other than those described above, though extensor muscles were specially looked for. In the case of the muscles of the pedipalp. not one functions as an extensor of either D or F segment. Every one of the muscles that insert on the C-D or E-F joints has been tested in the following way: one of the sclerotised points of attachment has been freed and the muscle pulled in its "normal" direction of action. In each case the muscle gave the functional effect that would have been predicted for it from a consideration of its line of pull. In no case was there any extensor action.

Furthermore, when the main nerve was cut be~~fore~~tween the ganglion and the joints concerned, and stimulated electrically, neither of the joints showed any signs of extension, flexion being the only active response. Again, animals were injected with 0.1 ml. $MgSO_4$ solution in the D-E arthrodial membrane. This solution was approximately isotonic with scorpion blood and should not have upset the osmotic relations of the limb to any great extent. Magnesium ions are said (Hoyle, 1953) to have a paralysing effect on an arthropod neuromuscular preparation and they appeared, in fact, to have such an effect. Contractions of the claw to mechanical stimuli got smaller and smaller, and ceased after a minute, leaving the claw wide open. The other claw, acting as a control, showed no such fall-off in reaction and within five minutes the experimental one was reacting normally once more. The fact that the claw was held wide open at the height of narcosis of the flexor muscle and that the claw would reopen if the joint was forcibly closed suggests that the extensor movement is not due to any muscular action.

Lastly, as will be remembered from the description of the form of the joints, neither C-D nor E-F could be extended by a muscle originating proximally, and there is certainly no sign of muscles in the segment distal to the C-D joint affecting C-D, while there are no muscles at all in F. It would appear from this consideration of the facts that there are no muscles effecting extension of either the C-D or E-F joint in the pedipalp, and another mechanism must be sought.

Since, as has just been shown, the extension of D and F segments is not dependent on muscles, a study was made of the behaviour of the C-D and E-F joints after these had been cleared of all muscles. Without any muscles present a freshly isolated pedipalp would show an automatic extension of each of the relevant segments as it was manually flexed. The actual course of the movement was watched under a binocular microscope and marked on to paper held beneath the claw. The measurements are all mean values from a number of trials.

The mean of the maximal extension in the claws of three different animals was 50° but it was quite clear that the rate of extension over those 50° was not the same. Up to 6° there is a quick opening, too fast to be measured. From 6 to 25° the opening is slower, of variable duration, and may take as long as 5 minutes. Under particular conditions, e.g. after greasing or wetting the articulation, this movement may be abolished and the claw will stay in the position in which it is put as long as this is between the extension angles of 6 and 25°. From 25° to the maximal degree of opening, a rapid jerk or "click" operates and the duration of the movement is once more too brief to measure. The claw may thus open to 6° then be pushed to 25°, remaining still each time the pushing stops. As the claw is placed in the 25° position it suddenly clicks open to its maximal extent. These observations immediately suggest at least two, possibly three, separate extension mechanisms. From the upper limit of their characteristic range of operations these three hypothetical mechanisms were named the 60°, the 25° - and the 50° - (or click-) mechanism. 6°?

The nature of the click is very like the snap as one end of a stretched piece of elastic is released; it brings to mind the "elastic interarticular membrane" proposed by Petrunkevitch (1910) as the explanation of the leg extension of spiders. Ellis (1944) states that, in the tarantula, the interarticular membranes at the joints concerned have no extensor effect. On the face of it, this appears a reasonable postulate in the case of scorpions as well. ~~[illegible] without the evidence.~~ If the "interarticular membrane" can act as an extensor in the case of the D and F segments, notwithstanding the fact that it has no particular features adapting it to such a function, it would appear inexplicable that, at the other joints, extensor muscles have been provided. The interarticular membranes, if capable of coping with the extension at two joints, would make the presence of extensor muscles redundant at any other joint of the limb. It would seem that, if the arthrodial membrane is responsible for the extension some special feature must be sought at the membrane of the joints concerned.

Further examination of the E-F joints of several species of scorpion suggests that such a special feature may well be present on the arthrodial membrane: it consists of the pair of "sclerites" which were described earlier (page 198). (Plate VIII) Another pair has also been described at the C-D joint, ~~and a further two are to be found on the E-F joint of the leg.~~ So far no reference has been found to these structures in the literature and, with ~~[illegible]~~ one exception which will be discussed later (p. 246), they have been found on no animal but the scorpion. In some species, e.g. *Uroplectes sp.* the light colour of the arthrodial membrane, as well as the sclerite, make the latter very difficult to recognise. It was thought that such considerations might explain the failure of Snodgrass to observe such a mechanism in his scorpion, *Centruroides sp.* Dr. Baerg of Arkansas University kindly sent across specimens of two species of *Centruroides*, *vittatus* and *suffusus*, for examination. The sclerites are clearly present in both pedipalp joints (Fig. 60b), an observation which was checked by Baerg himself in the States.

The position of the sclerites is important, in that it supports the possibility of their having an extensor function. At each of the joints where they occur there is (a) a straight line-pivot and (b) the lack of an extensor muscle: this type of sclerite has never yet been found where these two conditions are not fulfilled. It is true that, in the C-D joint of the leg (but not of the pedipalp), although there is no apparent extensor muscle, nevertheless no sclerite is present. In this case, however, the joint is not of a line-pivot type. In the three appendages, chelicera, pedipalp and leg, there are seventeen joints all told; amongst these only three show a line-pivot type of articulation. It is striking that each one of these three possesses arthrodial sclerites and lacks any muscular extensor. The case of the C-D joint of the leg will be discussed later and for the moment we will assume that there may be a connection between the sclerites and limb extension.

As can be seen from Fig. 60a, each of these sclerites runs

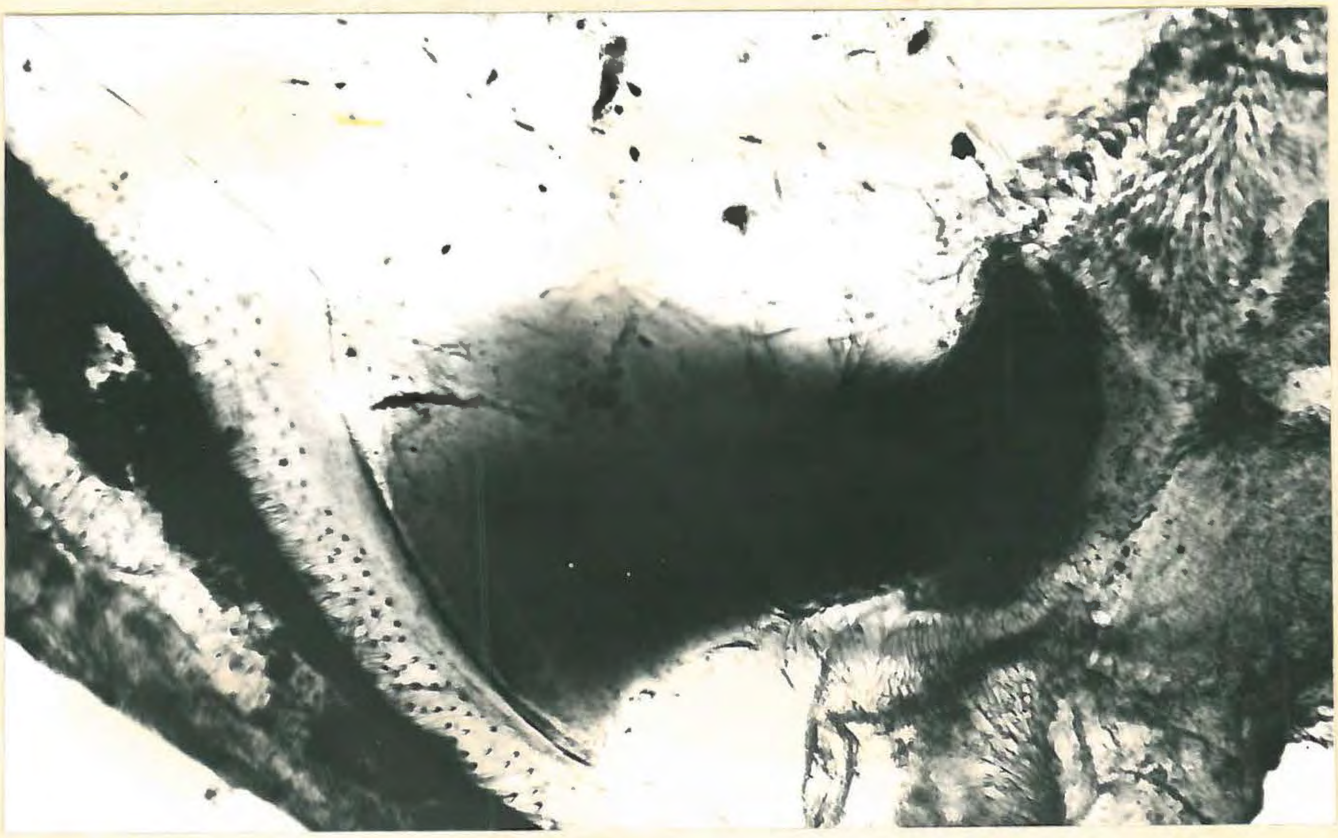


Plate VIII. Photomicrograph of a preparation of the E-F articular region of the pedipalp of O. latimanus. The sclerite shows up more darkly than the surrounding parts of sclerotised chitin.

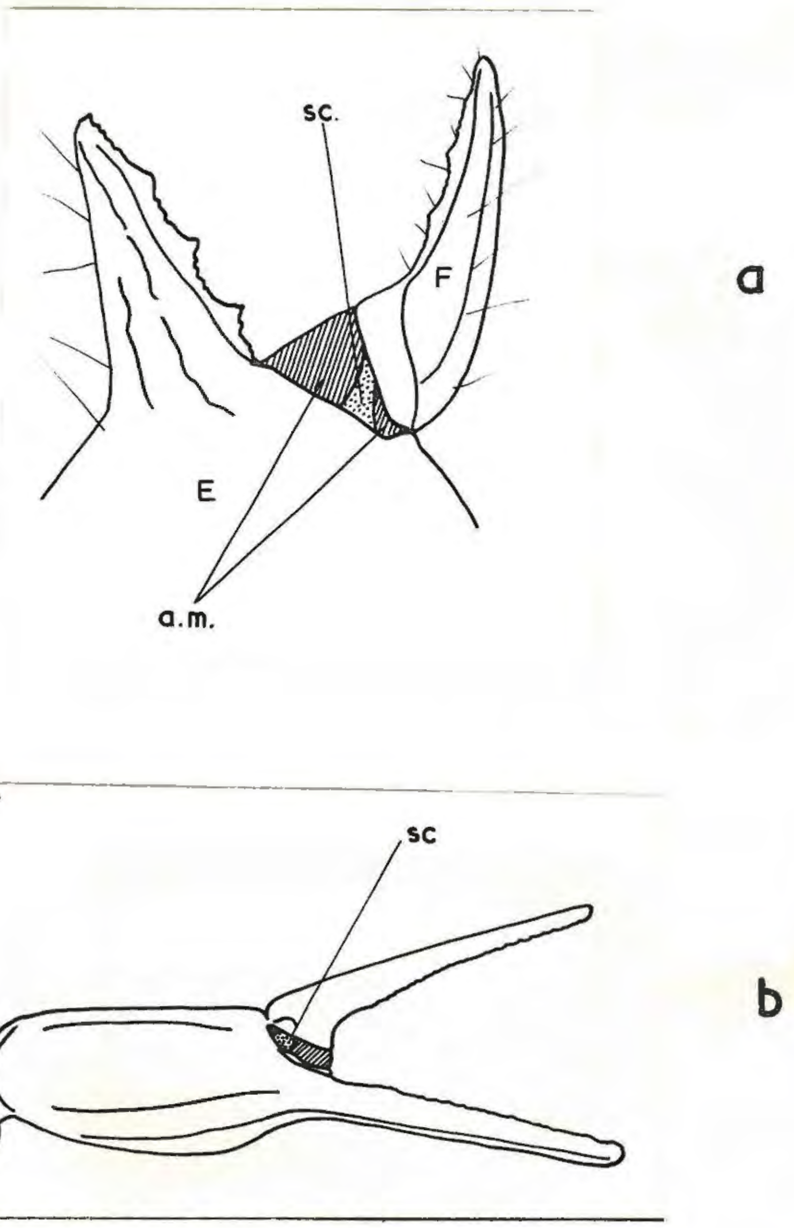


Fig. 60. (a) Chitinous sclerite on the E-F joint of the pedipalp/seen from the inner or anterior surface of the/hand. The soft articular membrane, a.m., is cross hatched, the sclerite, sc., lying across it, is stippled.
(b) Pedipalpar sclerite, sc., in Centruroides vittatus

in O. latimanus
(presumably

across the corner of the membrane as a small strap. When the joint is flexed the sclerite is folded from its "I" shape to that of an "N". Clearly it could act as a compression spring and might be able to develop sufficient force to extend the joint. Certainly the isolated sclerites offer considerable resistance to folding, but clearly further evidence is needed to demonstrate that the sclerites do in fact act so as to extend the joint.

as in all Museum specimens When a scorpion is killed in carbon bisulphide and fixed, the claws remain rigidly closed, presumably because the closer muscles contract and are fixed as the animal dies. If, however, the main nerve of the pedipalp is first cut and then the animal is killed and fixed, the claw remains wide open. Under these latter conditions, before the animal is stiff, the claw may be pushed closed and it reopens immediately. Cut the sclerites on either side of the E-F arthrodial membrane and the claw will stay in whatever position it is put or open partially. This operation may be carried out on the C-D joint and here too the results point to the sclerites being responsible for the automatic opening in the freshly killed animal. If the sclerites are both cut on a living animal, it will walk about with the control claw open in the normal way, but the experimental claw remains closed. It is true that this claw can be opened slightly, but in no circumstances has a claw ever been seen to open maximally once the sclerites have been destroyed. Finally and most convincingly, use may be made of a claw from which all muscles have been removed. If it has been treated so that the 25° mechanism has been abolished, i.e. so that the finger will stay fixed in any position from 6-25°, opening from 25-50° is a click, while both sclerites are intact. Once one of the sclerites is cut on this claw, the click disappears and only a fairly fast opening occurs, taking about 5 seconds. If the remaining sclerite is cut, the movement ceases and F will remain stationary in any position between 6 and 50°. If the interarticular membrane itself is cut before the sclerites are destroyed, the claw continues to open automatically so that Ellis' conclusion that the interarticular membrane in the

closing

Tarantula plays no part in extension applies also, sensu stricto, to the scorpion. The actual arthrodial membrane does not function as an extensor mechanism by virtue of its elasticity, but in the scorpion it does so indirectly by way of the arthrodial sclerites, structures which so far I have not observed in any spider.

Snodgrass (1952) comments on the lack of a muscular extensor in the scorpion claw and suggests that extension is effected by the "elasticity of the hinge of the finger of the hand" which "keeps it open until closed by the finger muscles." He goes into no further detail nor does he figure the "hinge" so that it is not clear exactly what he meant by the term. He makes no mention of the condition in the C-D joint where presumably a similar state could be expected. In spite of this, it seems most probable that "hinge" refers to the structure that has been called the "pivot" throughout this study: indeed, if all the soft tissues, the arthrodial membranes and sclerites are removed from the E and F segments so that only the segments and the pivot remain, the finger does in fact reopen on its pivot if it is closed manually. This opening is only to 6° and, since it would appear that little further can be done to investigate the matter without destroying the joint altogether, it will be assumed that the basis of the 6° opening lies with the pivot itself.

So much for the click-and-6° mechanism, and we turn to the question of the opening from 6 - 25°. It is quite clear that, if the sclerites and pivot were functioning alone in extension, this 6 - 25° would probably be the range least effectively controlled. When a sclerite is in the maximally folded state, namely as a of Fig. 61, the pressure that it exerts is being wasted because it tends to push the E and F segments apart horizontally, force h of Fig. 61a. What is wanted is a force which pushes them apart vertically, v of Fig. 61c. As the sclerite is further unfolded (b of Fig. 61) its h force is transformed more nearly in to a v force, that which would most effectively separate E and F. It might well be that in the claw cleared of muscles, the mechanism at work from 6 - 25° is just this weaker stage

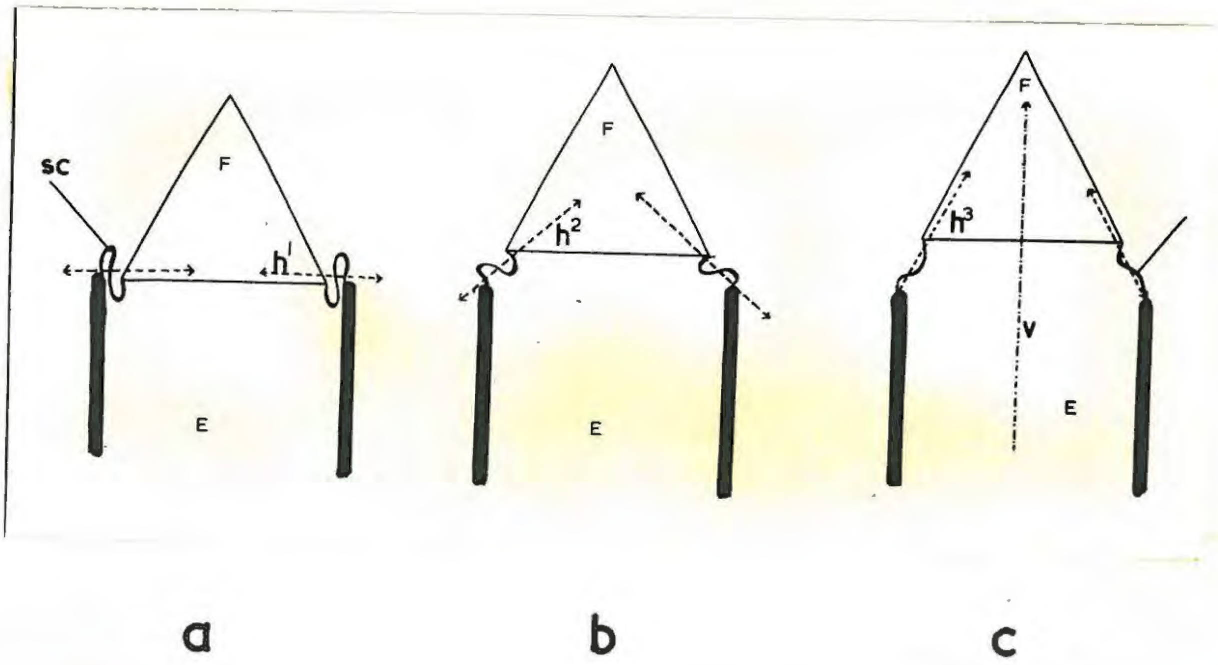


Fig. 61. Representation of the mechanics of the opening of the claw in the pedipalp of *O. latimanus*. As the triangle **F** moves vertically away from **E**, swinging on the straight line joint, the claw opens. The two sclerites are represented by the thin curved lines, *sc.*, connecting **E** and **F**. In (a) they are folded to an "N" shape and any force they exert in an attempt to unfold is expended along the line h^1 which is at right angles to the force *v*. (cf. Fig. 61c) which is that required to open the claw. As the claw opens (b and c), the force of the unfolding sclerite h^2 and h^3 respectively, more closely approximates to that of *v*.

of the click mechanism. However, several observations speak against this being the case in the normal animal. In the live animal or freshly isolated claw there is no sign of a weak range of extension. There would seem to be no reason for assuming that the process of removing the muscles affects the initial unfolding of the sclerite more than the final. Again, in living animals which had the sclerites removed from one claw, a full opening was never seen but the claw could clearly be opened about as far as 25°.

Indeed, from the limitations of the sclerite mechanism which were considered above, one might expect the additional mechanism to work most effectively over the initial stages of opening. With the exception of that part controlled by the pivot, this is the range over which opening appears to be most slowed down in the "demuscled" claw. It is over this range that a mechanism suggested by Ellis for spiders would work most effectively, namely extension produced by a rise in blood pressure. Such a mechanism would undoubtedly be upset more than either pivot or sclerite by the opening of the segment and removal of the muscles. These appear sufficient grounds anyway for investigating the possibilities of such an extension in the scorpion.

In O. latimanus it is noticeable that during the movements of the claw, the degree of bulging of the arthrodial membranes varies. This raised the question, "Is the converse true? Does the degree of bulging of the arthrodial membranes affect the claw movement?" Using either a freshly isolated claw or an entire animal recently killed, flexing C segment on to D puts a pressure on to the C-D arthrodial membrane and the claw opens. Straightening C-D causes the claw to close again. It seems that the increase of fluid pressure, as the arthrodial membrane is constricted, "blows" the F joint into the extended position. An attempt was made to test whether it is mechanically possible to extend D and F with fluid pressure. A limb was amputated at the A-B joint and fine rubber tubing filled with Ringer solution was fitted over B. The tubing was connected to a plastic bottle so that the pressure could be increased by constricting the bottle. The claw was held partly closed by the weight of a glass recording lever fixed directly on to the finger. With pressure on the Ringer, the arthrodial membranes were filled with liquid and the claw opened. When the hand was not fixed for recording of the claw movements, a similar extension of segment D could be seen. As soon as the liquid was sucked back, the parts were flexed once more. It is clear from this observation that, as far as the mechanics of the joints go, blood pressure could cause the extension of both D and F segments of the scorpion pedipalp. However, this can be shown for the locust tibia as well, and there is no reason to believe that this animal does not use its extensor muscles, so that the next question is whether this hydraulic opening does occur naturally in the scorpion.

Ellis (1944) made a study of the blood system of the spider leg and reports a vascular supply whose peculiarities, he implies, are concerned with the extension of the leg. In the case of the scorpion no detailed study has yet been made of the blood vessels of the pedipalp. An attempt was made, however, to interfere with the pressure relations within the appendage. If the tip of a spider leg is cut off (Ellis) the animal is no longer able to extend its leg. The tip of F was cut off so that a blood flow was established. The scorpion, however, was still able to extend both finger and D segment in the normal manner. The fact that the wound was still bleeding indicates that the phenomenon is not explicable in terms of a pressure built up behind a blood clot. If a rise of blood pressure "blows" F into the extended position one might expect a drop of blood at the cut surface of F to pulsate as the claw opens and closes in a live animal: such a drop was watched under the binocular. No pulsation was visible though the blood was clearly not in the form of a clot. If the sclerites are also cut the claw will not fully open after this, but clearly some extension is possible beyond that to 6°. Also, when in an isolated pedipalp, that has both its tip and sclerites cut off, the internal hydrostatic pressure is raised, the piece of F that remains is extended. It is true that the opening is not as effective as it is when the tip has not been removed, but it is nevertheless possible for the fluid presure to extend the claw maximally.

