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THE MUSCULATURE OF THE PROTHORACIC LEGS AND ITS INNERVATION IN *HIERODULA MEMBRANACEA* (MANTIDEA)

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CONTENTS

The musculature of the fore limbs and the innervation pattern of the muscles in the praying mantid *Hierodula membranacea* (Burm.) are described. There are three antagonistic pairs of muscles (promotors–remotors, abductors–adductors, anterior rotator–posterior rotators) operating the prothoracic–coxal joint around three different axes. At the coxo-trochanteral, femoro-tibial and tibio-tarsal joints there are flexor and extensor muscles, but at the tarsal–pretarsal joint only flexors are present. The trochanteral extensor is a complex muscle, with both parallel-fibred and pennate parts. The trochanteral–femoral joint is operated by a single muscle, the femoral reductor.

There are six pairs of prothoracic nerves, the first of which innervates the musculature of the neck and pro-mesothoracic joints. The other five nerves are all

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concerned with the innervation of the muscles and sense organs of the prothoracic legs. Some of the motor neuron somata in the prothorathic ganglion have been identified by using the cobalt chloride backstaining technique.

The leg musculature, its innervation pattern and the location of the motor neuron somata are compared with those of other orthopteroid insects.

1. INTRODUCTION

The fore limbs of praying mantids are highly adapted for the capture of prey, being long, massive and well armed with spines. Prey is captured by a rapid, precisely directed movement of the limbs (the strike) and afterwards held securely by contraction of the large tibial flexor muscle. The fore limbs and the strike are of interest from a number of points of view including comparative anatomy, mechanics and neurobiology. The purpose of the anatomical study described here is threefold. First it provides a description of the fore limb muscles of *Hierodula membranacea* as a background to a parallel study of the mechanics of the predatory strike (Gray & Mill 1983). Previous anatomical descriptions of mantid fore limb musculature dealt with different genera (*Stagmomantis carolina* (Leverault 1938) and *Mantis religiosa* (La Greca & Raucci 1949), although Maki (1938) dealt briefly and incompletely with the thoracic musculature of *Hierodula patellifera*. Second, it describes the gross neuronal anatomy of the prothorax and the position of some of the neuron somata in the prothoracic ganglion thus providing a basis for future studies on the neural control of fore limb movements. Third, it provides anatomical comparisons with relatively unmodified limbs from other insect species and with the hind limbs of mantids. Some additional skeletal specializations of the fore limbs, that is, the apodeme suspensions, are described elsewhere (Gray & Mill 1983).

2. MATERIALS AND METHODS

Hierodula membranacea (Burm.) is a large, bright green mantid, and the adults are about 8 cm long. The culture of the animals used in this study is described in detail by Gray (1981). Briefly, juveniles were reared together, initially in containers measuring 17 by 11 by 7 cm, and fed on *Drosophila*. After the fourth or fifth instar they were transferred to a larger cage (30 by 30 by 30 cm) and fed on blowflies. Adult females were kept in individual cages and oothecae, when laid, were removed and placed in a separate container. The temperature was maintained at 25–27 °C, and the humidity was kept fairly high.

Whole and dissected specimens of both sexes, either fresh or in 70% alcohol (following fixation in Brazil 1904) (Gray 1954), were examined using a Zeiss Epitechnoscope. Illumination was provided by a Schott Mainz KL 150B light source.

The unusual posture and specializations of the forelegs pose some problems for the directional terminology of the legs. Some authors faced with this difficulty (for example, in the cockroach (Pringle 1938), and in the mantid (Leverault 1938; La Greca & Raucci 1949)) have named the surfaces of the limbs according to their positions in the living animal. This system has the virtue of being simple to apply, though not so easy to understand for one unfamiliar with the normal orientation of the legs in the animal described. The system also makes interspecific comparisons somewhat difficult.

To overcome these problems the directional terminology applied here to the mantid fore limb is derived from that applicable to a relatively unspecialized leg. The leg is assumed to be oriented at right angles to the side of the body, with all leg segments lying more or less horizontally. The surfaces of the femur and tibia that are brought together when the femoro-tibial joint is flexed are ventral. To apply this to *H. membranacea*: (i) the coxa is rotated posteriorly through 90°; (ii) the coxa is abducted through 90°; (iii) the coxa is promoted so as to be perpendicular to the line of the body. The surfaces of the leg segments can now be named (figure 1).

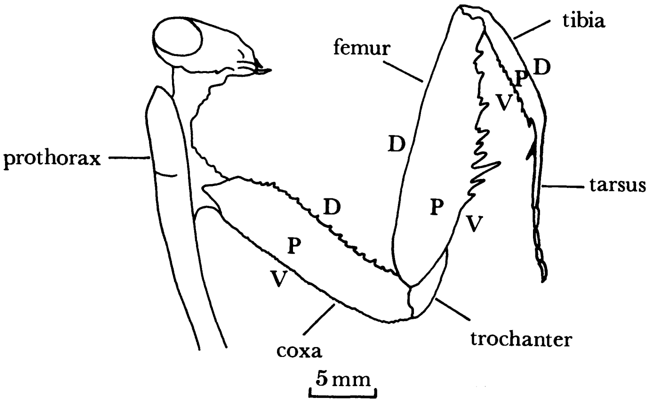

FIGURE 1. Side view of the head and prothorax to show the orientation of the segments in the right fore leg. P, posterior; V, ventral; D, dorsal.