Superficially these observations seem to imply that "natural" changes of blood pressure are not important in claw opening in the scorpion. However further tests were made.

An attempt was made to reduce the blood volume of the animal by desiccating it over $CaCl_2$. After several days the animal seemed slower at opening its claw and finally the claws were not opened at all. If forcibly opened they slowly reclosed. The animal was in such a bad condition that it was unable to drink on its own. An injection of 0.3 ml. Ringer was therefore made into the animal at the C-D joint. This caused both claws to open slowly. The animal was left for half an hour, by which time it was walking slowly about. It drank water after a little persuasion and it was clear that the use of the claws was returning. They were held open unless the animal was stimulated mechanically, when they would snap shut and then reopen if the object stimulating the animal was not caught. The course of observations made it clear that, when the ability to open its claw is removed from a scorpion by desiccation, it can be returned by increasing the water content of the animal. The result, however, is equivocal in so far as it does not distinguish between a direct effect of the water on the opening mechanism and an indirect one on some factor inhibiting the opening. It is possible that desiccation produces an effect of rigor on the closing muscle, thus preventing the opening mechanism from functioning although it would otherwise be perfectly able to do so. The water might alleviate the muscle effects and so allow opening. Since rigor effects of desiccation would most likely be due to the great increase of osmotic concentration around the muscle and alleviation be due to the dilution of this, theeffect of injecting a Ringer of three times the usual concentration was tried.

In this case as well the effect~~s~~ of the injection was to allow the scorpion to open its claws once more. The observation as a whole, and also the rapidity with which capability returned to the claws, indicate that loss of the power to open the claws was due to the lack of fluid in the body rather than any resultant concentration of tissue fluid.

As yet the blood pressure has not been measured but from the manner in which it spurts from any prick through the scorpion skin, it must be fairly high. necessarily this happen

The observations quoted above are unequivocal, but those involving removal of the distal portion of segment F appear to speak against any hydrostatic mechanism being involved in the extension of the segments F and D. This need not, however, be the case. There is one point which must first be considered. It is clear from the animal's behaviour that extension of F and D may occur separately and the extensor mechanism may be expected to act independently on either joint. This could not be provided by the indiscriminate blowing effect of the"Ringer pump" and indeed, when the tip of F was removed and pressure applied to an isolated limb, Ringer could be forced out of the wound as the claw was extended. Of course it is true in the living animal that if F and D were both flexed and the animal needed to extend D only and to keep F closed, the closer muscles of the hand could be entirely responsible for preventing F segments reacting to a general rise in pressure in the pedipalp. The blood pressure would thus be selectively effective and extension would occur only where the flexor muscles were quite relaxed. It seems as well, however, to look for a blood pressure mechanism whereby the two segments may be extended independently. The system suggested for the spider leg by Ellis is, in fact, of this type. The main blood vessel of the leg runs dorsally except through the two joints which are without extensor muscles. At each of these it dips ventrally and gives off a branch which runs down towards the articular membrane. Ellis suggests that the main artery is occluded and the branch filled to "balloon" out the articular membrane and thus extend the joint.

If this were true for the scorpions, cutting off the finger distal to the E-F joint would mean cutting the F artery after it had given off the branch to the arthrodial membrane. Little bleeding might be expected from the cut during the extension movements since the blood that flows in the F artery during flexion would at this time have been diverted into the arthrodial branch. This assumption would explain why the living animal can extend its claws quite easily even after the finger has been cut and the sclerites destroyed. This fact, that the damage created by cutting the finger lies distal to the point where the mechanism is at work, would also explain how the isolated pedipalp may have its claw extended by Ringer being blown into it, though bubbles of fluid are leaking out at the cut surface.

The lack of any blood pulsation at the tip of the cut surface is also explicable in terms of a blood pump working on the same principle as that suggested in the spider leg. No blood spurts out as the claw is extended because the cut is distal to the part which is being engorged with blood and there is a block between the two points. As the claw is flexed the blood is not sucked back from the cut tip because at this time blood is being released into the main artery from the blood pump. Under the conditions assumed in the hypothesis developed by Ellis, an interference in the blood supply might be expected to upset the opening mechanism only if it is made proximal to the joint concerned, i.e. interference with the main artery in the D-E joint might be expected to foul the opening of the claw. Such a cut was made, and it caused a definite fall in the speed of the opening of the claw. The blood loss seemed greater during the extension than flexion. However, maximal opening was still possible at times. Both sclerites were then cut on both sides; ~~[illegible]~~ the claw was now kept almost entirely closed and what little opening occurred could well have been due to the action of the pivot mechanism alone.

As the matter rests, no evidence speaks against an extension by blood pressure. Support lies only in the observation recorded above, the results of desiccation and water loading, and the fact that it is mechanically possible to extend the joints concerned with very little fluid. In addition, however, this mechanism would make good sense when combined with another of the sclerite type, for when the claw is maximally closed and the sclerite most ineffective, the whole of the base of F is exposed to the pressure of the blood. ~~Lastly, as will emerge later from a consideration of arachnid phylogeny, this mechanism would fit in well with the history of the scorpions as presented in this study~~. However, before anything more definite can be said on the subject, the anatomy of the scorpion blood system must be investigated to see whether there does in fact exist a mechanism capable of selective extension of the two joints by blood pressure. Until this is done, it is as well to notice that, though one and even two methods of achieving a single end have been found in a single animal, there is always the possibility of a third being used in addition.

The Form of Muscular Origins and Insertions.

Turning to the second problem, namely muscles inserting in what are apparently suboptimal positions, examples could be taken from the B-C, C-D, or E-F joint, but the phenomenon is perhaps best illustrated by looking at the insertion of the F muscles on to the F segment. Considering the mechanics of the system only, it might be expected that, to obtain optimal effects of flexion, the muscle insertion should lie diametrically opposite the pivot line and not to one side of the mid-line. As has been pointed out, the two major flexors do in fact insert at the optimal position on the E-F joint. The rest, however, insert on to F in an arc of about 90°. This peculiarity might well have arisen during the conversion of a walking leg to a pedipalp and might be ascribed to morphogenetic limitations arising from such a conversion. This hypothesis seems groundless, however; the leg segment corresponding to "F" of the claw is moved by a single straight-pulling muscle and none of the complexity encountered in the pedipalp is found here.

The origin of the peculiarity might again perhaps be sought in the events associated with the increase of musculature necessary to make the claw efficient. It is clear that only a limited number of fibres pulling on a particular point can be effectively "straight-pulling". Though F1 is considered as a straight-pulling muscle, it is obvious that this is the pull line of only the majority of the fibres. With this in view it appears that two possibilities are open to an animal that needs to increase the amount of muscle pulling on a joint.

(1) The first is to modify the form of the segment containing the muscle so that it can accommodate a greater number of directly pulling fibres. This could be done in one of two ways: (a) the base of the segment may be thickened so that a cone of fibres may be formed with apex at the insertion; (b) alternatively, the device used by the anomuran crabs may be used, namely an endoskeletal plate acting as a bed for muscle origins may be built into the hand.

(2) The second possibility is to keep the base of the segment light and to have additional muscles pulling obliquely on the insertion. There appears another choice in the way that this is brought about: (a) the new muscle slips may either be attached to a common tendon pulling at the "optimal" insertion, or (b) each may be given a separate insertion on to the joint. In both these cases, the scorpion has followed the line from the second of the alternatives: it has additional oblique muscles and has given these separate insertions on each side of F1.

While the course followed in the evolution of the claw muscles is clear, the elucidation of the mechanical factors which led to the selection of the existing organisation must inevitably involve speculation. Nevertheless, the question will be approached in the following manner. The claw of the scorpion and that of the crab will be assumed to have evolved to the same sub-chelate condition: both are in need of only slight modification of the fingers but vast enlargement of the musculature to produce an efficient "claw". Evolution may be envisaged as running along the following lines:

Consider Fig. 62, I. The only difference between the situation in the scorpion and the crab is that the latter has the opener muscle, B, as well as the closer muscle, A. The problem in either case is to increase the area of origin for A without affecting the insertion angles to any great extent. This seems possible in one or more of three different ways.

Method 1. The joint line (Fig. 62, IIa) may be rotated so that the point p moves proximally and the origin of A can be increased by the distal movement of A^1.

Method 2. Keeping the point A^1 fixed, the origin of A may enlarge upon the proximal face of the segment, with a corresponding enlargement of the base, so as to accommodate the greater origin of A and the E-D articulation (Fig. 62, IIb).

Method 3. Finally the area of origin may be increased by the development of an endoskeletal plate running distally in the muscle A and offering a greater area of attachment for fibres of this muscle (Fig. 62, IIc and d).

In the case of crabs, 1 would not prove satisfactory, as the rotation of the joint to the position shown in IIa would necessitate an alteration in the direction of the pull of the opener muscle B which involved moving its origin to the position shown in IIa - in which there is no skeletal support available.

Where the animal's behaviour makes no call of "snapping", i.e. efficient opening as well as closing, it may well be that the crab claw does in some cases have the joint at less than a right angle to the long axis of the hand. In <u>Potamon perlatus</u>, for instance, the joint line is about 65° from the long axis of the propus. In the main, however, methods 2 and 3 have been adopted by the crabs. The

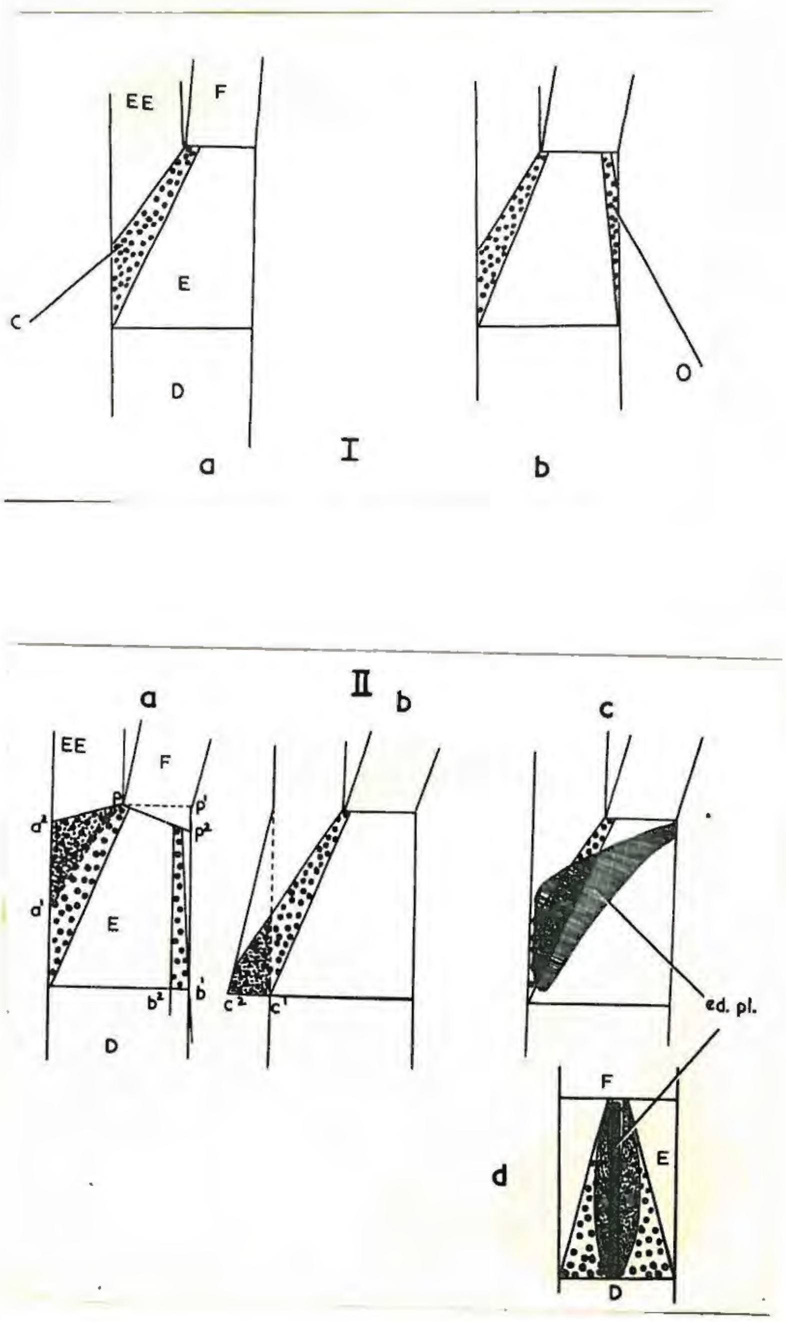


Fig. 62. Representation of possible solutions to the problem of the development of extra muscle origins within the claw of a scorpion and a crab. With the exception of **IId**, all representations are those of muscles acting in the plane of movement of F on E.

I. Small unspecialised muscles of hypothetical ancestors
  (a) Only closer muscle, c., present, as in scorpions.
  (b) Smaller opener, o., present as well as closer, as in crabs.

II. Three different solutions which allow the closer muscle to retain the same pull angle.
  (a) Solution by swinging the line of the joint from P-P^1 to P-P^2. New origin made available is A^1 to A^2. However without shifting the insertion of the opener or changing its angle of pull, the change of orientation of the pivot line results in the muscle having no possible origin, b^1 - b^2 not being part of the exoskeleton.
  (b) Solution by bulging out exoskeleton at the side of segment E. New area of origin, C^1 - C^2.
  (c) and (d) Solution by inserting endoskeletal plate, ed.pl.; d is schematized section at right angles to that of IIc and shows the extent of the new origin provided by the endoskeletal plate.

propus is broadened at its base so that its articulation with the carpus covers only a limited central area (Fig. 62, IIb). In addition, there is a strong endoskeletal plate in the propus and this takes the origin of many of the closer fibres.

The scorpion~~s~~, lacking an opener muscle, seems to have concentrated on making the E-F joint oblique. In *O. latimanus* (Fig. 47) it is about 25° from the long axis of the hand. In those species in which there is a powerful closer muscle developed, that portion of the hand on which the Fl line-of-pull ends has been bowed out considerably to give Fl a larger area of origin. That is, following the modification of the joint line E-F (Method 1), the form of the segment E is modified in some cases to enhance the area of origin (Method 2).

When further closing power is required, greater bowing of the E segment to enlarge the origin of Fl becomes impossible without upsetting the balance of the hand; additional closer muscles are added but they have to take their origin on the free areas that remain in segment E. The geometry of the segment compels muscles using these origins and a flexor insertion to operate with a very oblique pull.

It is now necessary to turn from a consideration of flexor origins to flexor insertions. The question arises "what determined that these additional muscles should have separate insertions and not be attached on the common tendon with the Fl insertion?"

An examination of the geometry of the system, together with experiments with models, suggests that the arrangement of separate insertions may sometimes be more efficient than the employment of a common tendon. Two relevant effects appear to be coming into play in the closing movements. If a muscle is not straight-pulling but has its insertion on the apex of the moving member, it will waste part of its force in pulling the apex towards its origin. Again, if the apical insertion already carries a direct pulling flexor muscle and the coflexor muscle, oblique because of its origin, inserts with the major flexor, then the coflexor will pull the major flexor out of true, and some effort will be wasted.

These effects have been studied upon a model of the joint acting against the force developed by a strip of rubber. Such a system is represented diagrammatically in Fig. 63. The pull-line of a muscle is represented thus: the insertion is denoted by the first letter, A, B or C of the fig., the origin by the subsequent number, 1, 2, 3 or 4 of the fig. A1 is thus a muscle with "optimal" insertion and with direct pull; B3 inserts sub-optimally and has an oblique origin while A3 shares the optimal insertion with A1 and pulls to the origin of B3.

The first issue is that of the shared insertion. If a force of 10 gms. is applied to both A1 and B3 simultaneously, and then to A1 and A3, the joint closes further with the former arrangement than with the latter. Of course, 20 gms. acting on A1 alone will be more effective than either of these arrangements. However, it is clear that the effect is not due to B3 having a more efficient position than A3 because when a 10 gm. weight is put first on A3 and then on B3, the joint is closed to the same degree in either case. From this result the conclusion is drawn that A3, by pulling A1 out of true, "wastes" some of the effort which could go into the A1 pull. At different angles of claw extension the same phenomenon can be seen, and in each case the effect is slight but quite clearly distinguishable.

The consequences of the development of a common tendon as distinct from a shared insertion can be studied by producing a further pull, not on the A insertion but on to the A1 muscle itself, a of Fig. ~~20~~ 63. The effect of A1 plus a2 is less than that of A1 plus A3, which we have just seen is weaker than that of A1 and B3.

From these results it appears that:

1. The coflexor may be less effective in assisting the major flexor if they pull on a common tendon, and
2. A more effective system may result if the coflexor insertion is moved along the arc to a position further from the "optimal"

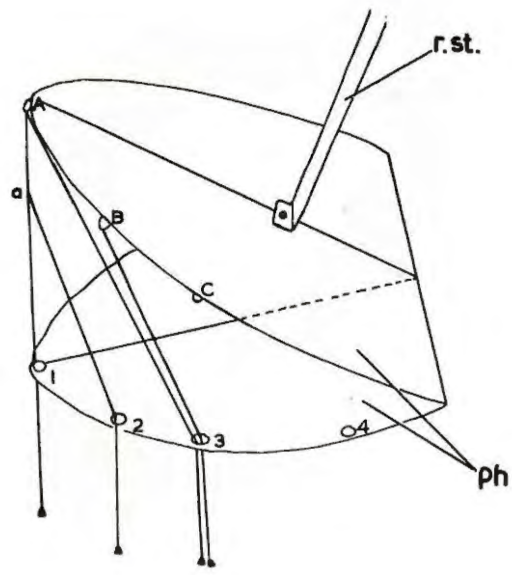


Fig. 63. Diagrammatic illustration of a model used in testing the effectiveness of separate or shared insertions of muscles closing the claw. Weights, represented by small triangles, attached to threads, can pull the two wooden flanges, ph., together, acting against the strip of rubber, r.st. Insertions are marked by the letters A, B, C and a; the origins which determine the angle of pull of the thread are 1, 2, 3 and 4.

insertion, i.e. from A to B.

This raises the question: "Supposing the insertion of the coflexor is remote from that of the major flexor, so that there is no interference with the pull of the latter, is the insertion of the coflexor still critical to any extent?". As had already been seen, the effect of a 10 gm. weight on A3 and B3 is the same. If, however, an equal weight is put on B3 and then on C3, or alternatively first on C4 and then on B4, the muscles with the B insertion are in both cases clearly more efficient closers than those with the C insertion.

Such an effect arises from the fact that the moment of the force at B is greater than that at C so long as the muscles are not pulling very obliquely. With a very oblique pull on B, the reduction in the effective vector will outweight the effect of the advantages gained from an increased moment. In practice, the advantage ~~gained~~ gained by a larger moment appears to be the greater and to limit the extension of insertions towards the pivot.

There are then two opposing effects determining the position of insertion of the co-flexor of a direct pulling muscle. To obtain maximal advantage from the moment it needs to be inserted as close to the apex, that is as close to the major flexor insertion, as possible. But, as we have seen, too close an approximation limits efficiency as the co-flexor tends to pull the major flexor out of true. A compromise is necessary and results in the major flexor and coflexor having distinct points of insertion.

Functions of Pedipalp Segments.

Before we attempt to work out the functions of the segment A, it may be useful to look at those of an hypothetical generalised limb. These can clearly be divided into two classes; in the one the important component of the segment is the joint, while in the second class, the podomere proper plays the dominant rôle.

Consider the former class first. The most obvious example of this is the use of a joint to give extra mobility to the limb, so that it can be made to bend further in a given direction. The extra bend may be used in the activity of the limb, or may be of more importance in tucking the limb out of the way for protection. Instead of an extra bending, a certain joint may be responsible for a bend in some plane particular to itself. Like that of the rotating insect-trochanter, the movement of a joint may affect the whole limb and sometimes only one joint is capable of effecting this particular movement.

In the second class the podomere plays the dominant rôle. In certain cases a podomere may have particular importance as a site of attachment of muscles. In others it acquires functional importance in being bent so as to give the limb axis a new plane of direction in which it can be held without extra muscular contraction. Again, the podomere may be especially elongated so as to increase the length of the appendage as a whole. In ambulatory appendages a single extension of a podomere may raise the centre of gravity too far from the ground for stability. In this condition the adjacent joints become of importance for their flexion allows a compensatory lowering of the body. The extra length can further be inconvenient in those limbs which are folded away when not in use. To meet this difficulty an adjacent podomere may also be elongated to permit a balanc~~ing~~ed folding pattern. Lastly, a particular podomere may be used for the manipulation of material of various kinds, e.g. food, nest-building material, water streams. This manipulation may be in conjunction with another segment, e.g. in the claws of scorpions, or alone, e.g. in the intromittent organ of a spider's pedipalp or the scaphognathite of the decapod maxilla. Other categories of segment function will become apparent in the discussion of the pedipalp segments.

It must be made clear that when the principal functions of the limb podomere or joints are being discussed it is normally not possible to distinguish whether the structure depends on the use to which it is put, or whether the animal does what it can with the material available. In part, however, this study can be used for this discrimination. The pedipalp, as has been repeatedly stated, must be derived from a walking leg. Where the two structures are essentially similar, as in the relative lengths of the first four podomeres, the modifications of behaviour associated with the function of the pedipalp have been grafted upon the structure inherited from the "leg-form". Where the corresponding parts are very different, the behaviour specific to the pedipalp has in some way influenced the pedipalp structure to a large extent. Further discussion along these lines will, however, be given in the section on comparative anatomy.

Now to return to segment A. In a consideration of the movements and therefore to some extent the functions of A, it must be noticed that, of five sets of muscles, four are concerned, in part at least, with the movement of A to and from the mouth region. Only A2 has almost no component acting through the 270-90° plane. The fact that the chelicerae, the joint articulation and the gnathobases limit the dorso-ventral movement, supports the hypothesis that these lateral movements are the most important.

The general facies of the podomere reflects three functional considerations. Because of the dorsal ridge and the hardened ring about its proximal joint, segment A provides suitable areas of origin for the many muscles operating the important A-B joint with its universal articulation. Secondly, it is sufficiently long to permit segment B, which can move in a plane at right angles to the main action plane of A, i.e. the 360° and 180°, to be clear of the chelicerae, limbs and gnathobases. None of these functions takes into account the lateral movement which has been postulated as the most important of the segment.

A feature which has, however, not yet been taken into account in the possible functions of A, is the soft, hair-covered portion forming the median side of the segment (see Fig. 47). When the segments A of right and left sides are apart, i.e. A6 and the other muscles which assist it are relaxed and A3 is contracted, these parts form the sides of a hairy preoral cavity, whose other limits are the labrum and the gnathobases (Fig. 7). There is a possibility that the muscles of the pharynx contract in anti-phase to those of the walls of the pre-oral cavity. This will result in fluid being driven into the distended pharynx by the walls of the preoral cavity. The preoral cavity and the pharynx will thus act together; the main suction may well come from the pharyngeal apparatus but it could be assisted by the pumping movements made by the walls of the preoral cavity. In favour of this view are the following observations.

When the animal is feeding and not trying to hold prey with its claws, not only the base of leg I but the whole of the pedipalp moves regularly. The movement of the latter can be seen to be initiated from the A segment, for though this is not visible, the A-B joint is, and there is no flexion at this or any of the more distal joints. It is therefore clear that it must arise from the movement of segment A upon the body; a movement dependent upon such muscles as A6, A5, together with A2. Such a movement is in keeping with the suggestion that pumping movements of the preoral cavity are involved in feeding.

The formation of the joint, the distribution of the muscles, the soft, hair-covered membrane of the medio-lateral regions, and the movements of the other segments during feeding, all point to A serving a gnathobasic function as well as the other functions postulated above.

Turning to the function of the A-B joint and B segment, it may be remembered that at the close of the consideration of the function of the B muscles, the conclusion was reached that these and the A-B joint allowed almost any movement of B on A. This would imply that this part of the pedipalp is of considerable importance in general movements of the limb. Two possible measures of this importance will be quoted. The first is achieved by merely painting a white dot on the B segment and watching this through much of the undisturbed behaviour of the animal. This was done for each one of the pedipalp segments and, comparing the resulting observations subjectively, the B segment does appear to originate more of the movements than the other more distal segments. The second intimation of the importance is of a more striking nature, though not as reliable in that the animal concerned had been tampered with. After certain experiments on the scorpions, the wound made was blocked with plasticine, the animals were fed and put back into their dishes. In many of these cases the main pedipalp nerve had been cut in the proximal part of segment C. Thus the only possible muscular movements of the pedipalp that could be initiated from the central nervous system were those involving the A or B muscles. In spite of this the pedipalps can be moved in so natural ~~a~~manner both in threat and in attempts at eating that it needs some attention to notice that the more distal segments are not being moved at all relative to the proximal ones or to each other.

The second feature which would appear of functional importance in the B segment concerns, not the movements of the segment, but the podomere itself. This contains a bend of 90° so that where the long axis of the limb enters B pointing slightly latero-anteriorly, it leaves B in a latero-posterior direction (Fig. 47), when the animal is at rest. Slight evidence of this bend is also observable in the B segments of the legs where the limbs are directed backwards, presumably in part to support the weight of the limbless opisthosoma. In the pedipalp it is, however, far more marked. Here it serves mainly to keep a free passage to the mouth and in front of the chelicerae. These latter organs are used so extensively in the behaviour of the scorpion, e.g. in eating, digging, mating, washing, stridulation, that it would appear of importance that a clear space be available for their operation. It is this curve in conjunction with the shape and possible movements of segments C and D which allows the pedipalps to approach the mouth from the side, i.e. without blocking the space for cheliceral action.

Lastly, and not quoted as one of the distinguishing functions of B, this segment has a particularly hard and irregular exoskeleton, which is associated with the C muscle origins.

In part the main function of the B-C joint and the C segment has already been considered; that of bringing the claws towards the mouth region. The length of the segment not only increases the grasping range of the claws but would appear to be used in the same way as the length in an antenna, for on C segment are the first of the tricobothria in addition to the stouter hairs that were found also on A and B.

In the D joint and D segment all the functional considerations given to the C segment arise once more; the tricobothria, extra length, and support of muscles moving the more distal segments. The anterior, i.e. grasping and sensory action, as well as that directed towards the mouth region has been accentuated in two aspects of the D segment. Firstly there is a distinct curve in the podomere itself (Fig. 47) so that E is more anterior than it would have been had D been a straight segment. Secondly, it is clear from the type of joint at the C-D articulation that movement of D through the 90° plane is not powerful or important here. D can be extended so that the long axis of C and D lies in a straight line but never to the extent that D is "bent back" on C. The mere fact that no muscular extensor is present to straighten D on C implies that such an action is not a "power stroke" in the main behaviour characteristics of <u>O. latimanus</u>.

Lastly, and quite distinct from any function of C, D segment has been used distally in providing a dorso-ventral brake on the movement of E on D. As was suggested during the functional consideration of the D muscles, segment E needs to be able to rotate through 270° and 90° planes, but needs, if anything, a check on the 360° and 180° planes, since it is through the 330-120° plane that F operates on E. To achieve this check, the distal ends of D have been drawn forward to form an articulation which allows only the movements that are functionally desirable for the E-F complex (Fig. 55c).

The most obvious and possibly the main function of the D-E joint and E segment has already been implied; the manipulation of F and EE, the claws, to within grasping range of the target. The mobility permissible at this D-E joint is best illustrated by observing some of the contortions in which the animal indulges while it washes its claws (Fig. 4a).

The bizarre shape of the E segment of O. latimanus, especially in the female, is clearly due to the fact that this provides origin for the powerful closer muscle of the claw. In scorpions in which the sting is used in preference to the claws as weapons of offense or defense, the shape of the E segment is correspondingly more like that of the other limb segments (cf. Parabuthus in discussion on stridulation). Not only is the shape of E distorted to provide suitable origin for the closer muscles but the actual surface of the exoskeleton is gnarled and hard. Not only must the origins be provided but they must be areas which will give stable origins.

In all scorpions E segment forms the immobile half of the claw apparatus as EE. This, as of course is the case with F, curves slightly towards the mouth and the teeth of the two fingers interlock.

Lastly the sensory function of the E segment must be noted. It is on the hand that the vast majority of the trichobothria occur. The importance of this function for both E and F is obvious,not only from the way in which the animal "tests" new environments as it walks forward and reacts to any touch against them but also from the way in which these parts are kept especially clean of dust and caked mud.

The function and importance of segment F appear to need almost no description. The sensory function has already been ~~emtn~~mentioned and the heavy closing muscles indicate that EE and F can be brought together with some force. Not only can the animal exert a fair pressure with its claws (an animal of 4.9 gm. can lift a 100 gm. weight in her one claw) but the tension can be held for a considerable time. In this respect the males appear weaker than the females, a fact that is not surprising, considering the difference in size and shape of the closer muscle.

As well as in the actual grasping at prey or enemies, the claws are used regularly in threat, courtship, and parental care. In addition, claw holds have been observed to be used in climbing steep surfaces (see plate IX), while in the section dealing with burrowing, it is pointed out that the scorpion can often be seen pushing itself backwards out of the burrow with alternate strokes of the claws. They have never been seen to be used as tooth picks, as was reported by Fabre (1907) for Buthus occitanus, in which the chelicerae were cleaned by the claws. They would, however, seem in part responsible for cleaning the dorsal carapace, (p. 13).

Plate IX. O. latimanus climbing out of a dish. Note the use of the pedipalps to drag the animal's body over the edge.

4. Gross Anatomy of the Nerves of the Pedipalp.

Since several different neuro-muscular preparations of the pedipalp were used for experiment and more were tried, it was necessary to know the nervous anatomy of the whole limb. All this knowledge is not indeed essential for comprehension of the more successful preparations used but since it appears never to have been described before, and also because it makes the picture of the limb more complete, the whole will be dealt with here. All details are recorded in diagrams (Figs. 64 - 68) and tables only.

The main pair of pedipalp nerve trunks are the most anterior and the thickest of five pairs coming off the sub-oesophageal ganglion, fig. 64. This lies, as indicated in its name, ventral to the gut and ~~is just above the~~ main blood vessel ~~or heart chamber~~. The muscles which effect movement of segment A are innervated by nerves which arise from the trunk almost as it enters segment A. Thus they will be labelled "a" nerves, though in truth the convention set forth earlier demands that nerves so named should arise in segment A itself.

Nerve.	Branch	Axon type.	Organ supplied.	Comments.
a0	$a0^1$	motor	A5	
a1	$a1^1$	"	A1	
	$a1^2$	"	A2	
	$a1^3$	"	A4	
	$a1^4$	"	A3	
	$a1^5$	"	$C4^1$	
	$a1^6$	mixed	-	travels distally, joining a2 complex to innervate C muscles
a2	$a2^1$	motor	B1	
	$a2^2$	"	B2	
	$a2^3$	"	$C4^2$	
	$a2^4$	" (?)	$C4^1$	
	$a2^5$	"	C3	
	$a2^6$	"	C2	
	$a2^7$	sensory	B-C arthrodial regn. about 270°	
	$a2^8$	"	distal C. 90°	

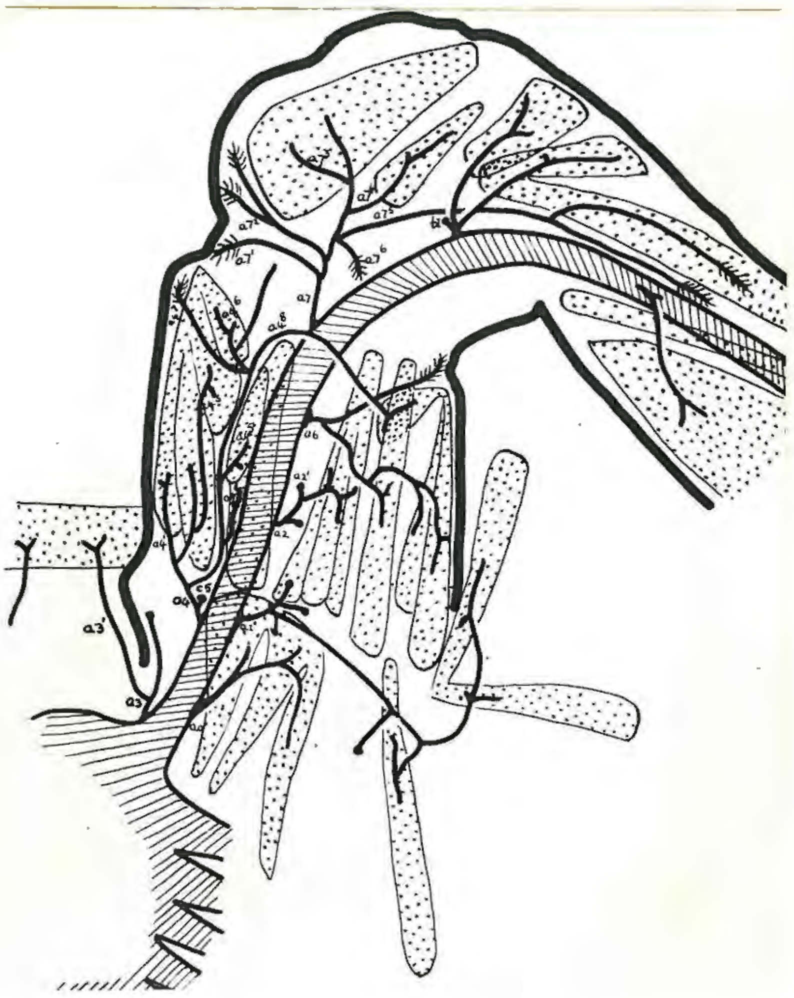


Fig. 64. Nerves of pedipalp segments, A, B and part of C.

Nerve.	Branch.	Axon type	Organ supplied	Comments.
a3	$a3^1$	motor	A6 (?)	Possibly sensory. Motor innervation to A6 may arise directly from ganglion, as mentioned by McClendon (1904)
	$a3^2$	sensory	proximal A 270°	
	$a3^3$	"	gnathobasic region of A	
a4	$a4^1$	motor	$B6^3$	
	$a4^2$	"	$B6^2$	
	$a4^3$	"	$B6^4$	
	$a4^4$	"	$B5^2$	
	$a4^5$	"	$B5^1$	
	$a4^6$	"	$B6^1$	
	$a4^7$	sensory	most of gnathobasic region as well as part A-B joint at 270°	
	$a4^8$	motor	B3	
a5	$a5^1$	sensory	A-B arthrodial 360°	
a6	$a6^1$	"	" " 30-120°	
	$a6^2$	motor	B4	
a7	$a7^1$	sensory	A-B arthrodial 270-360°	
	$a7^2$	"	central part of B, 200-360°	
	$a7^3$	motor	C6	
	$a7^4$	"	C5	
	$a7^5$	sensory	central part of C, 200-360°	
	$a7^6$	"	central part of B, 360-90°	
b1	$b1^1$	sensory	distal C 270°	
	$b1^2$	motor	C1	
	$b1^3$	"	$D3^3$	
c1	$c1^1$	"	$D3^2$	
	$c1^2$	"	$D3^1$	
c2	$c2^1$	sensory	distal part and arthrodial region of C, 80-100°	

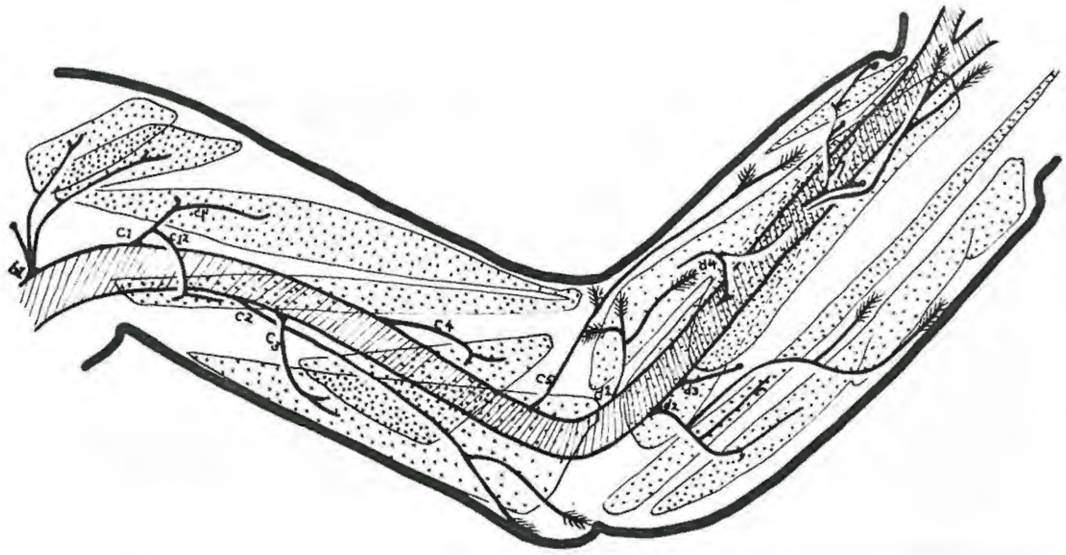


Fig. 66. Nerves of segments C and D of the pedipalp.

Nerve.	Branch	Axon type	Organ supplied	Comments.
c3	$c3^1$	Motor	D1	
c4	$c4^1$	"	D2	
c5	$c5^1$	sensory	arthrodial region C-D 230-280°	
	$c5^2$	"	central part D, 230-280°	
d1	$d1^1$	"	arthrodial region & proximal end of D, 270-360°	
d2	$d2^1$	"	central & proximal region of D,360-120°	
	$d2^2$	motor	F2	
	$d2^3$	"	E1	
d3	$d3^1$	motor	E2	
d4	$d4^1$	"	E8	
d5	$d5^1$	"	E3	
	$d5^2$	"	E5	
	$d5^3$	"	E4	
	$d5^4$	"	E6	
	$d5^5$	"	E7	
d6	$d6^1$	sensory	arthrodial region D-E 220-360°	
e1	$e1^1$	"	arthrodial region D-E, 350-10°	
	$e1^2$	"	central part of E 270-360°	innervation of inner flat of the hand
	$e1^3$	"	central part of E 180-280°	
e2	$e2^1$	"	arthrodial region D-E 140-200°	
	$e2^2$	"	central & distal part of E 140-200°	passes through muscle E6
	e23	"	arthrodial region E-F 270° and basal part of EE 270°	
e3	$e3^1$	motor	F8	
	$e3^2$	"	F9	
e4	$e4^1$	"	F10	
e5	$e5^1$	sensory	central & distal part of E 350-10°; also distal part of EE.	passes through muscle E4

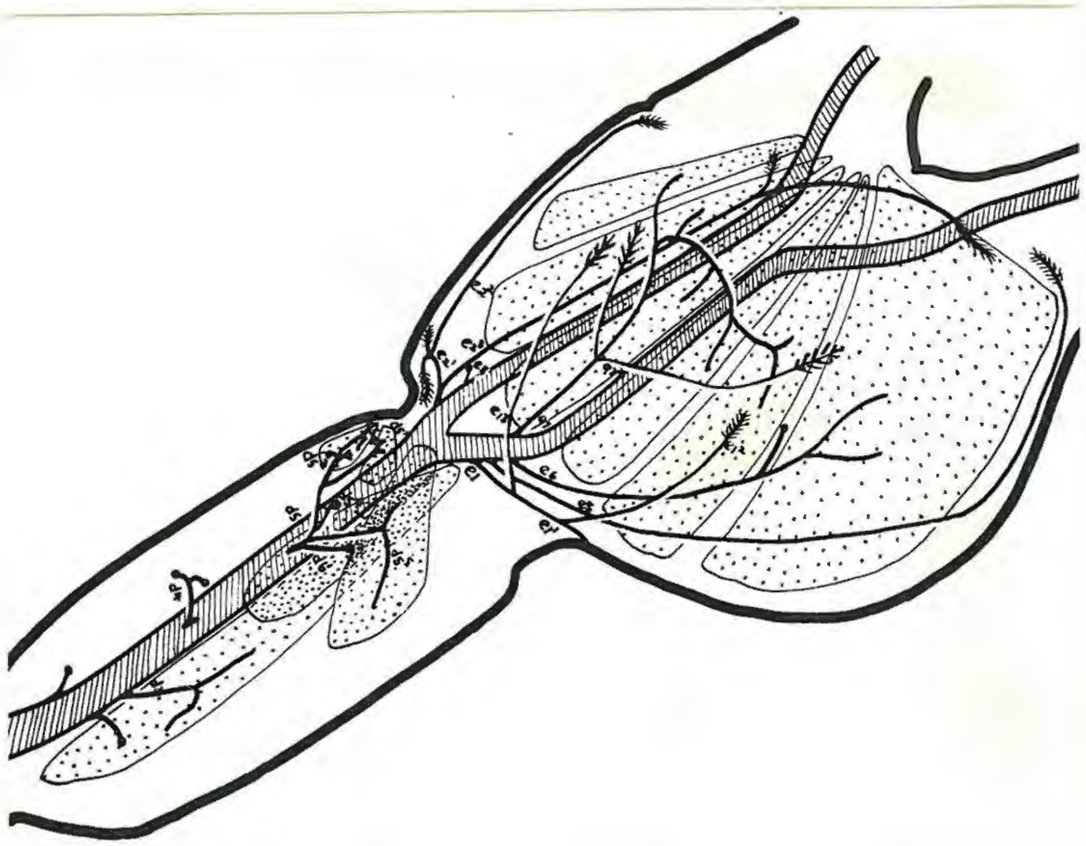


Fig. 67. Nerves of segment D and part of segment E of the pedipalp.

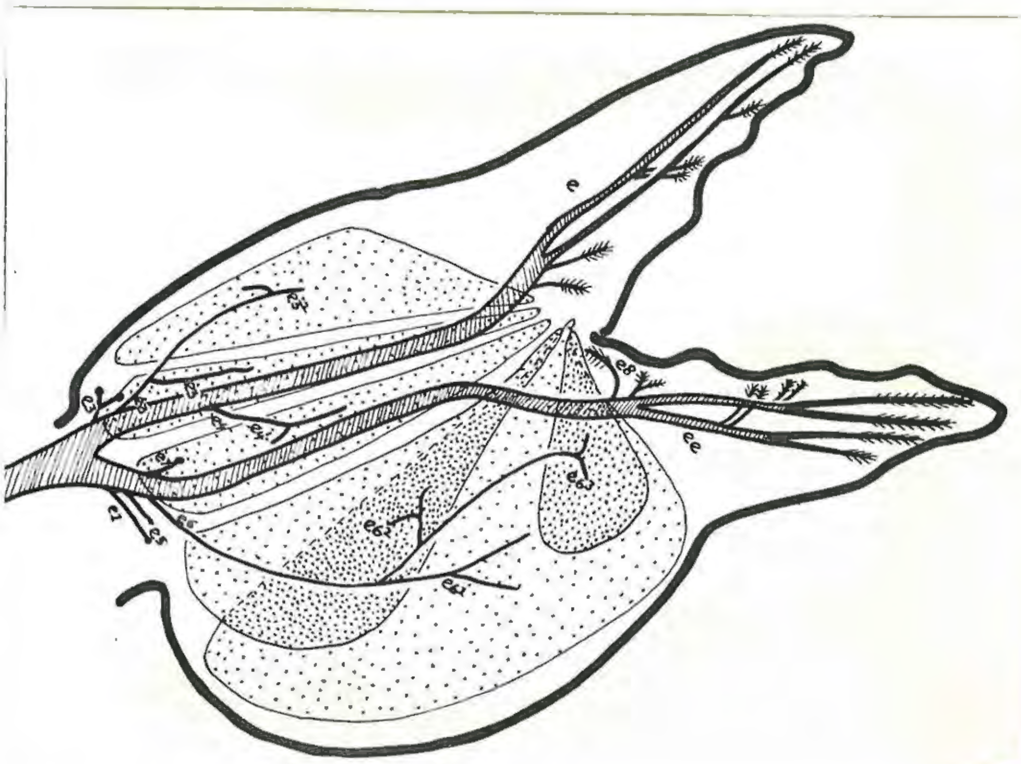


Fig. 68. Nerves of segmentsE and F of the pedipalp

Nerve.	Branch	Axon type	Part supplied	Comments.
e6	$e6^1$	motor	F1	
	$e6^2$	"	F11	
	$e6^3$	"	F12	
e7	$e7^1$	sensory	central part of E 270–360°	innervates outer
	$e7^2$	"	central part of E 180–270°	flat of the hand
	$e7^3$	motor	F3	
	$e7^4$	"	F4	
	$e7^5$	"	F5	
	$e7^6$	"	F6	
	$e7^7$	"	F7	

From its major division, as the main nerve enters segment E, the two trunks e and ee run respectively in to segment F and the EE portion of E. As ee passes beyond the area of muscle in E proper, it gives off nerve e8 innervating part of the E-F joint. More distally both e and ee branch repeatedly, giving off numerous small short twigs to the trichobothria and other sensory hairs of the claws. The organisation of these branchings are shown in Fig. 68. Since sensory axons are of no immediate interest here, they have been left without designation.

5. Gross Myology and Nervous Anatomy of the Tail.

It was proposed earlier (p. 179) to describe the muscular and nervous anatomy of the tail as a whole and not that of segments Y and Z only. Description of all segments other than these latter will be short and without detail. The system of description used for the pedipalp will also be used here, namely, the segments will be dealt with alphabetically, first functionally and then to some extent comparatively.