When naming and describing muscles the origin is defined as the dorsal or proximal attachment, the insertion as the ventral or distal attachment (for example, Davis 1968). A single muscle is defined as a fibre or bundle of fibres that (i) originate on the same sclerite; (ii) are contiguous for most of their length; and (iii) form a unitary morphological insertion (Maki 1938; Davis 1968; Alsop 1978). Leverault (1938) and La Greca & Raucci (1949) used a similar definition, except that where bundles of muscle fibres inserted on the same apodeme and were thought to perform similar functions they classed them as one muscle, regardless of whether they originated on the same sclerite or ran contiguous for most of their length. According to this latter system, bundles that originated in clearly different places were regarded as parts of the same muscle and labelled a, b, c, etc. Hence some muscles described in *Stagmomantis carolina* and *Mantis religiosa* as single muscles made up of several parts, are described below as a number of separate muscles.

For examination of fine nerve branches, some specimens were injected with reduced methylene blue (McConnell 1933). The preparation was left for 2 h at room temperature, opened up in 8% ammonium molybdate, left for a further 30 min and dissected in 70% alcohol.

The nerve roots are numbered from the anterior backwards, and the connectives are not numbered; this is the system used by most authors. The detailed numbering is a modified version of that devised by Mill (1965) for dragonfly larvae.

A preliminary study of the distribution of the motor neurons was made by using backstaining with cobalt chloride. Staining was carried out in a staining bath made from a block of clear perspex. Each block contained two holes 13 mm in diameter and 6 mm deep. They were separated at their closest point by 1 mm, where a 1.5 mm square channel was cut through the top of the perspex dividing wall.

Prothoracic ganglia were dissected out of freshly killed specimens. The nerve under study was dissected so as to allow 6 mm of nerve, where possible, beyond its final branch. All other nerve roots were cut off short. One of the wells of the staining bath was filled with saline (NaCl, 7.5 g; KCl, 0.1 g; $CaCl_2$, 0.2 g; $NaHCO_3$, 0.2 g; H_2O, 1000 ml), to which about 0.2 mg of glucose was added. The other well contained distilled water. The ganglion was placed in the saline, and the nerve branch under study was laid through the channel into the distilled water before being sealed in place with a 50:50 vaseline:heavy paraffin–oil mixture. The exposed branch was freshly cut in the distilled water and left for 1 min, since this is supposed to cause dilation of the cut axons' ends thus rendering subsequent penetration of the dye more reliable. The water was then replaced by 7.5% $CoCl_2$ solution and the bath placed in a petri dish containing moist cotton wool for 12–48 h at room temperature.

The ganglion was removed and placed in a solid watch glass containing 5 ml of saline and two drops of saturated ammonium sulphide solution for 15 min. It was washed thoroughly in fresh saline, dehydrated through a graded series of ethyl alcohols, cleared with xylene and embedded in Canada balsam. The slides used for whole mounts were made from aluminium sheet with a 12 mm diameter hole in the centre. By mounting the ganglion between two coverslips in this hole it could be viewed from either side under the microscope.

The muscle names used are based upon those of Leverault (1938), and Leverault's numbers for the muscles are given in brackets after each of the names. Disagreements with previous descriptions of mantid prothoracic anatomy are discussed where they arise and a comparison is also made between the muscles of the mantid prothorax that are involved in the strike and those of orthopteroid insects that do not have the raptorial specializations of the mantid.

3. OBSERVATIONS

The most notable adaptation of *Hierodula membranacea* to its raptorial habits is its unusually large (over 35% body length) and mobile prothorax. The protergum is the main structural member, forming in effect a 'U' cross-section strut. The limbs are highly modified in relation to those of the pterothorax. Most significantly the coxa is considerably elongated, being nearly as long as the femur. The coxa, trochanter, femur and tibia are all very robust and the latter two are heavily armed with spines (which are involved in prey capture). Furthermore the limb joints, particularly the prothoracic–coxal (P–C) joint, are highly mobile. Specializations of some of the apodeme suspensions have been observed which are believed to be involved in maintaining effective moment arms over wide ranges of movement (Gray & Mill 1983).

(*a*) *Musculature*

(i) *Prothoracic musculature*

The positions and attachments of the prothoracic muscles of *H. membranacea* are similar to those of *S. carolina* (Leverault 1938) and *M. religiosa* (La Greca & Raucci 1949). The muscles are redescribed here, first, to provide a full description of the thoracic musculature of *H. membranacea* and, second, so that their innervation can be described. Differences between the species do occur as some muscles have been identified as having a different function in *H. membranacea* from that described for them in *S. carolina* by Leverault.

(ii) *Prothoracic–coxal joint*

The musculature of the insect prothoracic–coxal (P–C) joint can be divided into six primary functional groups which work as three antagonistic pairs around the three axes defined by

Snodgrass (1935). These axes are those of promotion–remotion, abduction–adduction and anterior–posterior rotation (figure 2).