Articulation

"The segments have no specific articulations on each other, but are strongly connected, and in such a manner that their principal movement is in the vertical plane, most freely in a dorsal direction." So says Snodgrass (1952) of the tail segments of the scorpion.

This is quite true for the first four joints of the tail of O. latimanus (Fig. 69). There is no actual articulation of two sclerotised parts on each other and the arthrodial membrane runs around the joint without interruption. Movement in the vertical plane is very free while a more limited movement occurs through the lateral plane. This is achieved in two ways:- firstly the arthrodial membrane is narrower at each of the sides of a joint and secondly, while the anterior and posterior edges of the segments are hollowed out on their dorsal and ventral surfaces, this is not the case laterally. As a result, lateral movements are hindered as the segments tend to foul against each other. In spite of the lesser width of the arthrodial membranes at the sides, considerable rotation is possible at all four of these joints so that the tail is capable of a large amount of twist. By the rotation at these joints alone the sting can in fact be twisted through 180°.

The description given by Snodgrass does not, however, apply to the X-Y or the Y-Z joint of O. latimanus. The former is di-condylic the ball being part of the X segment, while Y provides the socket in which the ball sits. The articulations lie at 160° and 200° so that movement through the vertical plane only is allowed. At this X-Y joint then, there is no possibility of rotatory or lateral movements.

In the last joint little movement other than that through the vertical plane is possible. Here, however, this is not because of a strict articulation of one sclerotisation with another: there is no true articulation as in the case of the X-Y joint. The lateral movements of Z on Y are prevented by the sclerotised ridges of the sides of Y. Just as in the case of the D-E joint of the pedipalp, these distalward protrusions prevent movements in one plane without preventing rotation (Fig. 69). The rotatory movement is, however, limited by the narrowness laterally of the arthrodial membrane between Y and Z. In point of fact, the only movement of Z on Y that has been seen in O. latimanus and almost the only one possible in a dead animal, is that through the vertical plane. Snodgrass speaks convincingly of the flexibility that is achieved at this joint to allow the sting to reach almost any point near the scorpion. It is clear that, in O. latimanus anyway, this essential flexibility of the sting is achieved at the first four joints of the tail and not at the Y-Z joint itself.

Muscles moving Segment U (Fig. 70)

Muscle	Insertion L.	Pull L.	Comments.
U1	360 – 10	120	Paired, indistinctly two-branched.
U2	45 – 65	20	Paired, short and stout
U3	95 – 120	40	Paired, two large distinct branches, smaller is more oblique.
U4	145 – 150	90	Paired. Like U5 this has been previously overlooked
U5	150 – 165	80	Paired
U6	165 – 195	90	Single. Two major branches, both oblique.

Functional Relations of the Muscles Moving Segment U.

With one or a combination of any of eleven muscles moving segment U on the last segment of the abdomen, there can be few movements that are not adequately catered for. The two main antagonists are the single muscle U6 and the paired U1, causing depression and elevation respectively of the U segment. When the two U1 muscles contract

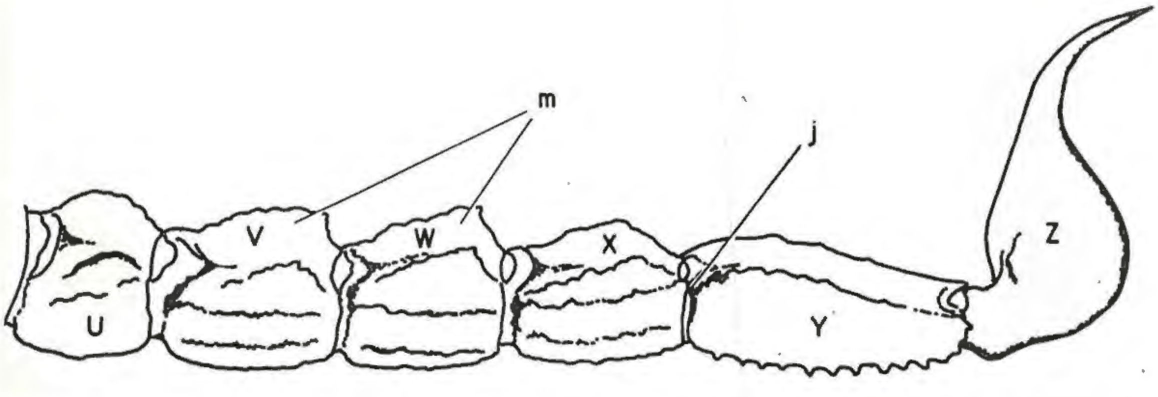


Fig. 69. Tail of O. latimanus in dorso-lateral view, showing j., limiting movement of Y on X and and m., muscle mounds.

independently they each produce a rotator effect and are antagonistic towards each other in this (Fig. 70a). The same state of affairs is also true for the two branches of the U6 muscle. This has one deep division and both of the branches produced by this are subdivided. U6-right and U6-left each give oblique pulls when operating separately, but together the rotator effect is cancelled out, and a straight depressor pull results.

The U2 muscle has, in addition to its lateral component, a strong rotator pull antagonistic to that of the ipsilateral U1. Of course this rotator effect of U2 is not always antagonistic to that of the U 1 muscle: should the right side U4 contract with the right side branch of U6 and the left U1, then the lateral, dorsal and ventral components are cancelled out, the rotator effects are summed and a strong negative twist results.

The other pair of muscles with a lateral component is the large U3. Again there is an additional rotator effect and again it is a positive pull on the right side.

The two pairs of muscles, U4 and U5, are rather puzzling. Both are very small but quite distinct. If their size allows them to be effective at all, U4 would depress U through 118°, an effect which could apparently be achieved quite easily by U6 with slight assistance from U3. The other muscle, U5, has almost the same pull angle as the outermost branches of the U6 muscle and the insertions are very close together. The functional significance of these two muscles is therefore not apparent. A clue to why they are present may be seen in the fact that the homologue of the U4 muscle is not found in any of the more distal tail segments while U5 tends to fuse more and more completely with the U6 branches. In the abdominal segments, muscles which are apparently homologous with U4 and U5 do occur. They are oblique and are concerned with pulling the pleura inwards. They are much larger and are apparently functional. It may well be that U4 and U5 represent vestiges of these abdominal muscles for, passing distally, they have become obliterated.

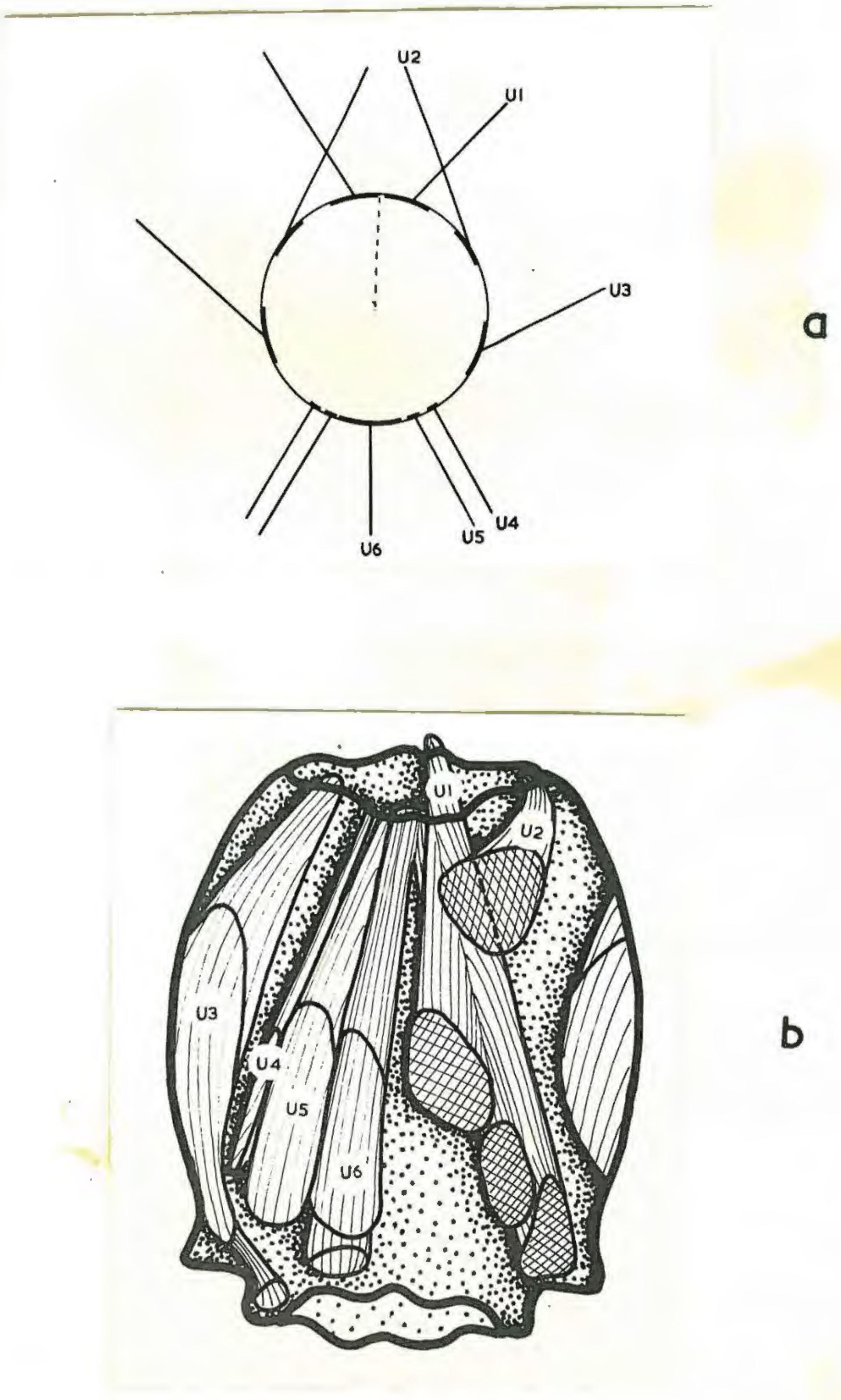


Fig. 70. (a) Ring diagram of muscles moving segment U.
(b) Anatomical sketch: those muscles with dorsal origins on the right side of the diagram, those with ventral origins on the left.

The muscles effecting movements of V, W and X may all be considered together since the same trends can be seen in them. Firstly, as has just been said, there is no homologue of U4 and that of U5 combines more closely with that of U6, the more distal is the segment (Fig. 71). The two main branches of U6 which are well separated and give therefore oblique pulls are posteriorly represented by muscles ~~in~~ whose branches become progressively less distinct as the more distal segments are reached. As a result, less of a rotator pull is possible and the muscle becomes progressively more purely a straight depressor; thus X6 is almost entirely a straight pulling muscle with practically no rotator ability.

The short stout U2 muscle with its strong rotator pull becomes increasingly smaller, longer and less oblique in the more distal segments and, in point of fact, there is no Y2 muscle at all. This reduction of the tail muscle "2" is reflected externally in the disappearance distally of the "mounds" (*m* of Fig. 69) characteristic of the dorsal surface of the tails of most scorpions. It is in the cup which is formed internally by this mound that the tail muscle "2" takes origin.

Lastly there is a tendency to separate the insertions of the ~~tew~~ two homologues of the U1 muscles, and thus to make each less oblique.

Besides lacking altogether a Y2, the group of Y muscles is further simplified by the Y5 muscle being almost indistinguishable from the Y 6, whose fibres are almost entirely straight pulling. In the muscles moving the sting the process is carried further and only four muscles effect the movement of Z on Y. There is no sign of a "6" muscle insertin g on to Z and those muscles that are present, namely Z1 and Z3, are incapable of any marked rotation, Z1 being almost straight pulling while Z3 has only a slight obliquity of pull.

The tendency which appears to unify the various trends which have been recognised in this consideration of the comparative anatomy of the muscles of the tail is this: - from the almost free articulation of the abdomen-U joint to the most distal joint there can be seen decreasing flexibility. This lies not only at the joints themselves

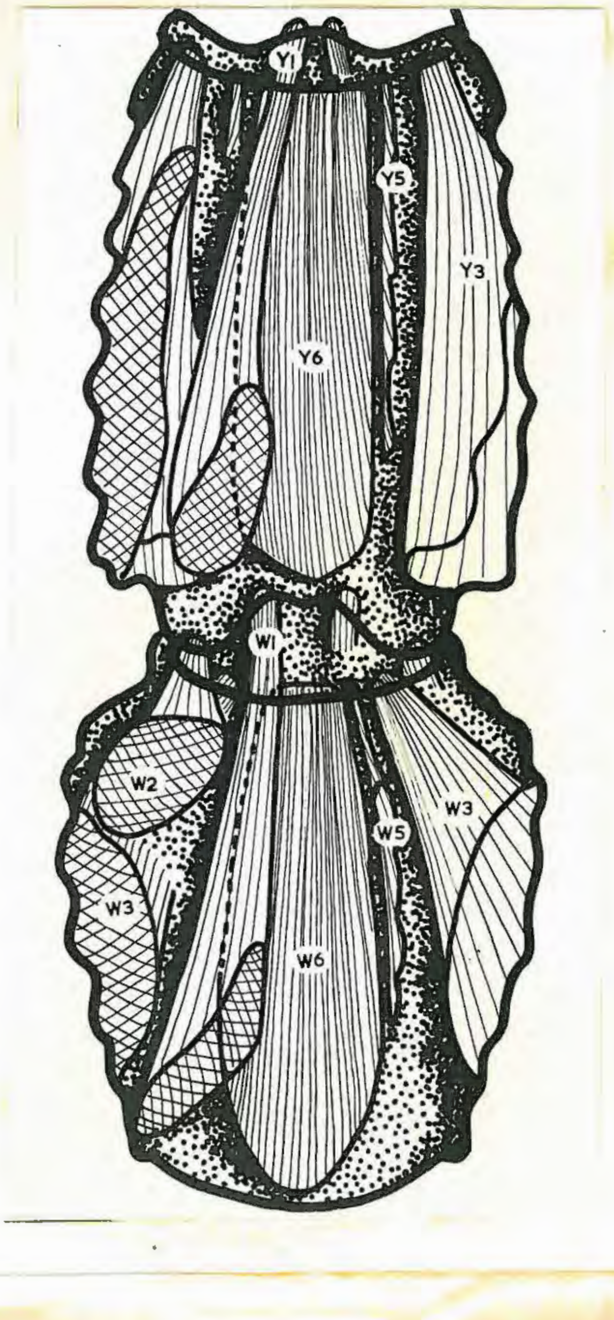


Fig. 71. Muscles moving segments X and Y of the tail. Muscles with more dorsal origins shown on the left of the drawing. All muscles labelled W in the drawing should be labelled X.

but also in the muscles. Not only are muscles reduced in number but their rotator action is decreased. It may well be that such a tendency should be looked at, not in terms of serial homology only, but of the practical needs of the animal. If the sting is to be effective, the scorpion must be able to bring it to bear on the point where it is needed. For this, flexibility of movement is more specially required at the base of the tail. On the other hand, the action of stinging requires only a downward plunge. Here clearly, flexibility is not required, and might even be a hindrance. To meet this need, passing distally towards the sting, movement is increasingly limited to the vertical plane. The same idea may be seen by an analogy with the apparatus needed for micro-manipulation. Remote from the actual point of operation, flexibility which affects the tip of the micro-needle or -electrode is useful. Once the main orientation has been completed and only movement in a single plane is required, flexibility in the needle or electrode itself, even if it could be controlled to some extent, is a marked disadvantage in the operation.

More detailed anatomy of Z and Y muscles.

With the functional considerations of both of these sets of muscles clear, it is still necessary to describe the details of Y and Z, both the muscles and the segments themselves. The former segment was that opened to get at the nerves supplying the sting muscles, while the latter contains the actual muscles used in the most successful neuro-muscular preparation.

Muscle	Insertion angle.	Pull angle.	Comments.
Y1	20-60	90	Longer and straighter than X1
Y3	120-140 [illegible]	50	More or less same size and origin as X3.
Y5	148-150	90	Just a few strands of fibre
Y6	150-210	90	Not as heavy as X6, no effective division between branches.

Since in the main it is not the functional properties of the segment that are of use to the neuro-muscular physiologist but the anatomy, the latter will be described here; the former needs no more than the generalised account already given.

Ventrally the Y6 muscle covers almost the entire length of the segment; the width of this origin may be judged by the distance apart of the two outer ridges of the four that run along the ventral surface of segment X (Fig. 75).

Until they have been dissected clear of Y6, the pair of Y5 muscles can only just be distinguished; once dissected free, each is obviously a distinct muscle composed of a long, tendon-like strand on to which four separate muscle bundles attach. The insertion is also quite distinct from that of Y6, lying slightly more distally on segment Y.

Muscle Y3 has the large lateral and the same insertion angle that X3 has. It does not, of course, rotate the Y segment since the X-Y joint conformation prevents this, but because of its insertion it functions as a depressor of Y, i.e. an auxiliary depressor to the Y6 muscle.

The Y1 muscle is more slender than the Y3, and the two Y1 muscles are not widely separate from each other. The Y1 origin is limited almost entirely to the mid-dorsal ledge (Figs. 69 and 75), which occurs where the X segment expands more distally after its constriction at the W-X joint.

The spatial relationships of these muscles with the gut, nerves and blood vessels may be surmised from the diagram of the cross-section through the middle of segment X (Fig. 72). It is not clear what is the membrane that surrounds the gut. Fine and transparent except where creamy-white inclusions occur, it would appear to be a "haemocoelomic lining". The main point about it in connection with this study is that, in a physiological preparation of this segment, it is better not to break this membrane. If it is torn, the gut immediately bulges out and, with the gut pulsations, the gut walls

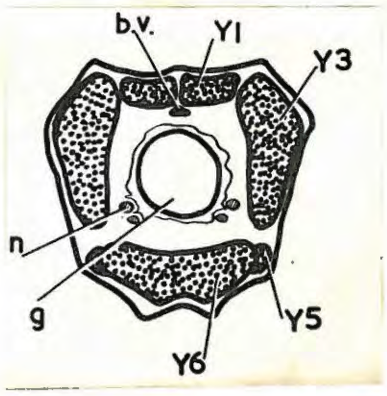


Fig. 72. Diagrammatic cross section through segment X of the tail. Muscles - stippled; paired lateral nerves - cross hatched; dorsal blood vessel (b.v.) - black; g., gut.

are in danger of getting torn on the dissecting instruments, an undesirable occurrence in that the gut content appears to affect adversely the performance of a preparation.

In segment Y there are only two pairs of muscles, Z1 and Z2, pulling on the next segment, the sting (Fig. 73).

Muscle	Insertion L.	Pull L.	Comments.
Z1	10-30	100	
Z3	115-130	60	

These are fairly long and not to any great extent oblique. However, it is clear from a comparison of the X-Y and Y-Z joints that a greater degree of freedom is allowed at the joint carrying the sting than at the X-Y joint, though it is by no means comparable with the freedom of movement in the W-X or other more proximal joints of the tail. The animal does not appear to use this freedom in that the sting has always been seen to be brought into a position where only a direct upward lunge is necessary to effect the injection stroke. The freedom would, however, allow any thrust at an extremely hard object to glance aside so that the sting point is not injured; as Pocock says (1893): "there can be little doubt that .... care is taken that there may be no risk of damaging the point of the sting against a substance too hard for it." It seems probable that the orientation of the sting resulting from such a glancing blow would be corrected by the rotator effect possible in both sets of sting muscles and that, in a second blow, a softer target area would be chosen, the sting again being brought into position for the direct lunge by the rotator ability of the more proximal tail segments.

The Z1 muscles are markedly smaller than the Z3 muscles. This is entirely explicable in functional terms as these latter muscles actually drive the point of the sting into the target by their contraction. The sting is always brought over the body before use, and, since the action is an upward thrust into the victim held in the scorpion's claws, it is effected by muscles which are morphologically the depressors of the sting, namely the Z3 muscles.

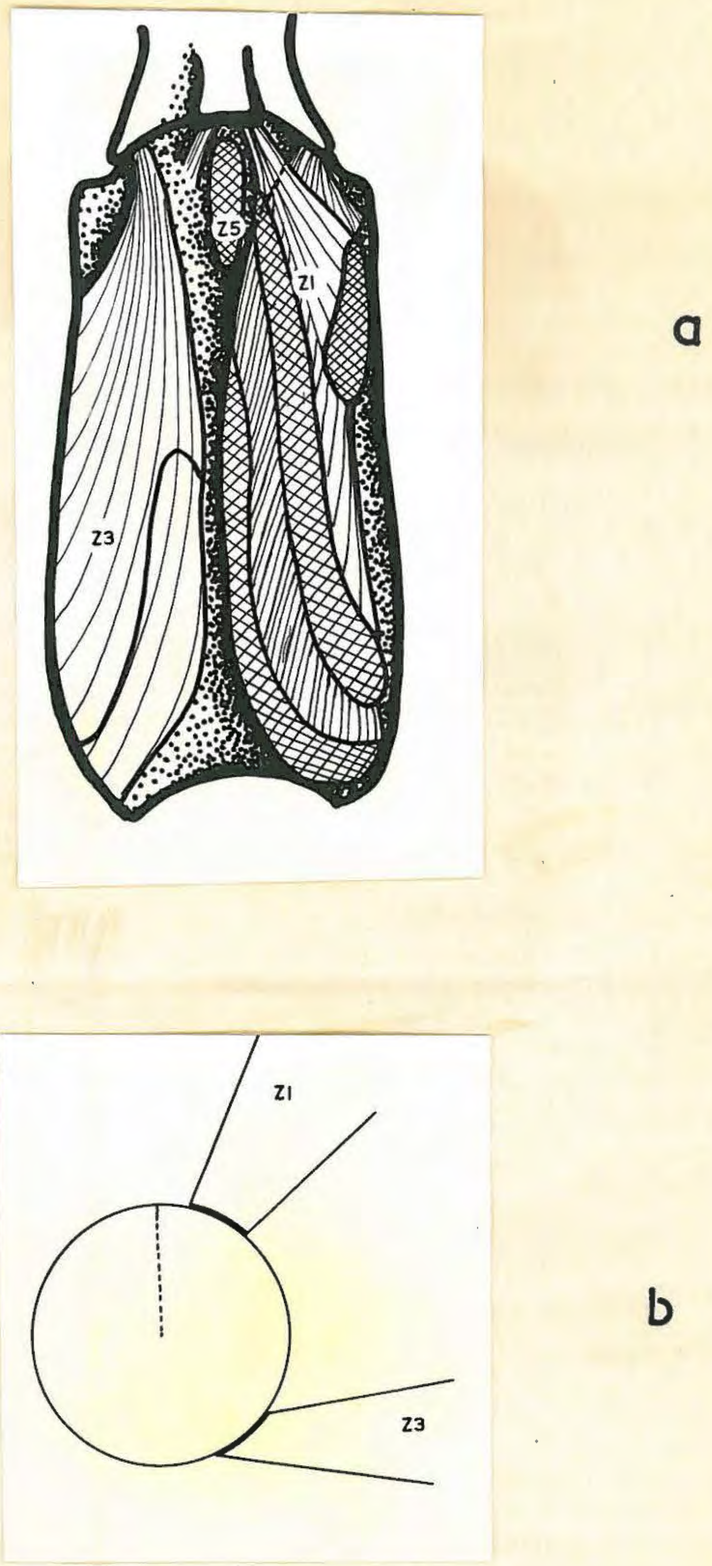


Fig. 73. (a) Z muscles of tail, those with more dorsal origin on the right.
(b) Ring diagram of Z muscles.

The insertions of the muscles may be seen clearly from Figs. 73a ~~abd~~ and 74. When the tail is stretched out along the ground and the tip is depressed, the insertions of the two Z1 muscles are easily accessible beneath the median dorsal articular membrane. The Z3 insertion is not on the lobe c1 of the sting (Fig. ~~73b~~ 74a) as might be expected, but at the base of a groove ventral to this. It is therefore not easy to reach this insertion without destroying either the lobe c1, the ~~rectal~~ anal lobes (Fig. ~~73b~~ 74a) or the distal part of the Y segment.

The origins are not easily discernible externally, especially as they are very close together (Fig. 75). The origin of a single Z3 muscle lies in a U shape around that of the ipsilateral Z1. If the plan of origin of the Y1 and Y3 muscles (Figs. 71 ~~[illegible]~~) is compared with that of Z1 and Z3 (Figs 73a and 75), it can be seen that the origin of the Z1 muscle has shifted laterally to an area homologous to that of the origin of Y3 in segment X. This means that in segment Y, the Z3 muscle cannot occupy the original position homologous with that of Y3, because part of this is already taken up by the Z1 origin. Why the Z1 origin is lateral is unknown, but it may be this shift in Y1 origin that necessitates the U-shape of the Z3 origin around the Z1 muscle. The major part of the Z3 origin is, however, ventral to that of the Z1.

It was said that only two pairs of muscles effected the movement of the sting. This does not, however, mean that only two pairs of muscles occur in segment Y. Inserting on to the ring of rectal plates, and taking origin on the mid-dorsal line between the Z1 muscles, is a pair of fine short muscles (Fig. 74a), the levator ani of Pavlovsky and Zarin (1926). If these are to be homologised with any of the other tail muscles, and there appears no reason why this should not be done, they seem homologous with the tail muscle 5; they would in fact be Z5 muscles. Their function is not clear; they appear to be used in defaecation and may be concerned with holding the rectal plates open while the long trail of excrement is pushed out by the gut and wiped free by the gross movements of the tail.

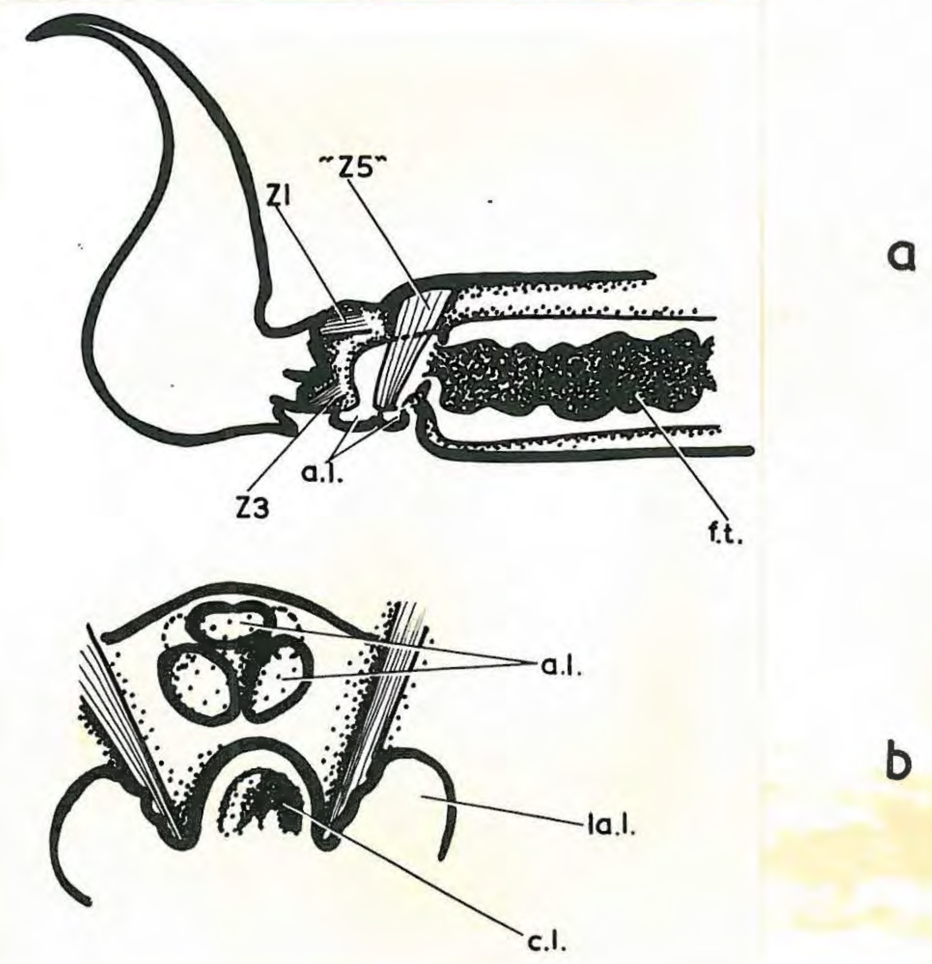


Fig. 74. Insertion of sting muscles in relation to gut and anus
(a) Diagrammatic representation of a lateral view. Faecal thread, f.t., and its covering membrane are shown.
(b) Ventral view of anal lobes, a.l., and base of sting with its central lobe, c.l., and two lateral lobes, la.l.

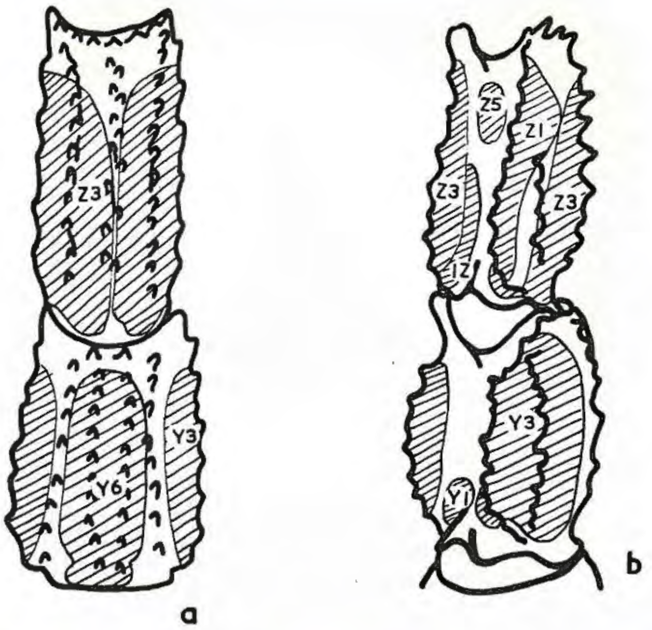


Fig. 75. Origins of Y and Z muscles of tail.
(a) Ventral view
(b) Latero-dorsal view.

Whatever their exact rôle, it is impossible for them to interfere with the movements of the sting and their only importance here is that they may provide a possible explanation of the persistence of muscle 5 throughout the tail segments. It was explained that vestiges of muscles still functional in the abdomen are to be seen in U4 and U5. In support of this view the fact was quoted that no V4 occurs. However, there does occur a muscle V5, a W5, an X5 and also a Y5; all quite distinct and each without any apparent functional value. It is true that it is virtually impossible to prove that these muscles do not have some functional justification and it is equally true that their presence could be accounted for just as "a vestige of abdominal muscles."

Neither of these approaches is fully satisfactory; the former because the structure can only acquire functional significance if some hitherto undiscovered physiological principle is invoked; the latter because it has been shown in so many cases that an "acknowledged" vestige, [redacted] may have some function.

If we take into consideration the fact that the more distal homologue, Z5, is in fact functionally explicable, a slightly different face is put upon the "vestige" explanation of the muscles V5, W5, X5 and Y5. It seems possible that when a serially repeated structure has become redundant for a limited number of segments in the middle of the body, while at either end of the series the structure is functionally valuable, the course of morphogenesis becomes unnecessarily complicated if the unwanted structures or its associated basic morphogenetic field are obliterated completely. It may be simpler and more efficient to modify the development so that the structure is not fully formed although the basic morphogenetic field remains intact. In the more distal segments where the structure is needed, the presence of the field is thus assured and the structure may once again be expressed fully in development and organisation. Such an explanation is, of course, entirely speculative and at the moment I am not aware of another case to which the theory could be applied. However, it does fit the known facts for this case and, until some better explanation is offered, this interpretation appears worhty of consideration.

The sting itself will not be described here. The muscles compressing the two poison sacs have been described by various authors (e.g. Snodgrass, 1953) and in this study only the nerves to these structures will be indicated. The form of the segment need only be mentioned when problems of attachment for recording the sting movements are being considered.

The Nervous Anatomy of the Tail (Figs. 77a and b and 78a and b).

To follow the nerve supply to each of the muscles described earlier, it is necessary to start with the system in the last mesosomal segment (Fig. 77a). Here the two nerve cords join to form a bi-lobed ganglion. This lies ventral to the gut and blood vessel. Running out laterally from it to both sides is a pair of nerves, tl of Fig. 77a. Each nerve branches after about 5 mm. and supplies the more dorsal muscles: U6 with tl^{1}, U5 with tl^{2} and U4 with tl^{3}. At this branching a small sensory nerve comes off and innervates the dorsal hairs of the exoskeleton. The rest of the tl nerve, termed the tlb, curves round to supply U1, U2 and U3. As it passes the dorso-ventral strips of muscle which line the pleural wall it gives off a small branch to them. The ~~tl6~~ tl^{6} nerve which supplies the U1 muscle turns and runs to them. The tl^{6} nerve gives off a branch just before it reaches the U1 muscle. This branch is tl^{7} and it supplies the U3^{1} branch of the U3 muscle. As will be seen, the two branches of U3 are innervated rather differently. It is as well to note this here, as it will be referred to later. After giving off the tl^{7} and tl^{6} nerves, tl becomes almost a network in the U3^{2} branch of U3. This plexus has been called tl^{5}. Two nerves do emerge from it and run forward once more; tl^{9} and a small sensory nerve tl^{8}. tl^{9} supplies the U2 muscle.

The innervation plan in the segments U, V, W and X follows very closely that described for the muscles of segment T. Where the

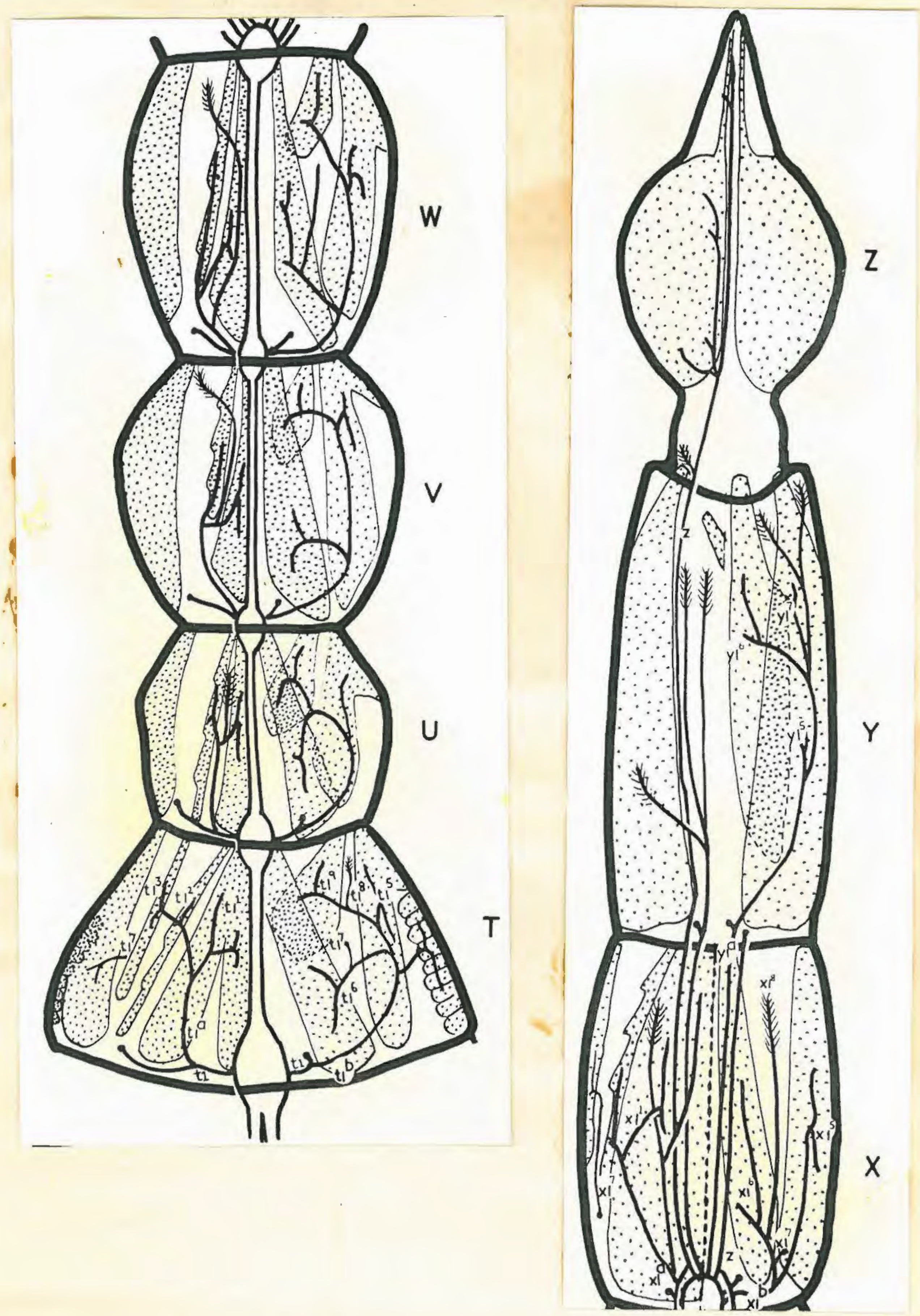


Fig. 77. (a) Nerves in tail segments T, U, V and W.
(b) Nerves in tail segments X, Y and Z.

homologue of a U muscle is missing, the homologous nerve is, of course, absent, and this alters the branching pattern to some extent. It also means that there is no ul^3 or xl^9. A further change is the gradual separation of the single pair of nerves coming from the ganglion that is the tl^a and tl^b of T segment. In segment X this separation is complete; xl^1, xl^2 and xl^4 are quite separate at their origin on the trunk from xl^5, xl^6, xl^7 and xl^8. The general tendency in most of the posterior part of the tail is to fuse nervous elements together and for this reason the separation might possibly indicate some functional separation of the Y6 from the Y_1 and Y6 muscles.

The ganglion in segment X is larger than that in any of the more proximal tail segments; it is also the last in the tail. The branching is as might be expected if the homologies implied in the labelling were correct. The nervous anatomy in segment Y also supports the interpretation given to the Z muscles. yl appears to be homologous with the xl nerve and with all the homologues of the latter. It will be remembered that when the innervation of U3 was being described, it was noted as being slightly peculiar. The nerve tl^b branches (Fig.78a). One twig of each of these two branches goes to supply U3. In the case of yl the same thing happens. After the nerve has forked to supply Z3 and Z1,the branch going to Z1 gives off another twig which runs to Z3. The yl nerve would thus seem to be homologous with the xl^b nerve of segment X, and this implies a homology of yl with xl^b, as well as z with xl^a , and is supported by the crossing of the nerves. Nerves z and xl^a both come off more laterally and proximally than their neighbouring nerve. Since both innervate muscles more medial than their neighbours, both are constrained to cross their neighbours at one point or another. The x nerves do it almost at their origin, while the z nerve only crosses to the mid-line at the level at which y innervates its muscles.

From this study of the serial homologies of nerves and muscles of the tail, it is clear that the muscles Z1 and Z3 are to be considered as simple single antagonistic pairs. Z3, despite its size, is not formed by the fusion of several muscles, and it therefore provides a single muscle preparation suitable for neuro-muscular studies.

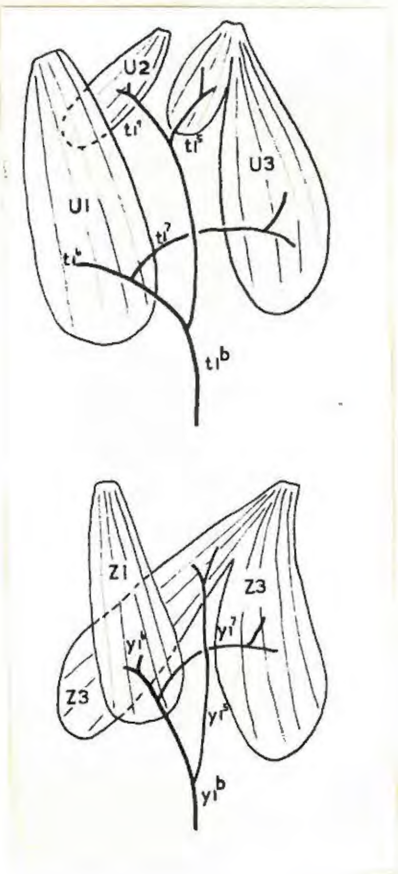


Fig. 78. The homology of tail nerves 1 and 3 as suggested by their innervation patterns.
Upper drawing, branchings of nerve tl^b; lower drawing, branchings of nerve Yl^b.

6. Comparative Anatomy of Arachnid Limbs.

Until recently the dominant outlook in the comparative study of arthropod limbs has been the comparison of either the number of segments, the flexions of the joints, or the most readily observable muscles in the appendages of various animals. It is now becoming clear that this, even if all three features are considered together, is not enough to allow us to comprehend the evolution of these limbs. The locomotory mechanics or other specialised function of any limb must be taken into account and, in the analysis, attention must be paid to all the muscles, to the precise mode of articulation of the podomeres as well as the limb flexions, the patterns of innervation, and, with the arachnids at least, to the vascular organisation of the limb.

With the need for such a programme, it is clear immediately that, as far as the arachnids are concerned, there is as yet not enough information available to build a satisfactory picture of the course of evolution of limb structure and to recognise the selective advantages at work in this evolutionary process. Moreover in many accounts of the anatomy of arachnid limbs the results presented have been strongly biassed by an outlook coloured by the methods of working of normal "vertebrate limb musculature" and, as a result, these have to be approached with critical caution.

Nevertheless there is one problem which can be directly approached by the classical methods of comparative anatomy, namely the relationship between the pedipalp and a walking leg of a scorpion.

Pedipalp and Leg.

It is clear that if one is to be derived from the other, the scorpion pedipalp must come from the leg and not vice versa. Since the leg has seven, possibly eight, podomeres, while the pedipalps have only six, it may be assumed that the pedipalp has lost at least one segment relative to the leg. In addition the terminal pair of claws of the leg is missing in the pedipalp.

It would seem that, in considering this question, the most reasonable assumption is that the most distal segments are the more likely to be lost and that, starting with the most proximal, the podomeres will be homologous. The consequences of this idea will be explored, the differences and similarities between successive segments will be pointed out and in this manner the validity of the hypothesis tested,and where necessary it will be modified.

To fadilitate comparison of the organisation of muscles along the length of a segmented limb, the convention previously used in relation to single joints, is here extended to whole limbs. As before the articular surface on to which muscles insert is represented as a circle, the mid-dorsal muscles being drawn at north, 360°. The circles of joints are drawn concentrically, that representing the most distal joint being nearest the centre of the diagram. A muscle that runs through several segments of a limb will be drawn as crossing several of these circles. Where a muscle has a ventral origin and dorsal insertion, the muscle in the diagram will curve around its circle, so that it will join on to the next at 360°. For simplification the whole muscle is not drawn but is represented as a thick line which indicates its line of pull, a convention already used where a large number of muscles lay particularly close together. (Fig. 80).

No description has yet been given here of the leg. It and its muscles have been figured in a few previous accounts, that of Snodgrass (1952) being the most satisfactory for it gives a brief description of the articulations as well as the muscles. Since much in that account is applicable to the leg of <u>O. latimanus</u>, it is felt that a separate and complete description is not warranted and that the relevant points may be comprehended from the diagrams and comments as the comparison proceeds.

The A segment of the pedipalp and legs have first to be considered. The former has already been described as a short, cylindrical segment moved by muscles A1 - A6. In the legs the A segments are triangular in form and those of legs III and IV are fused together laterally. The presence of a "dorsal ridge" running along the A segment of the pedipalp has already been described. A similar, but less well marked feature can be recognised in the A segments of the legs.

In *Centruroides*, Snodgrass (1952) states that the basal segments of the legs have "no points of articulation on the body and, except those of the first pair, are little movable." In *O. latimanus* however there is, as in the pedipalp, a single point of articulation with the body, though here it is at about 220°, rather than almost mid-dorsal. The pivots of legs III and IV articulate on to the corners of the sternum, those of I and II with the endosternite and the anterior tip of the sternum.

The A segments of legs I and II have been observed to move independently (p. 25) while those of III and IV have not. The shape of the A segments differs, one from the other, but this is hardly surprising owing to their different rôles and the presence of glands in legs I and II. A comparison of the musculature (Fig. 79) shows, however, that the four segments are homologous with each other and this musculature is further very similar to that moving the A segment of the pedipalp.

All these features support the suggestion that the basal segment of the five appendages are homologous.

Segments B of both pedipalp and legs ~~are~~ are clearly homologous. Both are short and curved, articulating with segment A by a wide, loose joint without any specific pivot. The curve in the claw segment is far more marked than that of the leg segment. In the legs, as in the pedipalp, segment B has a dorsal peg, opposite the ending of the dorsal ridge of segment A and taking the insertion of the most powerful B muscles. Comparing the B muscles in Figs. 80 a and ~~B~~ b, it is clear that they are homologous, a fact which also provides further evidence in favour of the homologies of the A segments where these muscles originate.