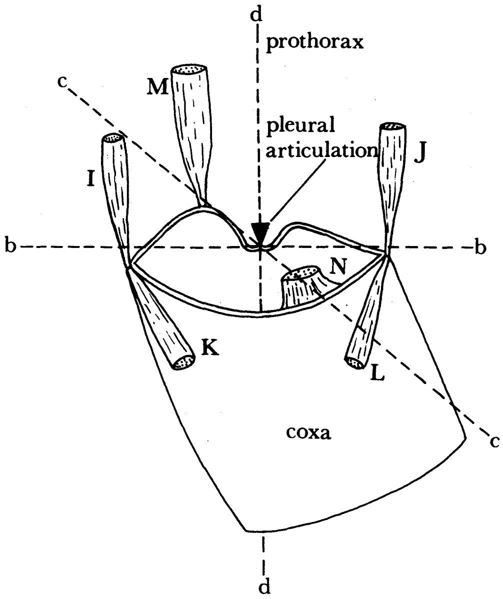

FIGURE 2. Schematic diagram of the mechanism of coxal movement with respect to the pleural articulation (▼). The view is drawn looking laterally from the midline. The three axes of movement are promotion (I) and remotion (J) on the transverse axis (c–c), abduction (M) and adduction (N) on the longitudinal axis (b–b), and anterior rotation (K) and posterior rotation (L) on the vertical axis (d–d). (After Snodgrass 1935.)

The musculature is described below in terms of the six functional groups listed. In practice, many muscles fulfil more than one function and, in these cases, they are classified according to the function that is regarded as primary.

Promotors. The *tergal* (L19a) and the *pleural* (L19b) *coxal promotors* (figures 3*a*, *b* and 4) are both large muscles originating on the anterior lateral portion of the tergum and on the anterior portion of the episternum, respectively. They insert on a strong apodeme which has a highly sclerotized anchorage on the anterior corner of the coxal rim. This contrasts with the statement of Snodgrass (1935) that the tergal promotor inserts on the trochantin, except where the trochantin is much reduced or is absent. In *H. membranacea* the trochantin is not reduced and indeed has four large muscles inserting on it. However, the rotation of the P–C joint has made these latter muscles adductors and another pair of muscles, presumably originating from Snodgrass's group M (the abductors) (figure 2) have taken over the function of promotors. This also provides a possible additional advantage, in that the promotor inserts directly onto the coxa which may be of importance in allowing fast and extensive promotions of the coxa.

Maki (1938) listed four promotors in *Hierodula patellifera* (17–20 in his system). These are the four coxal adductors that insert upon the trochantin. Presumably he identified these muscles as promotors from their insertion on the trochantin, even though only one of the four can exert a pull that is directed even slightly forwards. The tergal and pleural coxal promotors he named as the tergal and pleural coxal abductors (31 and 32, respectively, in his system).

Remotors. The *lateral* (L10a) and *posterior* (L10b) *coxal remotors* (figures 3*a*, *b* and 4) are the principal remotors of the coxa and are large muscles. The lateral muscle originates on the lateral