The B-C articulation is strictly dicondylic in both the claw and leg. In the legs the pivots are at 90° and 270°, whereas in the claw they are more nearly at 300° and 210°. The length of the C

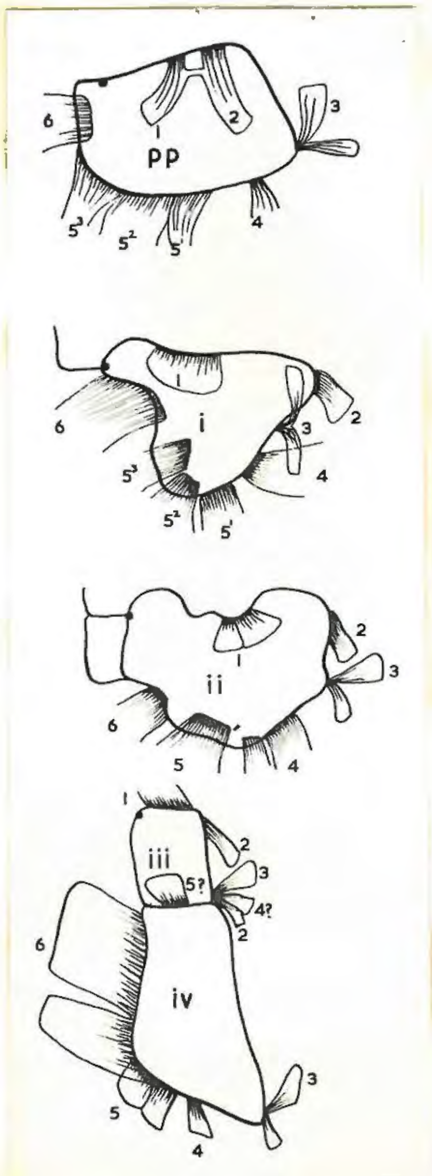


Fig. 79. Musculature of the A segments of the legs of *O. latimanus* compared with that of the pedipalp. The insertions of the muscles moving the segment are shown. The numbering of the pedipalp muscles is that already used (p. 186) and those muscles in the legs believed to be homologous with particular pedipalp muscles are correspondingly numbered.

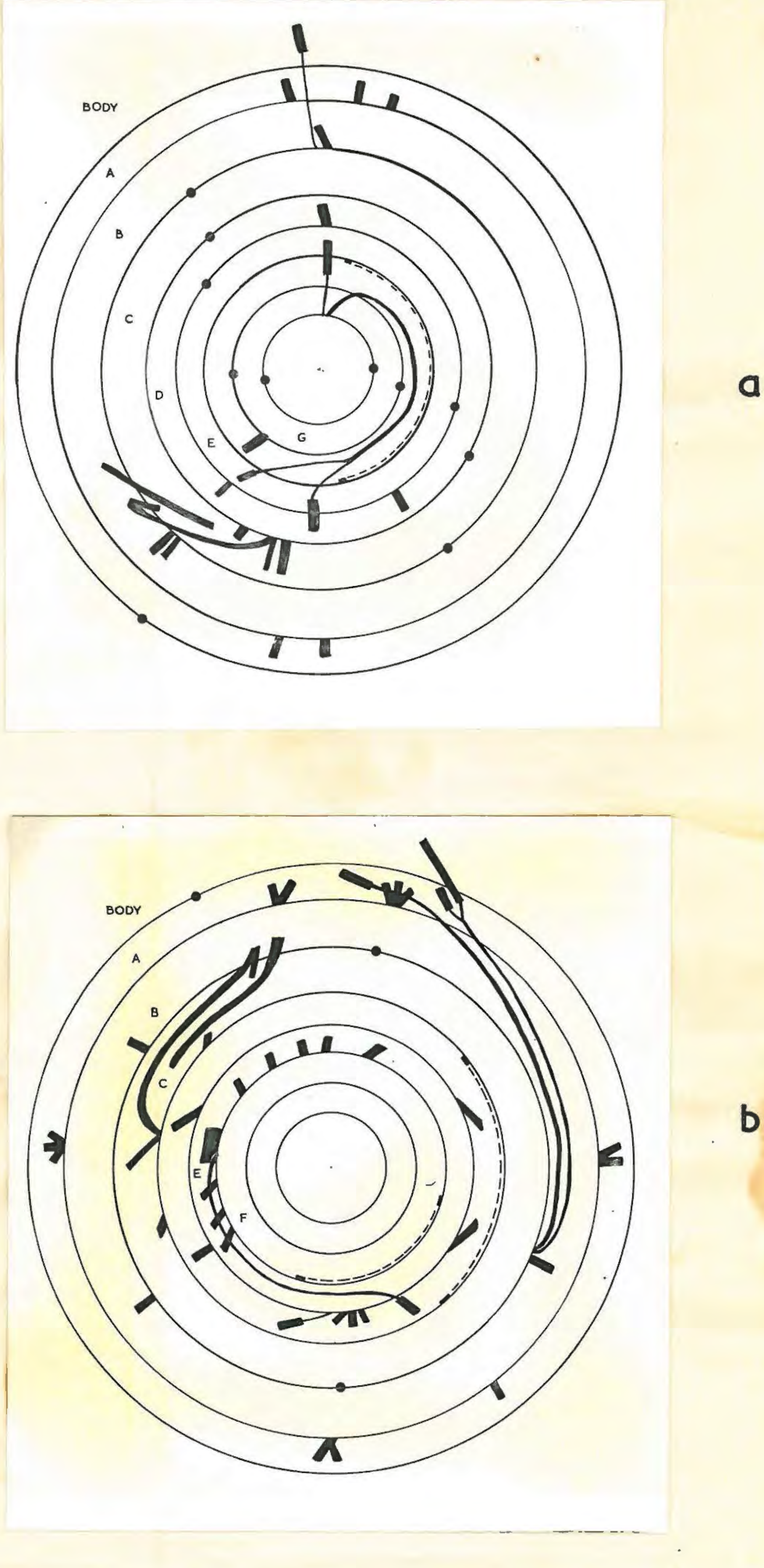


Fig. 80. Ring diagrams comparing the musculature of (a) the pedipalp and (b) the leg of O. latimanus

segment relative to B and D is the same in both claw and leg and the muscles effecting movement of C are very similar. C2 and C6 are clearly to be regarded as having the same functions in the legs as in the claw, while the lesser degree of elaboration of muscles C3 and $C4^2$ is of minor importance. There thus appears to be nothing which would invalidate the homology of segment C in claw and leg.

Segment D shows the first major difference between a pedipalp segment and the corresponding structure in the leg. This difference lies in the structure of the C-D joint. In the claw this is straight, stretching from 10° - 170° and giving movement across the 270° plane. With a dead animal a very slight rotator movement may be obtained provided the segment is somewhat extended. This rotation has not been observed in the living animal and it may be that it is an artifact. The C-D joint of the leg is dicondylic but the two condyles are not identical. One, at 300°, is composed of a peculiar ~~ord~~ rod on the proximal part of D which articulates on to a cup on C (Fig. 81a). At 75° there is the normal type of arthropod limb articulation, two slight pegs closely tied together and articulating on each other (Fig. 81b). Although the C-D joint of the leg is thus not a straight pivot, it allows for only restricted movement in the 360° plane; complete flexion is possible, but extension is limited to little more than a straightening of the C-D joint. In this the arrangement is functionally similar to that in the pedipalp.

Both in shape and size, relative to the adjacent segments, the D segments of the limbs and claws are very similar.

As in the pedipalp, there is no muscular extension mechanism for the C-D joint of the leg. The mechanism here still requires full study. By experiments similar to those made upon the pedipalp it has been shown that blood pressure could be used to extend the joint, but not that it, in fact, is. There is further the possibility that the rod at the 300° point of articulation may enter into the mechanism. Certainly there is no hinge comparable to that found at the corresponding

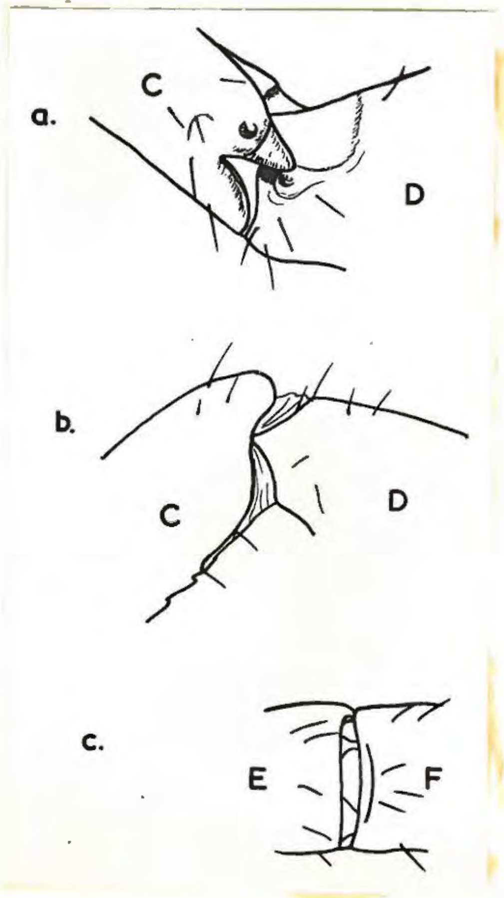


Fig. 81. Articulations in the leg of <u>O. latimanus</u>
(a) Articulation at the C-D joint; the hinge at 300° showing the peculiar rod-shaped structure.
(b) Articulation of the C-D joint; the hinge at 75° ~~at 120°~~ which is approximately of normal arthropod type.
(c) The hinges at the E-F joint.

joint on the pedipalp. The significance of the differences in these two joint mechanisms has still to be elucidated.

The formation of the D-E joint is a further feature which distinguishes segment D of the leg from that of the pedipalp. In the latter this joint is acondylic, lacking any specific articular pivot but limited in its movements by the conformation of the distal region of segment D. (Fig. 55c). Such a joint allows free rotation, but limits lateral movement to one plane. In the leg the joint between segments D and E is strictly dicondylic; both pivots are of the normal arthropod type and are situated at 90° and 280°. Further the form and size of segment E is very obviously different in leg and claw since it is this segment which has become the hand and immovable finger of the pedipalp. With the extreme looseness of the D-E articulation of the claw is associated a great elaboration of muscles which effect movement of E. This is, of course, not present in the strictly articulated leg segment. It must be noted that these two differences are not independent, but must be considered as a single functional syndrome.

Lastly a striking similarity which should be noticed here is that both E segments have passing through them the tendon of the muscle F2, which originated in segment D in both cases. On the whole it must be considered that the segments C, D and E are homologous, the greater freedom at the D-E joint of the claw being associated with manipulating the claw into a position where its snap can be effective.

The case for the homology of the next segment, F, is fairly clear. The E-F joint in both the leg and claw is a straight one, the first so far to occur in the leg. In the leg the articulation line runs from about 280° to 10°, while in the claw it stretches from 10° to 200°. Both joints operate strictly, though, in the leg, because of the softness of the surrounding tissue, this is not as striking as in the claw. The shape and size of the segments are of course not comparable since F in the pedipalp is the movable finger. Neither in the leg nor the claw is there any sign of a muscular extensor for F. The probable opener mechanism of the claw has been described above (p.200). Across one corner of the articular membrane of the E-F joint of the leg a chitinous hinge may be seen, looking very like the hinges of the C-D and E-F joints of the claw. If the other corner is observed very closely a second hinge, much lighter in colour and further from the corner of the membrane can just be made out (Fig. 81c). Because of the small size of the joint and also the limited movement between E and F, these hinges could not be tested for their function as were those of the claw. While it seems possible that these hinges have some very different rôle from that at the E-F joint in the pedipalp, this seems unlikely and until evidence to the contrary is found, it seems reasonable to assume identity of function and that, in this, the E-F joints of legs and pedipalp are similar.

A further difference between the F segments lies in the details of the flexor muscles. In the legs there is but a single flexor, while in the pedipalp there are eleven, some of them branched. The functional advantage of this system has already been discussed (p.211) and the difference must be attributed to the specialisation of the movable finger of the pedipalp.

From these considerations it would seem that the first six podomeres of the leg are homologous with those of the pedipalp and that, in this latter, the two most distal podomeres are missing. This difference is reflected in the muscle F2. In the pedipalp this originates in segment D and inserts in F, functioning as an additional closer. In the leg the muscle originates also in segment D, but its tendon passes, not only through E but also through F and G, to insert on the most distal podomere at 180°, acting as a flexor to the last segment. This difference permits two interpretations of the relations of the distal segments of the legs and pedipalp. Either segments G and H have become fused with F in the pedipalp, or the terminal segments have been totally eliminated, the insertion of F2 slipping back to the proximal end of F from that of H. It is to be noticed that, if the former explanation is correct, muscle F13 has been eliminated. Either way it is clear that in the evolution of a pedipalp from a walking leg, the proximal segments were modified to meet the new functional demands; any really radical alteration occurred only at the extremity of the limb. It seems likely that this "solution" might be determined by morphogenetic mechanisms, but it seems unlikely that the result found in this particular case represents a general rule of the course of evolutionary change when the number of podomeres of a primitive arthropod limb is reduced to meet some specialised requirement.

Finally, although a number of differences between limb and claw have been noted, little has been said of their significance. In general these differences are a reflection of a need for greater motility in the pedipalp: where articulations differ, those of the pedipalp are freer; where muscles are more plentiful, it is in the pedipalp. The extra overall length, hardness and greater sensory equipment are probably features which were added once the limb had acquired the motility which allowed it to be used in the feeding patterns. As it became increasingly modified and ceased to be able to play any rôle in locomotion, the limb was lifted from the ground. When this occurred it was not lifted straight but was given a slight positive rotation. The effect of this rotation can easily be recognised from a comparison of Figs. 80 a and B. In the joints it is especially clear, ending with the E-F joint which in the leg runs from 280° to 10° and in the claw starts at about 10° and ends at 200°. This rotation resulted in the movements which had previously been made relative to the earth now being made relative to whatever untested environment lay ahead, whether these movements were for the detection of enemies, the capture of prey, or the recognition of a mate.

The Walking Legs of the Arachnida.

A second problem which invites consideration is the interrelations of the podomeres in the walking legs of the arachnids. Here the difficulty of insufficient information becomes a real limitation.

The number of podomeres is variable between the different orders and the methods of comparative anatomy have so far failed to produce any satisfactory picture of homologies which meets with general acceptance.

No solution is offered here, but it would seem desirable to focus attention upon one common feature in the structure of the legs of all the larger arachnids which have been studied. The results presented here stem from observations on Limulus (Snodgrass 1952), on an unidentified solifuge (Ewing, 1928), on various spiders (Ellis, 1944, Parry, 1957), on Centruroides (Snodgrass, 1952), and on the pseudoscorpions Neobisium and Chthonius (Chamberlain, quoted by Vachon, 1949). In all cases but the last I have personally made dissections of the legs of local representatives of the groups concerned, and also of Limulus.

If an analysis is made of the muscular movements possible at the apical bend of the walking legs of these forms, it is found that, while there are flexor muscles acting on these joints, there is invariably no muscular extensor mechanism. Extension is effected by blood pressure, as in the spiders (Ellis, 1947, Parry, 1957) and in O. latimanus, or by hinge-type sclerites and possibly blood pressure in the solifuges (personal observation). Moreover, and probably correlated with this feature, the joint of the apical bend is never of the typical dicondylic type found in other arthropods, but is either a dicondylic joint of a peculiar type found in this position in Limulus (Snodgrass, 1952), or is a straight hinge.

It is possible to construct a hypothetical origin of such a system as this, starting with a soft-bodied "arthropod" resembling Peripatus. In the leg of Peripatus, while there are retractor muscles to the limb (Snodgrass, 1938), no extensor muscles occur: indeed in the absence of some type of skeletal system, whether it be an exoskeleton or an endoskeletal aciculum, it is not mechanically possible to effect extension by muscular activity. It is to be presumed that limb extension is effected by hydrostatic pressure and the observations of Alexander and Ewer (1956) on eversible sacs show that in Opisthopatus cinc~~i~~tipes Pur. localised increases in hydrostatic pressure can occur. It seems reasonable to assume that localised extension of the legs can be achieved by similar means, albeit the controlling mechanism has yet to be elucidated in both cases.

I will take as my ancestral form to an arachnid limb one similar to that of Peripatus described by Snodgrass, but having not only a retractor unguis, but also a ventrally placed protractor unguis (Fig. 82a). The development of increasing speed, a character which seems to be generally selected in arthropod evolution, requires the lengthening of the limb, and if this is to be mechanically sound, it must inevitably be associated with some bending. It is suggested that this bending was achieved by the development of an exoskeleton which must initially have been fairly soft. In this condition (Fig. 82~~b~~c) the contraction of the protractor unguis, passing across a pulley at the joint, would tend, not only to depress the terminal claws of the foot, but to flex the leg around the apical bend. The action of the retractor unguis, originating within the body and running to the claw by a long tendon, might well also cause flexion and for its effective action would require the movement of its origin to a position distal to the apical bend. I am not here concerned with the history of this muscle beyond establishing that, while it might have served as the basis for the development of a muscular extensor system at the apical bend, this could only occur provided sclerotisation was rapidly evolved, as may well have happened in the ancestors of the myriapod line, particularly if they were already terrestrial. If, however, the evolution of strong sclerotisation was slow, the muscle may have already been modified to retain its sole original function before it could have been elaborated to a secondary extensor of the apical joint.

It is suggested that the next stage in the evolution of the system was the enhancement of the flexor function by the development, from slips of the protractor unguis, of flags of muscle originating close to the apical joint and inserting on the tendon beyond the

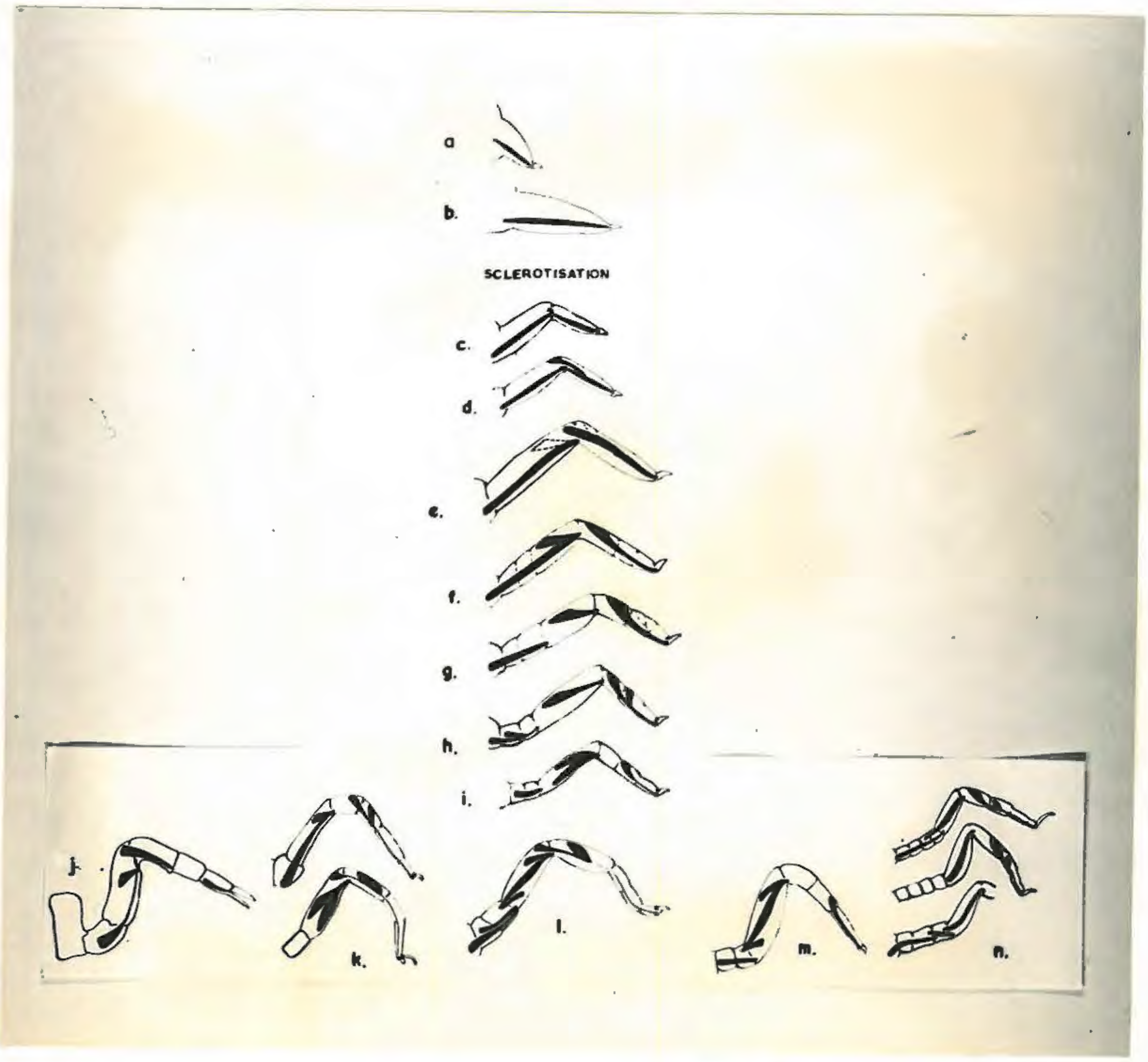


Fig. 82. A schematic representation of the evolutionary history of the flexor muscle system in the arachnids.

a - h, hypothetical stages in the fragmentation of the single protractor unguis muscle of the primitive arachnid leg to form a functional flexor: the process suggested is described in the text.

j - n, certain flexor muscles in the legs of living arachnids to show how certain of the stages represented in the series a - i can be recognised in existing forms.

j, Limulus. Leg IV.
k, Pseudoscorpion. Upper, Leg I; lower, Leg IV.
l, Scorpion
m, Spider
n, Solifuge. Upper, LegI; middle, Leg III (after Ewing); lower, Leg III (personal observation).

joint (Fig. 82d). This would moreover permit some independence of claw protraction from limb flexion. From this position, it would seem a relatively simple translation to one in which the proximal element established an insertion upon the pivot of the apical joint, thus becoming a pure flexor, while the distal element became a pure protractor of the claw. Extension continued to depend upon hydrostatic pressure.

This situation possibly still finds reflection in Limulus (Fig. 82j). In the fourth leg the flexor muscle of the apical joint runs across at least two podomeres, while the major protractor of the claw originates proximal to the apical joint. The same position possibly occurs in the pseudoscorpions (Fig. 82k). The protractor of the claw has a long tendon originating, in the fourth leg, proximally to the apical joint and running through several segments. The position in the first leg is less clear and requires further study.

It is generally agreed that, where it is mechanically possible, a short muscle and tendon will give more effective control than long ones, as the relative contribution of viscous-elastic components will be reduced. It is therefore to be expected that there will be a general tendency for the origin of the protractor of the claw to move increasingly distal (Fig. 82 e - i). The first stage in this migration is, perhaps, seen in the scorpions (Fig. 82l), where the major muscle now originates proximally to the apical joint although it still runs through several podomeres. The same tendency is more strongly marked in the spiders and solifuges (Fig. 82 m and n).

At the same time, and possibly for the same reason, the flexor muscle to the apical bend fragments in a manner akin to that postulated above for the initial fragmentation of the protractor unguis. But in this process the proximal fragments have been retained in the scorpions, spiders and solifuges as accessory flexors to newly evolved podomeres. The fact that in all cases these podomeres have their proper flexors (and extensors) as well, suggests that the process of fragmentation occurred subsequent to the establishment of the new proximal podomeres.

It would thus seem that in attempting to establish homologies between the podomeres of arachnid legs, the starting point should be those associated with the characteristic apical joint and that new podomeres have been evolved both proximally and distally to this point. If the idea developed above is correct, the myology of the leg can only act as a guide to the homologies of the podomeres if it is recognised that the accessory flexors are the product of modifications to an original muscle plan, whose persistence has been dictated by specialised functional considerations.

Whatever may be the validity of the speculations here put forward, the persistence, at least in those arachnid groups which have been studied, of hydrostatic extension at a major joint of the walking leg is a very striking feature. Clearly such a functional peculiarity, which is found not only in the Euarachnida, but in the Xiphosura as well, must reach back to the common ancestor of this group. It is a characteristic which distinguishes the arachnids from all other arthropods and possibly suggests that the subphylum developed an exoskeleton independently of the other arthropoda. Certainly the retention of a primitive hydrostatic mechanism points to a very early separation from the other groupings of the Phylum and, if it is indeed a reflection of the independent development of an exoskeleton, raises doubts as to the profitability of attempts to determine homologies between the podomeres of the arachnids and those of the other arthropods.

VII. PHYSIOLOGICAL OBSERVATIONS.

1. Introduction.

Amongst the living Arthropoda are found the following groups of animals:- Onycophora, Diplopoda, Chilopoda, Symphyla, Pauropoda Arachnida, Crustacea and Insecta. Of these the skeletal neuromuscular physiology of only the lattermost two has been studied to any extent. Pantin, Wiersma, Pringle, Ripley, Hoyle and other workers have shown the differences between the "oligoaxonic" system in these animals and the "polyaxonic" system in the vertebrates. Although it seems highly unlikely that the neuromuscular system of the remaining Arthropod groups will differ from that shown in the Insects and Decapod Crustacea, it seemed desirable to see whether the neuromuscular differences between Arthropod and Vertebrate are as general as we may reasonably expect.

On the other hand it may be that, while the neuromuscular system of the remaining groups is not in any way similar to that of the vertebrates, it nevertheless may be rather different from the arthropod systems studied so far. Our present knowledge of arthropod inter-relationships is very scanty. The phylum can even be considered invalid and regarded as a heterogeneous collection of animals whose superficial similarities are due to convergent evolution towards efficient locomotory and respiratory systems. It is possible that convergent or parallel evolution could have occurred in neuromuscular physiology, but the following consideration should be taken into account.

A system such as that of locomotion or respiration is related directly to the environment; selective forces operating through the environment will act directly on it. On the other hand, if we are considering a control system, the relationship with the environment is less direct; between the two will stand all the activities which are being controlled by the control system, e.g. locomotion and respiration. Neuromuscular co-ordination is one of the most obvious examples of such a control system. While similar selective forces could produce parallel adaptation in systems like those of locomotion and respiration, it seems unlikely or at least more unlikely, that this would occur in neuromuscular co-ordination on which selection would not be acting directly. As a consequence of this it is possible to expect that slight similarities and differences found in the arthropod neuromuscular control system may tell us more than we have so far understood of their inter-relationships.

The question facing us is "what group of the arthropods not yet studied could be expected to throw most light on the problems that we want to solve?" The answer is clearly the Arachnida. Amongst the reasons for this the following points may be picked out: firstly, the Myriapod-symphylan-insect line can be fitted into a coherent evolutionary sequence, but if the Onycophora, the Crustacea and the Arachnida must be considered at the same time, the difficulty in linking all these together becomes immense. If we know something of the neuromuscular physiology of the Crustacea and since the Myriapod-symphylan-insect line makes some measure of an evolutionary pattern without considering information on this score, light thrown either on the Onycophora or Arachnida might be most helpful in the question of inter-relationships.

Furthermore, there is amongst the Arachnids, as has been described above (p.200) an anatomical characteristic in the structure of the limbs which is of considerable interest. While in both the decapod crustacea and the orthoptera there is normally a complete set of antagonistic muscles operating each joint of the limb, this is not true in the Arachnida. Here, within a single limb, there are some segments which show antagonistic muscle pairs while in others there are single unopposed muscles. Clearly the problems of reciprocity in these two muscle systems must be distinct.

Finally the problem of "inhibitory" fibres appears to be one on which a study of the arachnid neuromuscular system may throw some light. Hoyle (1955) has found, in the locust, an axon which he calls a "facilitatory" axon and which he homologises with the inhibitory fibres of the decapod crustacea. This axon does not inhibit the effect of an excitatory fibre which was stimulated simultaneously with it. When stimulated it merely produces as hyperpolarisation of the muscle membrane, the converse of the depolarising effect of the excitatory axons ~~membrane~~. Hoyle suggests that, in a grass-feeding animal such as the locust, this hyperpolarising effect may be used to reverse the drop in resting potential of the muscle membrane caused by the high concentration of potassium which, owing to the herbivorous diet, is contained in the blood. The arachnids, carnivorous except for a few mites, should have no need for fibres of this kind and presumably they would not possess them. If arachnids lack the "facilitatory" fibres of the orthopteran type, the question of whether they possess the typical inhibitory fibre of the decapod crustacea presents itself. Its presence, or perhaps equally well, its absence, may help to explain what functional rôle it plays in the crustacea.

Previous Investigation.

Almost no experimental studies have been made upon the myoneural physiology of the arachnids. Rijlant (1934) has published records of action currents from the leg muscles of an unidentified scorpion. While these may throw some light upon central nervous function, they do not aid in the present investigation. In Limulus conduction rates and latent periods of nerves have been determined by Carlson (1906), while Monnier and Dubuisson (1931) have made a more elaborate study of the same character. Finally, and here most relevant, Prosser and Young (1937) make a passing reference to a neuromuscular preparation of the limb of Limulus used by Grossman as physiological class material at Woods' Hole.

Scope of the Present Study

In the present investigation attention was first paid to the development of preparations using the claw; this seemed the pedipalp appendage of choice by superficial analogy with the success attendant upon using the great chelae in studies on the decapod crustacea. A study of the muscular anatomy of the claw suggested that such an undertaking was likely to be difficult, but various attempts, described below, were made to develop satisfactory preparations using claw muscles. Finally it was decided that the anatomical complexity and the relative weakness of the individual muscles made the claw totally unsuitable for the first stage of any such investigation, namely an examination of the mechanical responses of these muscles. A preparation using the muscles moving the bulb of the sting was then developed. This has proved satisfactory and the main conclusions outlined below have been derived from such preparations.

The results presented, as stated in the introduction, are essentially preliminary in character and limited to a study of the mechanical activity of these muscles. They do, however, appear to show that the major features of the myo-neural physiology of a scorpion are very similar to those of a crustacean and to focus attention upon the need for more extensive studies upon this problem in insects other than the locust.

2. Methods.

All preparations employed in this study have involved entire animals: isolated appendages have not been used. Such a procedure offers two advantages - firstly any preparation is of a readily manageable size, while, secondly, the need for an elaborate perfusion system is avoided as the heart, continuing to function, pumps blood to the muscles being studied. Activity by the experimental animals was reduced to a minimum by shielding them as far as possible from light and screening them from the heat of necessary dissecting lamps by damp cotton wool.

Stimulator, Shielding and Electrodes.

The nerves were stimulated by negative square waves produced by a two stage multivibrator whose circuit is shown in Fig. 83. This is based upon a circuit developed by Ripley and Kirk (personal communication) and is an elaboration of the system described by Bernstein (1949). Except for some instability at low frequencies, the

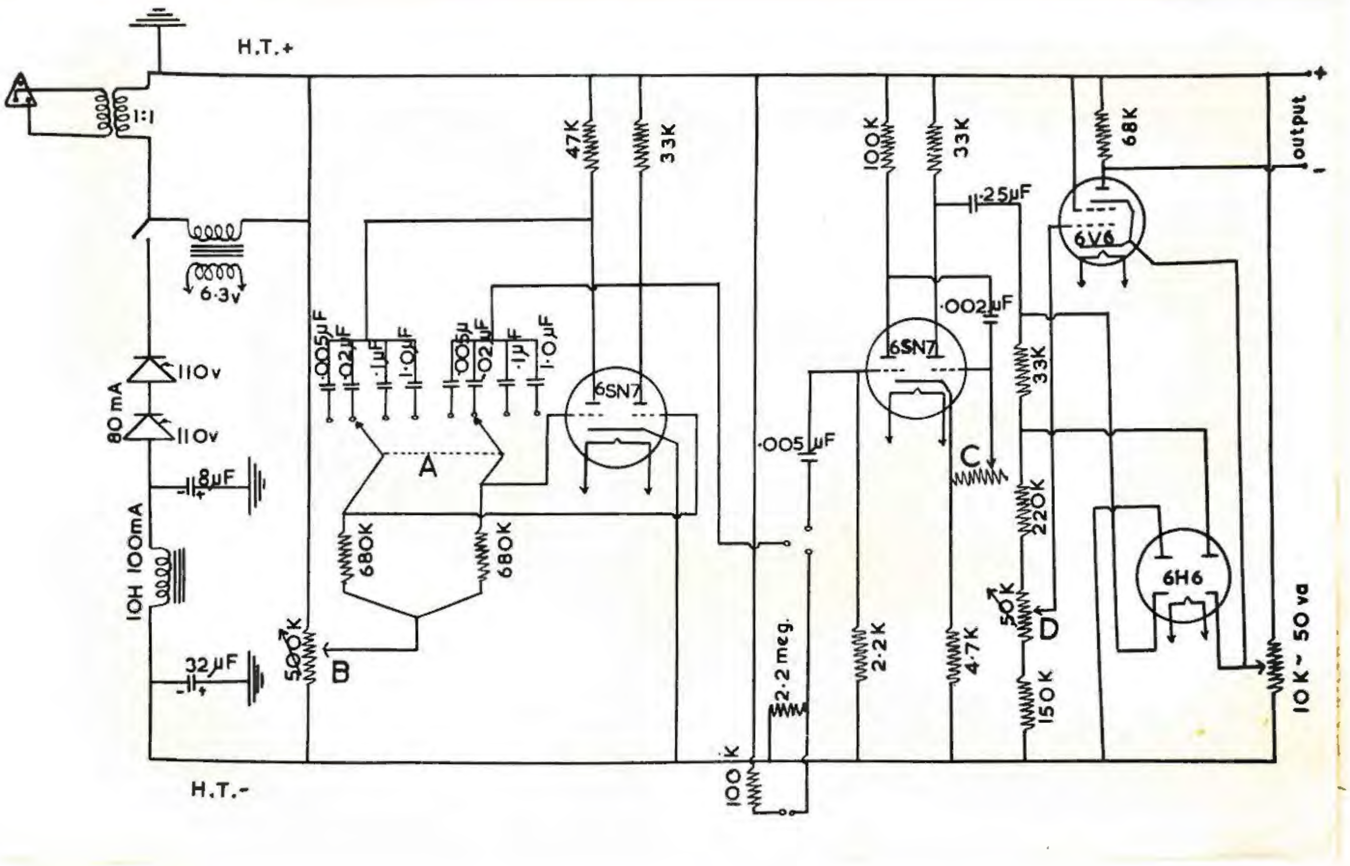


Fig. 83. Multivibrator circuit used as a stimulus generator. The circuit is modified from the original proposed by Bernstein (1950) and subsequently altered by Ripley and Kark.

A. Frequency range selector switch
B. Fine frequency control.
C. Pulse duration control.
D. Output amplitude control.

apparatus was satisfactory.

Examination of the output on an oscillograph showed that there was considerable mains hum in the output. Part of this came directly from the stimulator and was eliminated by the inclusion of a 1:1 transformer in the circuit. Part was, however, direct pick-up at the preparation. To reduce this to a minimum all preparations were enclosed as far as possible in small cages of wire gauze suitably earthed, so that the body of the animal was shielded except for an aperture of about one sq.cm., necessary for the manipulation of the electrodes.

All stimulation was applied to either nerves or muscles by way of fine platinum electrodes. The electrodes were manipulated independently: the anode was mounted on a simple ball and socket joint - the standard mounting of a small dissecting lens suitably modified - while the cathode was attached to a travelling microscope which provided the necessary fine control to allow nerve fibres to be handled with accuracy and delicacy.

Mechanical Recording Systems.

Early recordings were made directly upon a kymograph. It appears worth mentioning here a modification to standard technique which was developed and proved very useful. In normal practice, once a preparation has been set up for recording the writing point is moved towards the kymograph drum. Such a movement is frequently awkward and may involve a rotation of the recording lever which introduces unwanted tensions in the preparation. It seemed easier to reverse the traditional method and bring the kymograph to the recording lever. For this purpose an extension rod was fitted to the base of the kymograph and this was fixed to the rack and pinion motion of a disused microscope, the rack and pinion being attached horizontally to the bench. In this way the kymograph could easily be moved towards or away from the assembly or writing points with no disturbance to the preparation itself.

During the attempt to develop a suitable single muscle preparation from the claw, it became clear that the mechanical responses which were to be recorded were likely to produce very little tension and that ~~simple~~ direct mechanical recording would be unsuitable. Recourse was therefore made to the simple electro-mechanical transducer described by Hoyle (1955). This is a ~~simple~~ potentiometer system in which the voltage upon a fine platinum electrode free to move in a bath of 50% glycerine is measured by display on an oscillograph, using D.C. amplification. The system is shown diagrammatically in Fig. 84a.

Such a technique allows the mechanical movement of a muscle to be displayed upon the screen of an oscillograph. Since it was considered desirable to have a correlated record of the stimuli applied to the nerve, this information was applied to the other beam. It then became necessary to have some time marking system directly upon the photograph. After various attempts at using incandescent and neon bulbs, a satisfactory system was found using a miniature tuning valve - Philips DM 71 - modulated at mains frequency using the circuit shown in Fig. 84b. My thanks are due to Dr. Stack-Forsyth of the Department of Physics in this University for assistance in the development of this device.

Claw Preparations.

After various trials a method of holding the claw which gave control of its orientation was developed. A small shifting spanner was fixed into a stand with a heavy base. The head of the spanner was built up with solder to leave only a triangular hole in which the claw could be held firmly. The stand stood close to the block carrying the preparation. Two universal joints were inserted between the spanner and the base of the stand so that small changes in orientation at these two points allowed easy manipulation of the claw and permitted it to be orientated in any manner which might prove convenient for recording.

In such experiments as these it is necessary to have, if possible, preparations of single muscles. The closer of the finger, as has been described above, is moved by at least eleven distinct

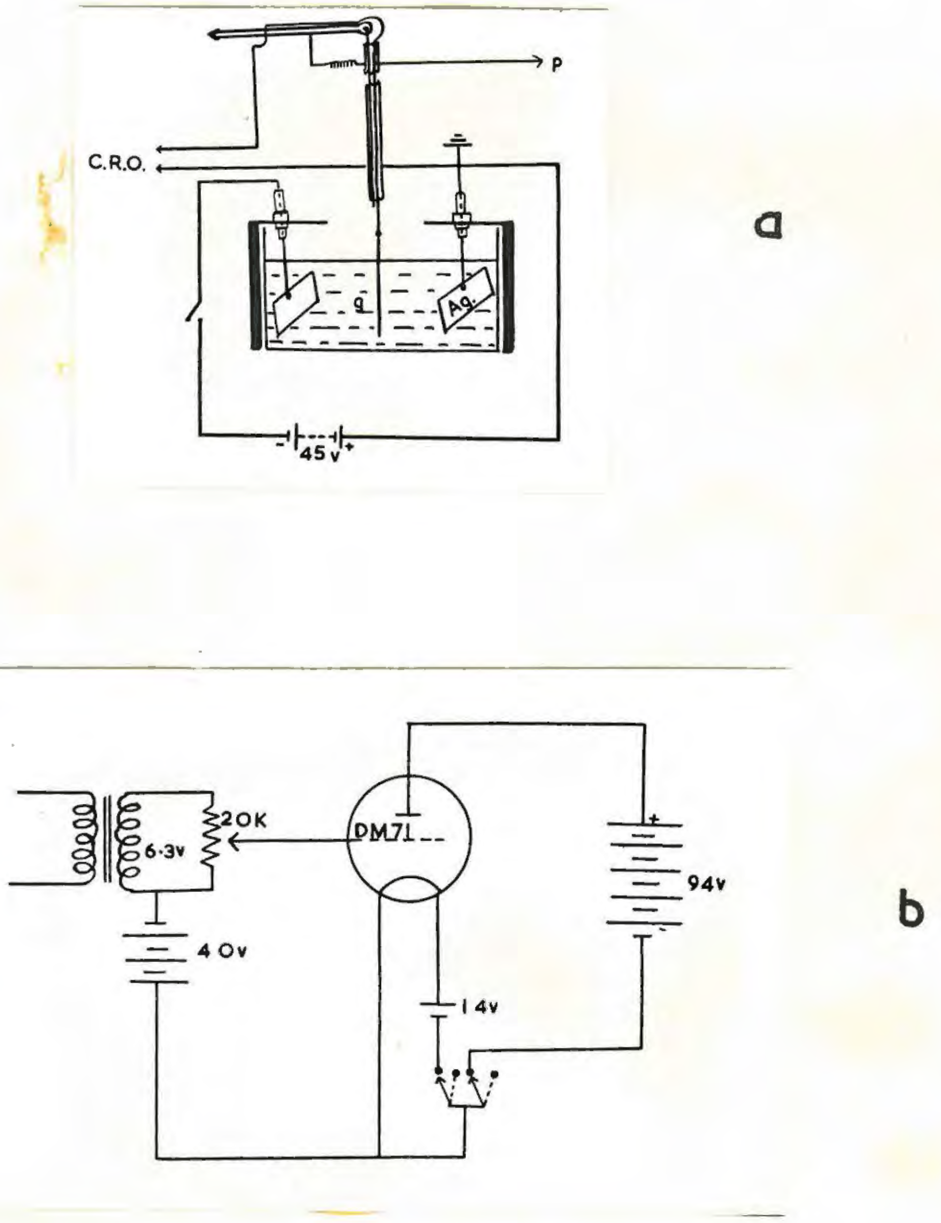


Fig. 84. (a) Sketch of electromechanical transducer. Ag., silver foil electrodes; g., 50% glycerine solution.
(b) Circuit used to drive valve DM 71 as a time marker.

muscles. The nerves which supply these muscles do not separate from the main trunk until it leaves segment D and it was found that these axons lay too near the claw itself to make it possible to stimulate the individual fibres.

However, the muscle F2, which lies alone in segment D and has a distinct innervation seemed to offer some possibilities of a satisfactory preparation. If the main nerve trunk be severed distal to the point at which it gives off nerve $d2^2$ to F2, and the whole nerve trunk proximal to the cut be stimulated, only F2 of the closer muscles will respond. Such preparations have been made successfully. The muscle is very weak and its movements can only be recorded satisfactorily by the use of the transducer. The preparation is, however, open to one serious objection. Ripley (1953) has shown, using the levator tibia of *Romelea*, that the mechanical response of this muscle when operating directly on the tibia is different from that obtained if the tendon of the muscle is isolated and recording is taken from it directly. The origin of this effect, which is very striking, is unclear. It may perhaps lie in the modifications produced in the contractions by the properties of the arthrodial membrane and joint, or, less probably, in mechanical interference between the levator and its antagonist. Either way it seemed desirable, if a true record of the activity of the muscle was to be obtained, to separate the muscle tendon distally and record its movements directly.

The muscle F2 has a long apodeme which, at first sight, seemed to offer a solution to this problem. However, for several reasons this did not prove satisfactory. Firstly it was necessary to dissect almost the whole length of the hand to expose sufficient length of the tendon which is very slender and almost invisible. This not only greatly upset the scorpion but also made the attachment of the claw in the spanner less secure. Secondly the apodeme itself is so thin that it was found to be very difficult to get a thread to grip on to it and lastly it is of such softness that the thread frequently cut through it or, in the throes of getting it tied securely, the whole muscle came adrift. Consequently it was felt that it would be better to record from a muscle whose insertion was left intact, but dissected free from the claw.

For such a preparation any one of the closer muscles might be used. It was clear that a muscle inserting on the periphery of F would be the easiest to isolate and that preference should be given to a straight pulling muscle as this would produce more mechanical displacement; at the same time the stronger the muscle the better. Muscle F9 appeared to fulfil almost all these requirements and an attempt was made to use it as a single muscle preparation.

The finger was cut off near its base, a tiny hole was bored through the inner face of what remained of F, and the chitin on either side of this hole was pared away until only the muscle insertions and the hole were left. Except for the attachment, the fragment of chitin was then disengaged completely from the E-F joint and cleared of the insertions of all muscles except F9. A thread was then passed through the hole in the chitin, the hand fixed in position in the spanner and the preparation was complete (Fig. 85). Once again the magnitude of the mechanical effect was very small and the use of a transducer necessary.

Tail Preparations.