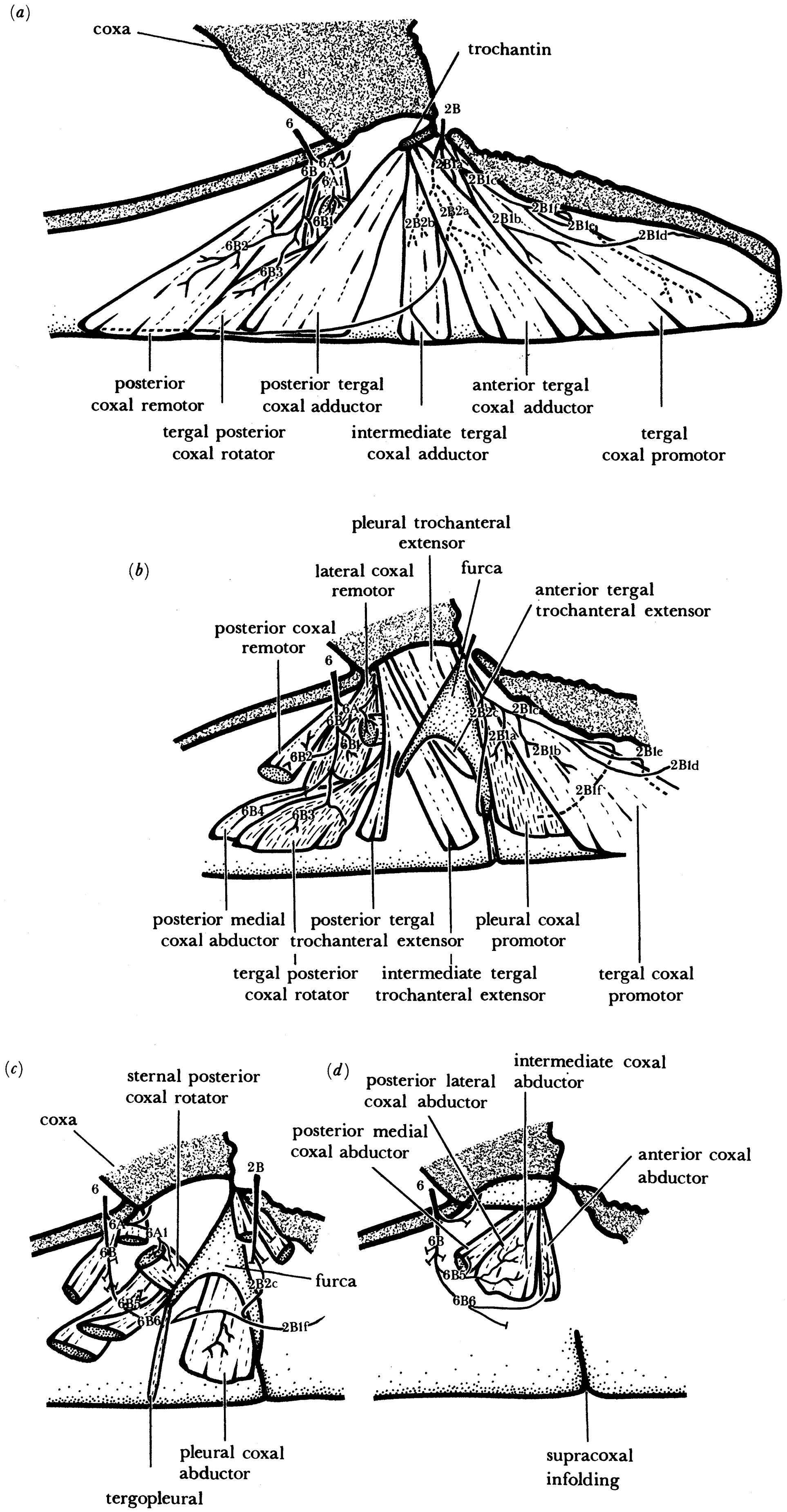

FIGURE 3. Basal coxal musculature and nerves of the right side of the prothorax, viewed from the mid-line. Successive layers of muscle have been removed in (*b*), (*c*) and (*d*).

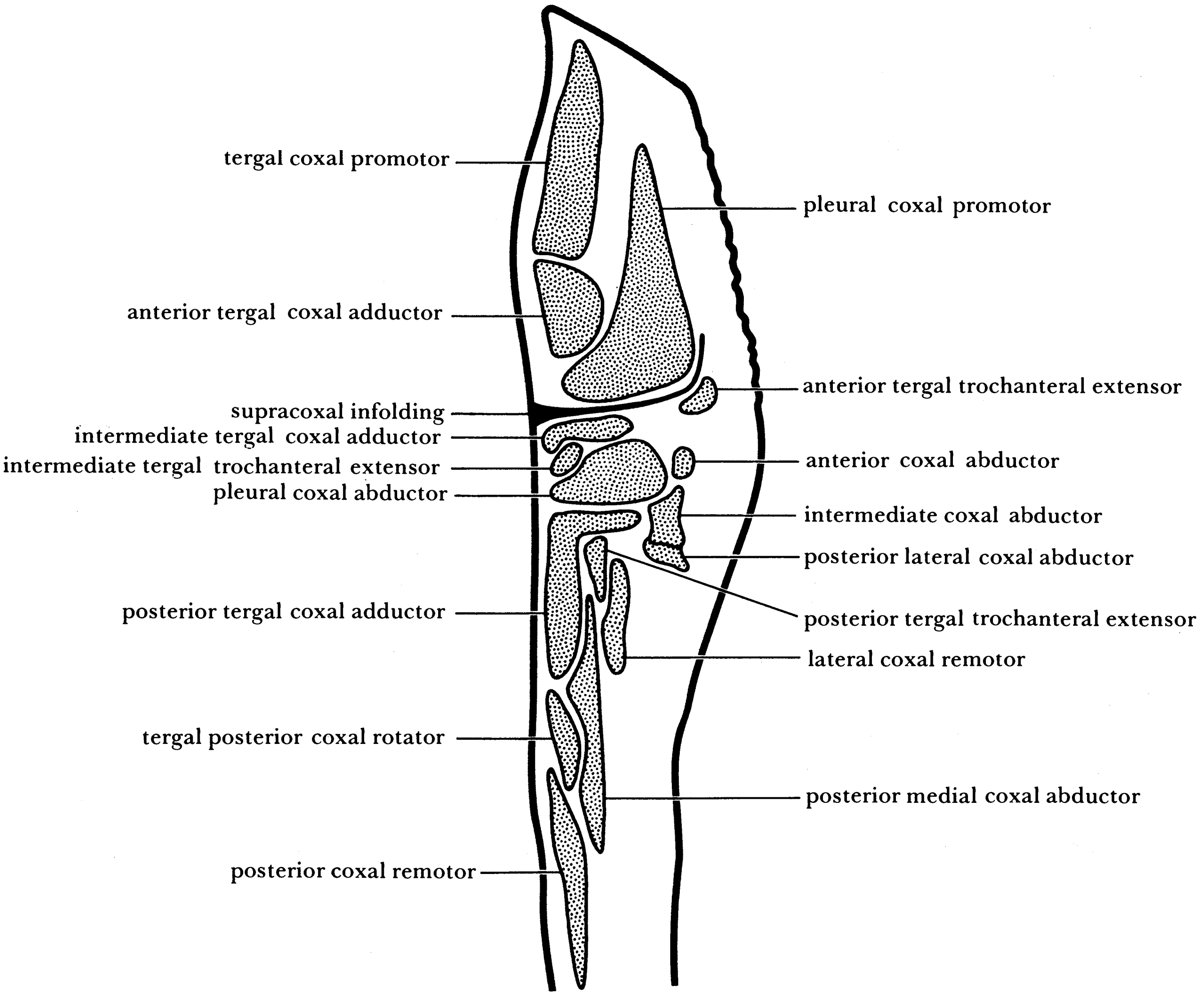

FIGURE 4. Dorsal view of the right side of the protergum to show the attachments of the basal coxal musculature of the prothorax.

part of the tergum, just posterior to the supracoxal inflexion. The posterior muscle originates on the mid-lateral tergum posterior to all the other coxal basal muscles. Both muscles insert on a tendon which originates from the posterio-lateral portion of the basal coxal rim. These are both typical remotors belonging to group J (Snodgrass 1935) (figure 2).

Abductors. There are five abductors (figures 3*b*, *c*, *d* and 4). The *anterior coxal abductor* (L16) is short and extremely thin, and it originates on the lateral part of the tergum, just behind the supracoxal infolding (figure 3*d*). The *intermediate coxal abductor* (L15) originates immediately posterior to this (figure 3*d*), while the origin of the *posterior lateral coxal abductor* (L14) lies so close to that of the intermediate muscle that they are almost indistinguishable (figure 3*d*). Indeed, in *H. membranacea* the insertions of these two muscles are so close that their separation is only possible by observation of the bilobed structure of their shared apodeme. However in *S. carolina* they are clearly distinguishable (Leverault 1938). The *posterior medial coxal abductor* (L17) is a large muscle which originates on the median lateral tergum well posterior to the other muscles of the group (figure 3*b*, *d*). All of these muscles insert on the proximal tip of the basal coxal rim behind the coxal articulation. They thus appear to belong to group J (remotors) of Snodgrass (1935) (figure 2). Maki (1938) identified them as remotors in *H. patellifera*, though they certainly could not have that function in *H. membranacea.*

The fifth abductor, the *pleural coxal abductor* (L20) is a tergopleural muscle, inserting on the epimeron and originating on the tergum, just posterior to the supracoxal infolding and medial to the anterior abductor (figure 3*c*). In *H. membranacea* the prothoracic epimeron is fused to the episternum and coxal articulation, but not to the sternum. Furthermore the episternum is flexible, allowing considerable movement of the coxal articulation and trochantin in the abduction–adduction plane. Thus contraction of this muscle, in conjunction with other abductor muscles, probably plays an important role in the high degree of freedom of movement of the coxa in the abduction–adduction plane.

In the cockroach *Periplaneta americana*, which also has a highly modified coxal articulation, with all six coxae lying almost flat against the body (an adaptation that enables the cockroach to enter narrow cracks), Carbonell (1947) found alterations of function of the basal coxal musculature similar to those found in the mantid. In addition he found no functional abductors (abduction resulting from cuticular elasticity) but several remotors. This supports the thesis that the coxal abductors of the mantid leg are derived from muscles that were originally remotors (group J) of Snodgrass (1935)), rather than being muscles of the abductor group that have somehow retained their function as the leg base shifted. Additional evidence comes from the positioning of the abductor insertions posterior to the coxal articulation, since Snodgrass (1935) states that the abductors of a 'typical' leg are anterior to the articulation.

Adductors. There are four adductors (figures 3*a*, 4 and 5), but adduction of the coxa is largely carried out by three of these which insert on the tip of the trochantin. The *anterior tergal coxal adductor* (L9a) originates on the median region of the tergum, just anterior to the supracoxal

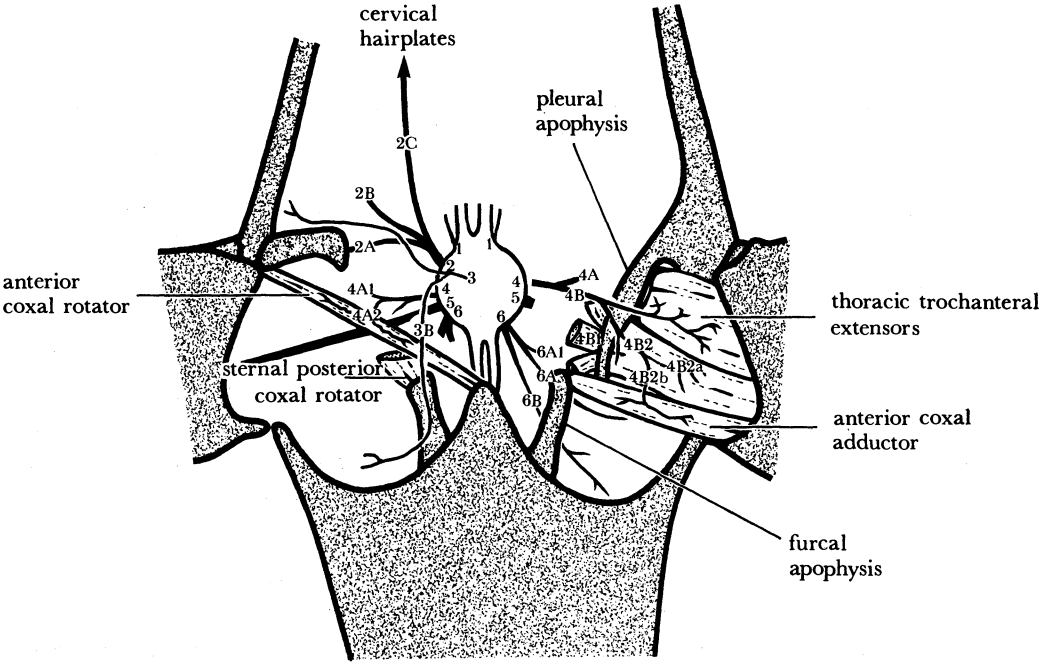

FIGURE 5. Ventral view of the prothoracic ganglion and some of the basal leg muscles.

infolding (figure 3*a*). Its pull is directed slightly forwards and probably provides a small posterior rotational component in addition to its main function of adduction. The *intermediate tergal coxal adductor* (L9b) originates on the median part of the tergum immediately posterior to the supracoxal infolding (figure 3*a*). In *M. religiosa* (La Greca & Raucci 1949) and *H. patellifera* (Maki 1938) this muscle has two distinguishable parts. However, in *S. carolina* (Leverault 1938) and *H. membranacea* it has a single origin. The *posterior tergal coxal adductor* (L9c) originates immediately posterior to the intermediate muscle (figure 3*a*). Its pull is directed well backwards and it has an anterior rotational component in addition to its role in adduction.