As has just been seen, the development of a single muscle preparation from the claw is possible, but it could not be regarded as very satisfactory. In an investigation such as this, it is desirable to work, if possible, with single axons, but experience showed that in such attempts the nerve trunks were very readily damaged and it seemed desirable to find some more effective preparation. Chelicerae, legs and pectines were considered. All are rather small and inaccessible, and the latter two are so poorly sclerotised as to make mechanical recording difficult. The anatomy of the sting, on the other hand, suggested that a valuable preparation might be made from its muscles. As has been described earlier, the bulb is moved by a pair of dorsal muscles, Z1, as well as their ventral antagonists, Z3. Both lie in the Y segment. These muscles are supplied by long

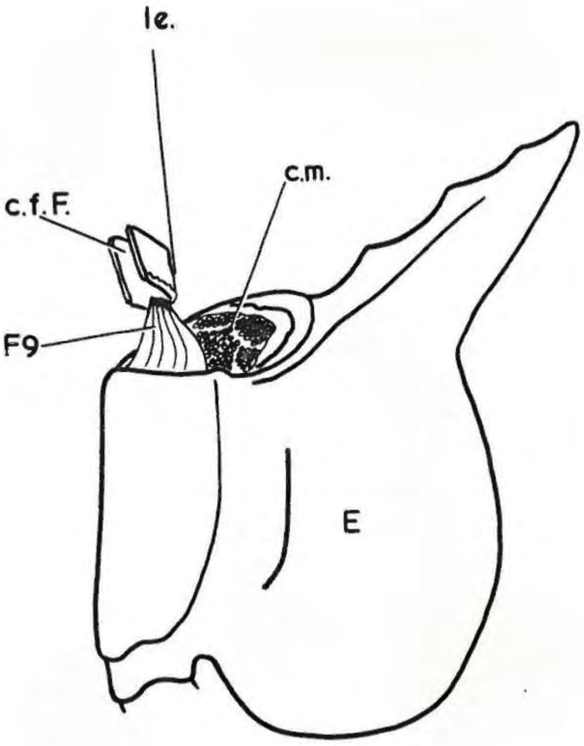


Fig. 85. Arrangement for mechanical recording of muscle F9. c.f.F., fragment of chitin carrying insertion of F9 muscle; c.m., severed muscles of claw; le., thread running to lever of recording system.

nerves arising from the ganglion at the proximal end of Y. Since these nerves run to these muscles alone, they offered a simpler system than the complex of axons in the main nerve of the claw. However, the branches running to the two muscles only separate very close to the muscles themselves and there seemed little possibility of cutting one or other branch without doing serious damage to the preparation. It was, on the other hand, relatively easy to separate the insertion of Z1 from the sting, so as to leave a pure Z3 preparation. Cutting the insertion of Z3 is not very difficult, though Z3 was preferred as experimental material as it is the more powerful muscle. Further, Z1 may be cut without risk of damaging the large ventral blood vessel, while in cutting through the insertion of Z3, this vessel was sometimes ruptured and the life of the preparation was noticeably shortened.

In making a preparation of the Z3 muscles two distinct operations are involved. Firstly, the insertions of Z1 must be cut and then the ventral surface of the Y segment removed to expose the nerves. To avoid turning the animal over for the second of these, a bridge was built (br) over the operating block (Fig. 86). The animal was fixed on to the block ventral surface downwards, its tail pinned straight out behind, and the Z1 insertions cut. The bridge was then swung into position and fixed by means of a bolt at the side, the tail was flexed over the block into its normal position and the surface of segment Y removed.

In such a preparation there is inevitably bleeding. This was especially marked when the insertions of Z1 were cut. It was found that this could be staunched effectively with celloidan solution, but that the celloidan would stick better if the area of the operation had first been painted with the solution before any incision was made. This preliminary celloidan coating was therefore invariably made before starting preparatory work.

To keep the exposed nerves moist a few drops of physiological saline were placed in the Y segment from time to time. Only two solutions were tried, namely those of van Harreveld (1936) and Shiff

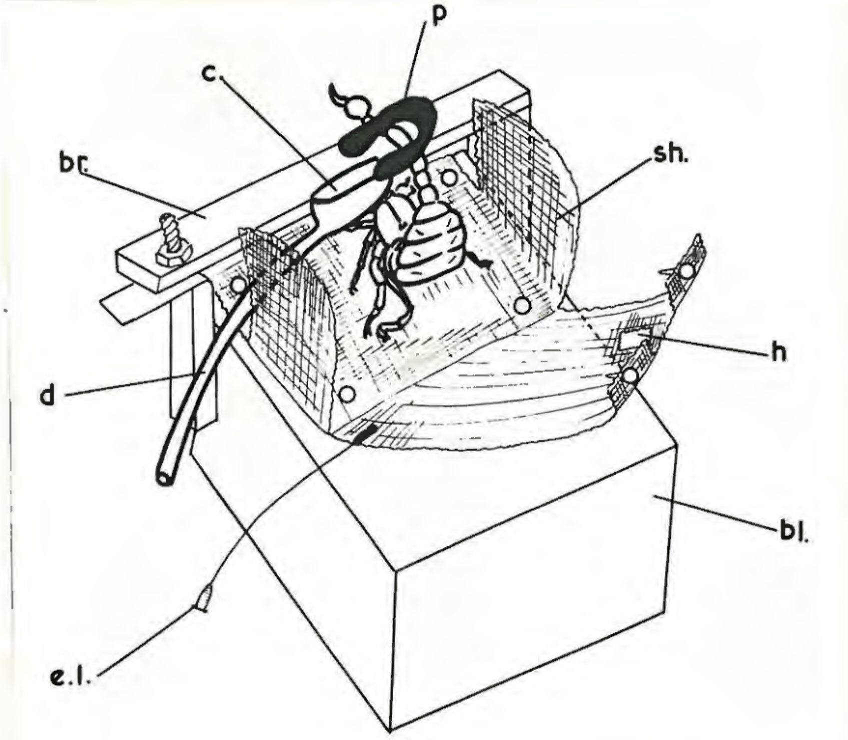


Fig. 86. Arrangement for recording mechanical movement of sting. bl., operating block; br., bridge over anterior region of scorpion; c., sealing wax cup collecting excess fluid from preparation; d., plastic drainage tube from cup; e.l., earth lead; h., hole in wire gauze to allow access for electrodes to nerves of tail; p., plasticine retaining tail on bridge; sh., wire gauze screening.

not in bibliography

and Ewer (1952). Both were originally developed for use with freshwater decapods and both appeared to be satisfactory if brought to pH 7.1, the pH of Opisthophthalmus blood quoted by Grasset et al. (1945). In the main, van Harreveld's solution was preferred as the other solution produces a precipitate at this pH.

To collect excess saline solution a cup, **c.**, moulded out of sealing wax was attached to the bridge, a hole was bored into the bottom, and plastic tubing, d, sealed in position to act as a drain (Fig. 86).

This preparation seemed to have a number of advantages not found in the claw preparations. Not only was the animal the correct way up, the incisions easy and clear of all blood vessels, but the bridge protected the greater part of the animal's body from both heat and light. Furthermore the tail and mesosoma were in a more natural position than formerly. Again, when, as sometimes happened, the physiological saline leaked around a claw preparation, it ran on to the operating block and certainly inundated the openings of the book lungs which were pressed against the block. It seems likely that a number of premature deaths which occurr~~r~~ed with such preparations were due to the animal being drowned. In the tail preparation, no matter how bad such a leak might be, the openings of the book lungs were safely out of the way.

Recording the mechanical responses of the tail was done in a number of ways. The actual movement of the Z segment itself could be used. Because the lance of the sting is smooth as well as curved, it was not possible to attach a thread to it directly and it was too hard to allow notches nitches to be cut in it. Sticking the lance into a small piece of cork, which was then kept wet and swollen was one way in which a purchase could be got upon the slippery sting (Fig. 87a): in the end, however, it was found simplest and safest to coat the whole segment with Samsonite and attach a thread to the "built-up" sting. (Fig. 87b).

Direct records from the Z1 and Z3 muscles are much more difficult to obtain. Initially an attempt was made to use the

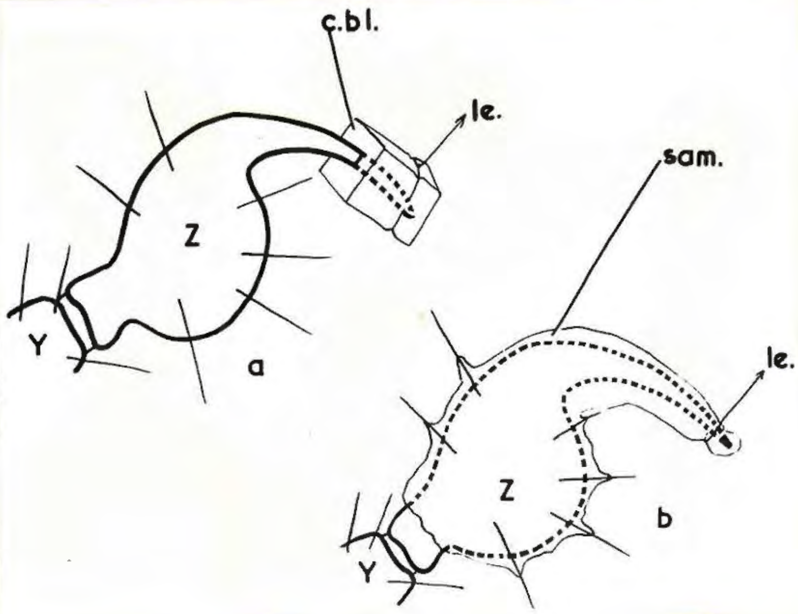


Fig. 87. Methods of attaching a recording thread, **le.**, to the bulb of the sting, **Z.**:
(a) using a cork block, **c.bl.**
(b) using a layer of Samsonite, **sam.**

muscle apodemes themselves, but these are extremely short and, unlike the apodemes of crab muscle, are not tough and fibrous. After a few attempts, this idea was abandoned in favour of "splitting the sting". This involved making the cuts shown in Fig. 88. In the main, it consisted in cutting off all but the base of segment Z. The cylinder of exoskeleton which is left has on it the insertions of all four Z muscles. The cylinder was split horizontally so that the insertions of Z1 and Z~~2~~3 muscles were separated and the chitinous plates which carry them freed from the Y segment by cutting through the sfot articular membrane - the cut 2 is to allow this to be done with some measure of facility. A vertical slit was then made through the lower of the two plates so that three small pieces of chitin resulted, each carrying the insertion of one or a pair of muscles. The insertions of the two Z1 muscles are too close together to allow their separation with any ease, and, in any case, such a course seemed unnecessary. To record from such an assembly of muscles size 20 trout fly hooks were pushed through each plate and attached by way of a terylene thread to the mobile electrode of a transducer. If this thread is moistened with saline it stiffens as it dries, leaving a fine, slightly rigid connecting rod between the muscle and the elctrode. Using two transducers it is possible, in this way, to record the activity of one of the Z3 muscles and its antagonists.

Such preparations respond well for periods of four to six hours, provided time is given between each stimulation for the nerves and muscles to recover.

3. Results.

As indicated in the introduction, the results so far obtained from this study are only preliminary and one question only will be considered here, namely does the myo-neural system, as exemplified by the Z~~2~~3 muscles of the tail, show the typical mechanical characteristics of other arthropods?

Three criteria may be used in attempting to answer such a question, namely:-

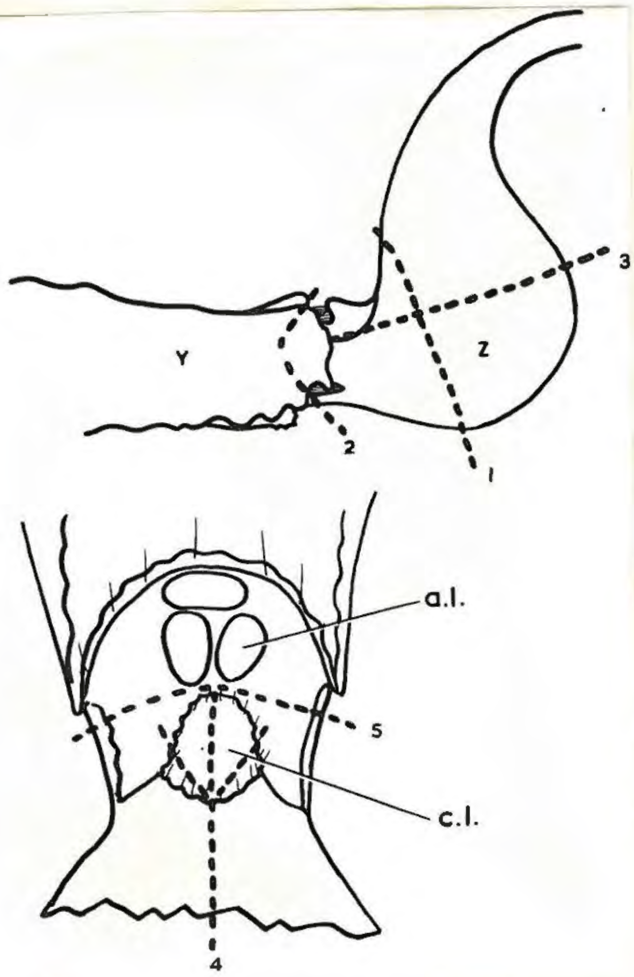


Fig. 88. Operative cuts for the exposure and isolation of muscles moving the tail bulb. For further explanation, see text. a.l., anal lobe; c.l., central lobe.

(a) does the system show frequency sensitive facilitation?

(b) does the system show a Blashko-Cattell and Kahn effect?

(c) are there inhibitory nerves which express their activity mechanically?

Responses to Single and Repetitive Stimuli.

Using shock of 1 msec. duration a fairly clear threshold to single shock was found at an amplitude of 0.4 v. To such a stimulus the muscle responds with a very small, fairly slow contraction, which can only be seen by direct observation (cf. Pantin, 1936). This response is about one-twentieth of the maximal contraction which can be obtained from the muscle and is unchanged as the intensity of stimulation is increased up to 3.5 v. It would appear that if a twitch system is present, it does not respond to single shocks while the absence of tension recruitment with increasing amplitude of stimulation points to the response being due to a single axon.

When stimuli are given at a frequency even as low as 6 cycles per second (c.p.s.) there is a very marked facilitation in the response (Fig. 89).

At higher frequencies the contractions gradually fuse. This fusion is well marked by 13 c.p.s. and at 20 c.p.s. the response is a smooth tetanus. If at 20 c.p.s. or higher the nerve is first stimulated at an intensity a little above threshold voltage, for a period and the intensity of the stimulation is then increased to 2.3 v. there is a sharp increase in the tension developed. Further increase in the stimulation intensity to 3.5 v. results in no further increase in the tension developed (Fig. 90). Results from experiments of this type suggest the presence of two motor axons of different threshold of stimulation. Further evidence for this comes from experiments at lower frequencies of stimulation, but high amplitude. Thus at 13 c.p.s. and 1.2 v. a clonus develops: this rises in tension as a sigmoid curve which is starting to flatten when a second increase in tension develops. It is suggested that this effect is due to the presence of two motor axons, the one facilitating more rapidly than the other.

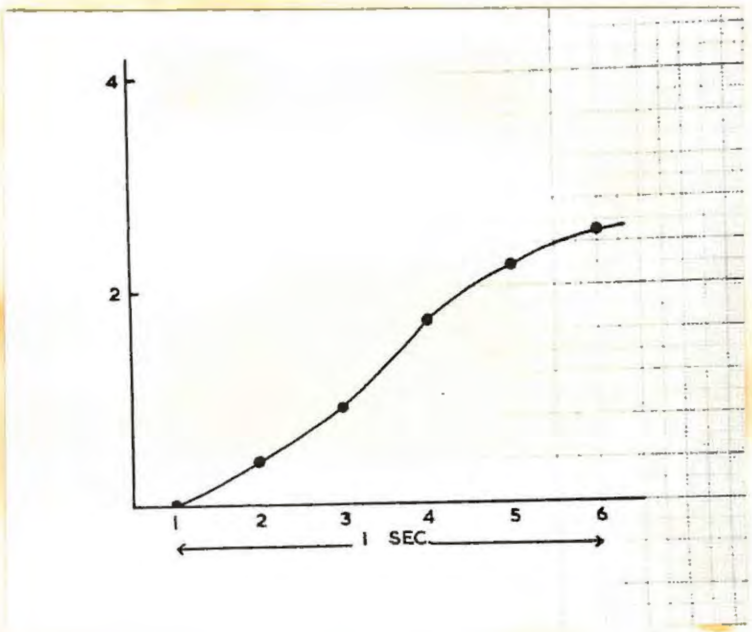


Fig. 89. Development of tension in the Z3 muscle in response to successive shocks. Abscissa - time; Ordinate - tension in arbitrary units. Each point represents the tension developed by a discrete contraction.

N.B. Oscillograph records were taken upon sensitive paper and not film. This is very unsatisfactory for showing fine detail when reproduced. Certain results are therefore presented in graphical form.

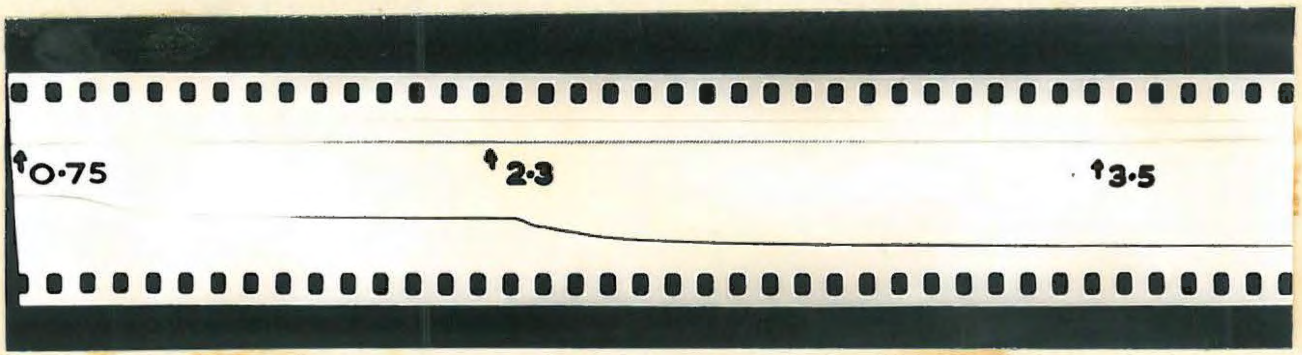


Fig. 90. Oscillograph trace showing tension recruitment with increasing intensity of stimulation. Upper line - time marker; middle line - record of stimulus; bottom line - mechanical response.

Changes in intensity of stimulus (in volts) indicated by arrows. Frequency of stimulation 80 c.p.s. Pulse duration 2 m.sec.

These various results point to the fact that the Z3 muscle is supplied by at least two motor acons which both show marked frequency facilitation and in this feature resemble conditions found in other arthropods.

The Blasho, Cattell and Kahn Effect.

Blashko, Cattell and Kahn (1931) demonstrated, using the muscles of the legs of crabs, that if a motor axon is stimulated at a steady but fairly low frequency until the tension developed is constant, the interpolation of one or more additional shocks will not only cause in increase in tension, but that this tension is now held by the lower frequency of stimulation. Such an effect has been demonstrated using the Z3 muscle. This effect is probably due to facilitation at the myo-neural junctions and its occurrence here may again be taken as evidence of such a phenomenon.

Inhibition.

The last question to be considered is whether there are any signs of mechanical inhibition. Evidence for such an effect has indeed been found and the results of a typical experiment are shown in Fig. 92. It can be seen that increasing the amplitdue of stimulation results in a decrease in the tension developed and that with a return to the original amplitude the tension is almost immediately restored. Hoyle (1955) has pointed out that inhibitory artifacts may arise at high intensities of stimulation owing to polarisation of the stimulating electrodes, and considers that the claim of Ripley and Ewer (1951) to have demonstrated mechanical inhibition in the levator tarsus of <u>Locusta</u> is due to such an effect. He finds that such polarisation can be avoided by placing a large capacity condenser in the cathode line leading to the electrode. The effect found here persists however, when a 0.2 μF condenser is included in the circuit.

It seems probable then that there is at least one inhibitory axon supplying the Z3 muscle in the scorpion tail.

4. Conclusions.

From the results presented above it would appear probable that the Z3 muscle is supplied by two motor axons and at least one

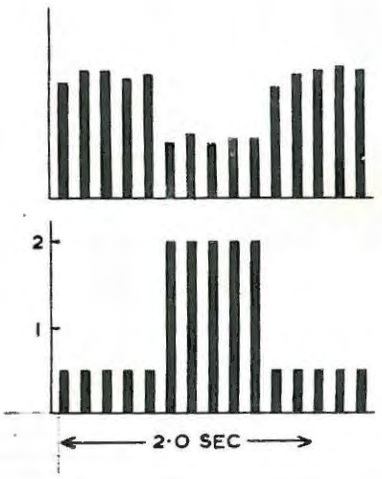


Fig. 92. Inhibition in the ZB muscle. Abscissa - time: Ordinate - upper figure, tension in arbitrary units; lower figure, stimulation intensity in volts. Stimulation frequency 6 c.p.s. It will be seen that increase in the intensity of stimulation results in a fall of the tension developed.

inhibitory axon. The result cannot be taken as final until it is accompanied by a study of the action currents associated with these events. Sufficient has been achieved, however, to show that the myoneural system found here does not differ, at least in its gross features, from that in other arthropods so far studied.

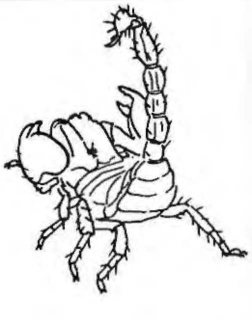
It has already been pointed out that the insects, as narrowly personfied by Locusta, differ from the decapod crustacea in having fibres which, although they hyperpolarise the muscle membranes, do not produce any mechanical inhibition. In this particular the scorpion appears to agree with the crustacea, but, as has been emphasised above, this difference may rather reflect the peculiarities of Locusta as a herbivore than have any general validity. In the study of arthropod myo-neural physiology the urgent need - apart from that of extending and deepening the present observations, is to determine whether the conditions found in Locusta are also encountered in carnivorous forms such as mantids and tettigonids, and to obtain a picture of the condition also in both the diplopods and chilopods.

VIII. ENVOI

Hyman (1955) has recently saluted the echinoderms as a phylum "especially designed to puzzle the zoologists". While not accepting the philosophical implications of this salutation, the arachnids might well be saluted as a group designed to puzzle the arthropodologist and their relative neglect may be a reflection, not of their small economic importance, their bad name as venomous animals or their place in the literature of psychoanalysis, but rather of the fact that we lack a key to the comprehension of their peculiarities.

If the modes of thought of men are, in general, socially conditioned, so too the modes of thought of a zoologist may be conditioned by his familiarity with one particular animal. Opisthophthalmus is a burrower and, possibly for this reason, it has appeared that many of those characteristics which are peculiar to the Euarachnida - the lack of antennae, the limitation of feeding appendages frequently to a single pair, the absence of a neck, the presence of only simple eyes, the highly developed responsiveness to ground vibrations and the possession of book lungs - all point to the group having evolved first as burrowing forms. Indeed this may be true of the Merostomata as well, for Limulus is known to burrow and Lankester (1883) say that it does so in a manner recalling that of the scorpion, Androctonus.

If this idea has validity it opens up the possibility that, in invading the land, the euarachnids, whose ancestors may well have been freshwater animals, moved out of the rivers or ponds, not up the banks but through the banks into the soil and that, much as the isopods carry with them the stains of migration through the littoral zone (Edney, 1955), so too the peculiarities of the modern arachnids reflect the very different route which brought them to dry land.



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