These muscles belong to group I (promotors) of Snodgrass (1935) (figure 2), but have come to perform a new function in the modified mantid fore limb (see the section on the promotors).

The fourth adductor, the *sternal coxal adductor* (L18) is a wide, flat muscle originating on the ventral surface of the furcal apophysis and inserting on the anterior part of the basal coxal rim (figure 5). It corresponds to muscle N of Snodgrass (1935) (figure 2) and also provides a little posterior rotation.

Anterior rotator. The *anterior coxal rotator* (L11) originates on the tip of the furcasternite, and inserts on the dorsal part of the basal coxal rim (figure 5). This represents muscle K (figure 2) (Snodgrass 1935).

Posterior rotators. There are two posterior rotators (figures 3*b*, *c*, 4 and 5). The *tergal posterior coxal rotator* (L13) is a long flat muscle which originates on the mid-lateral tergum posterior to the leg base (figure 3*b*) and inserts on the posterior coxal rim with the sternal posterior rotator (below), and the posterior lateral abductor. This muscle also provides some remotion.

The *sternal posterior coxal rotator* (L12) is a short, thick muscle which originates on the dorsal surface of the furcal apophysis (figures 3*c* and 5) and inserts on the coxa with the tergal posterior rotator. Some abduction is also provided by this muscle.

The sternal rotator belongs to group L of Snodgrass (1935), the tergal rotator to group J (figure 2). The rotation of the coxal base has resulted in this latter muscle becoming primarily a posterior rotator, with remotion only a secondary function.

In addition to the above muscles there are two small muscles intimately associated with the P–C joint, but apparently not directly involved with coxal movement.

(i) The *tergopleural muscle* (L21) (figure 3*c*) is a small muscle with no obvious function. It originates on the lateral region of the tergum some way posterior to the supracoxal infolding and inserts on the pleural apophysis. Presumably it is a homologue of the larger tergopleural muscles of the pterothoracic segments.

(ii) The *sternopleural muscle* (L22) is a very small muscle which holds the tips of the furcal (sternal) and pleural apophyses close together.

(iii) *Coxo-trochanteral joint*

Extensors. The *anterior tergal* (L23d), *intermediate tergal* (L23c), *posterior tergal* (L23e) and *pleural* (L23b) (*thoracic*) *trochanteral extensors* are long parallel-fibred muscles (figures 3*b*, 4 and 5*a*). The first three originate laterally behind the supracoxal infolding, while the pleural trochanteral extensor originates on the pleural infolding. All four merge to insert on the broad trochanteral extensor apodeme.

The *coxal trochanteral extensor* (L23a) is a large pennate muscle which originates on the ventral side of the coxa and inserts on the distal part of the extensor apodeme (figure 6*a*). The *anterior* (L24) and *posterior* (L25) *accessory trochanteral extensors* are very small muscles which originate

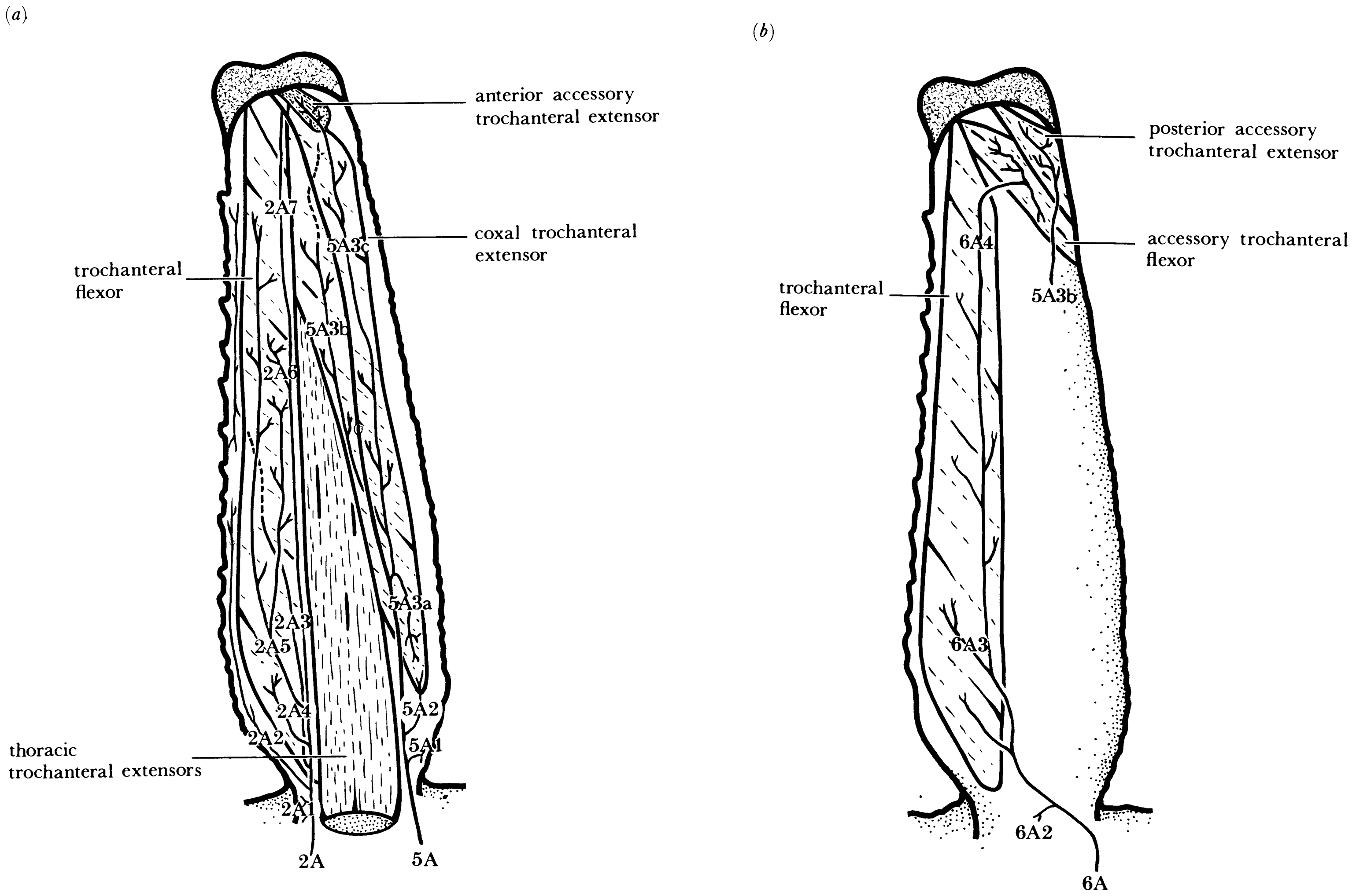

FIGURE 6. Muscles and nerves of the left procoxa. In (*b*) the coxal and thoracic trochanteral extensors and the anterior accessory trochanteral extensor have been removed.

in the distal, ventral region of the coxa and insert on the base of the main trochanteral extensor apodeme (figure 6*a*, *b*).

Functionally the trochanter can be considered as being extended by two muscles. (i) A muscle with long parallel fibres (10–12 mm long), consisting of the four tergal and pleural muscles, and termed collectively the thoracic trochanteral extensor (TTrE), and (ii) a pennate muscle, the coxal trochanteral extensor (CTrE), with fibres 3.5–4.5 mm long. The TTrE and CTrE have approximately the same volume. The two accessory muscles are so small that they can probably be disregarded functionally. In the posterior legs of *S. carolina* (Leverault 1938) and the legs of *Periplaneta americana* (Alsop 1978) these latter muscles are of approximately equal size to the main coxal trochanteral extensor muscle. The great difference in size between the accessory and the main muscles in the fore limb of the mantid is presumably due to the considerable lengthening of the coxa.

La Greca & Raucci (1949) described the accessory muscles in *M. religiosa* as an antagonistic pair (for abduction and adduction of the trochanter). As the coxo-trochanteral (C–T) joint in dictyopterans has only one degree of freedom of movement (extension–flexion) this seems hardly likely.

Flexors. The *trochanteral flexor* (L26) is a pennate muscle which originates in the medial anterior and posterior regions of the coxa, and inserts on the long flexor apodeme of the trochanter (figure 6*a*, *b*). In addition there is an *accessory trochanteral flexor* (L27) which is a small muscle originating in the distal, medial posterior region of the coxa and inserting on the posterior side of the base of the trochanteral flexor apodeme (figure 6*b*). This muscle, as with the accessory extensor muscles, is relatively much smaller than its counterparts in unmodified legs (for example, the rear legs of *S. carolina* (Leverault 1938) and the legs of *Periplaneta americana* (Alsop 1978)).

(iv) *Trochanto-femoral joint*

There is a single muscle operating this joint, the *femoral reductor* (L28) (figure 7*a*, *b*). It is composed of two fibre bundles, both of which originate on the anterior ventral region of the trochanter and insert on the anterior basal rim of the femur. There is no antagonist to this muscle, femoral production presumably occurring through cuticular elasticity.

(v) *Femoro-tibial joint*

Extensor. The *tibial extensor* (L29) is a long pennate muscle which originates on the posterior part of the femur and inserts on the long flexor apodeme of the tibia (figures 7*b*, 8*a*).

Leverault (1938) listed another tibial extensor in *S. carolina*, the median accessory extensor of the tibia (L30), originating on the proximal dorsal, anterior portion of the femur and inserting on a long, thin tendon which attaches to the dorsal side of the base of the tibial extensor apodeme. However, in *H. membranacea* (figures 7*a*, *b* and 8*a*) this is clearly a chordotonal organ, homologous with the pro- and mesothoracic femoral chordotonal organs of orthopterans (for example, Slifer 1935; Campbell 1961; Burns 1974), and this has been confirmed by a recent ultrastructural study (K. E. Haynes & P. J. Mill, unpublished observations). It has been suggested that this organ should be renamed the femoro-tibial (FT) chordotonal organ, to indicate its physiological role and at the same time bring the insect terminology into line with that used in crustaceans (Hughes & Mill 1974; Mill & Pill 1981). Alsop (1978) described a muscle in the same position in each leg of *P. americana*, yet suggested that its function may be proprioceptive, as it is too small to be of significance in moving the leg. Most likely this is also a femoro-tibial chordotonal organ.

Flexors. There is a *trochanteral tibial flexor* (L31b), which is a small muscle originating on the

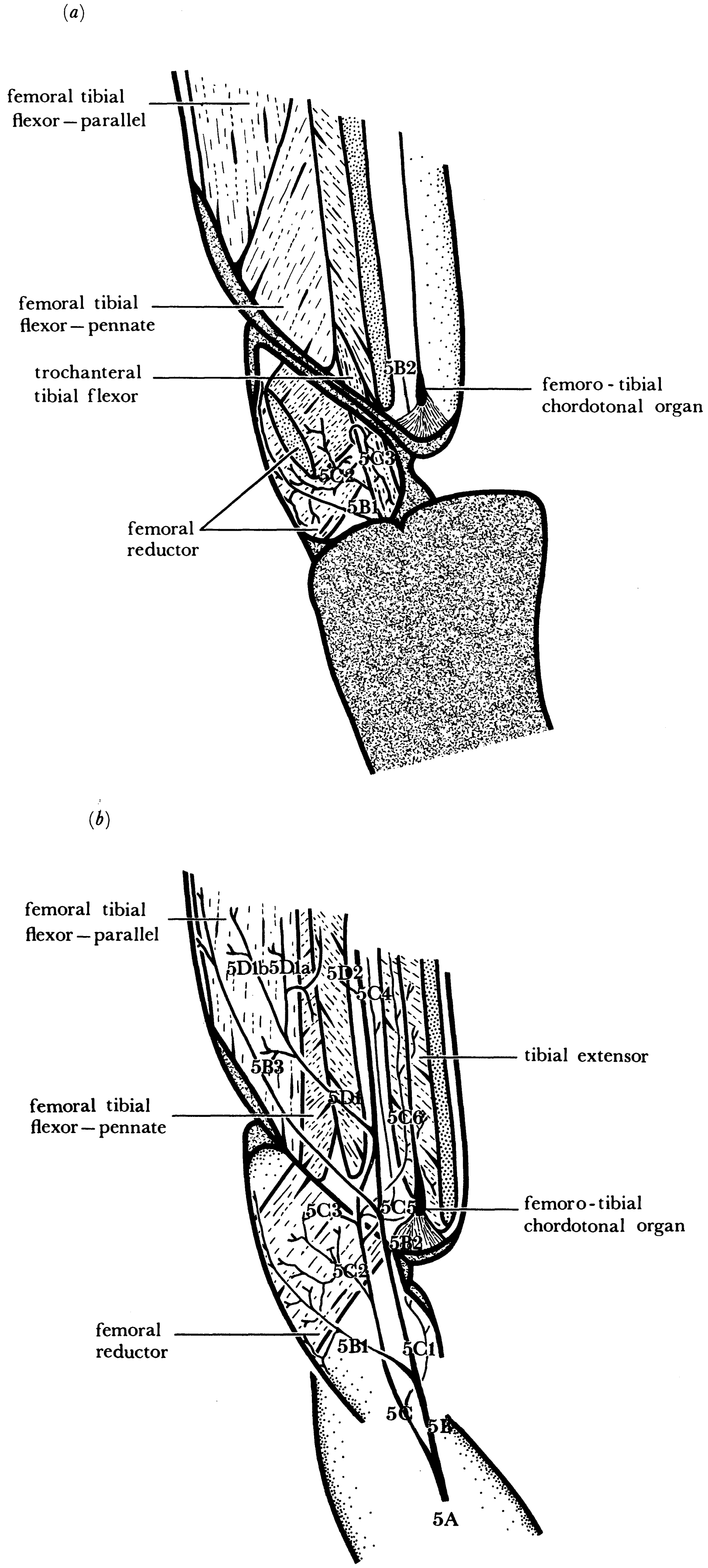

FIGURE 7. Muscles and nerves of the right protrochanter and the proximal part of the right profemur. In (*b*) the trochanteral tibial flexor and part of the pennate part of the femoral tibial flexor have been removed.

anterior wall of the trochanter and inserting on the proximal end of the long broad flexor apodeme of the tibia (figure 7*a*). In addition there are two large *femoral tibial flexors* (L31a), one with parallel fibres, the other with pennate fibres, and together these occupy most of the volume of the femur (figures 7*a*, *b* and 8*a*). The parallel-fibred muscle originates on the proximal, ventral part of the femur and inserts on the distal, ventral surface of the large flexor apodeme. The pennate-fibred muscle originates over the whole of the ventral part of the femur and inserts on the surface of the apodeme not occupied by the parallel-fibred muscle. Both of these muscles consist of several distinct bundles which might be named separately, if following a very narrow morphological definition of muscular identity. However, Leverault (1938) and La Greca & Raucci (1949) treated these two muscles as one, whereas Snodgrass (1929) made a distinction between them in the tibial flexor of *Dissosteira carolina* (muscles 107a and 107c) and, as is shown by Gray & Mill (1983), they probably play different functional roles in *H. membranacea*.

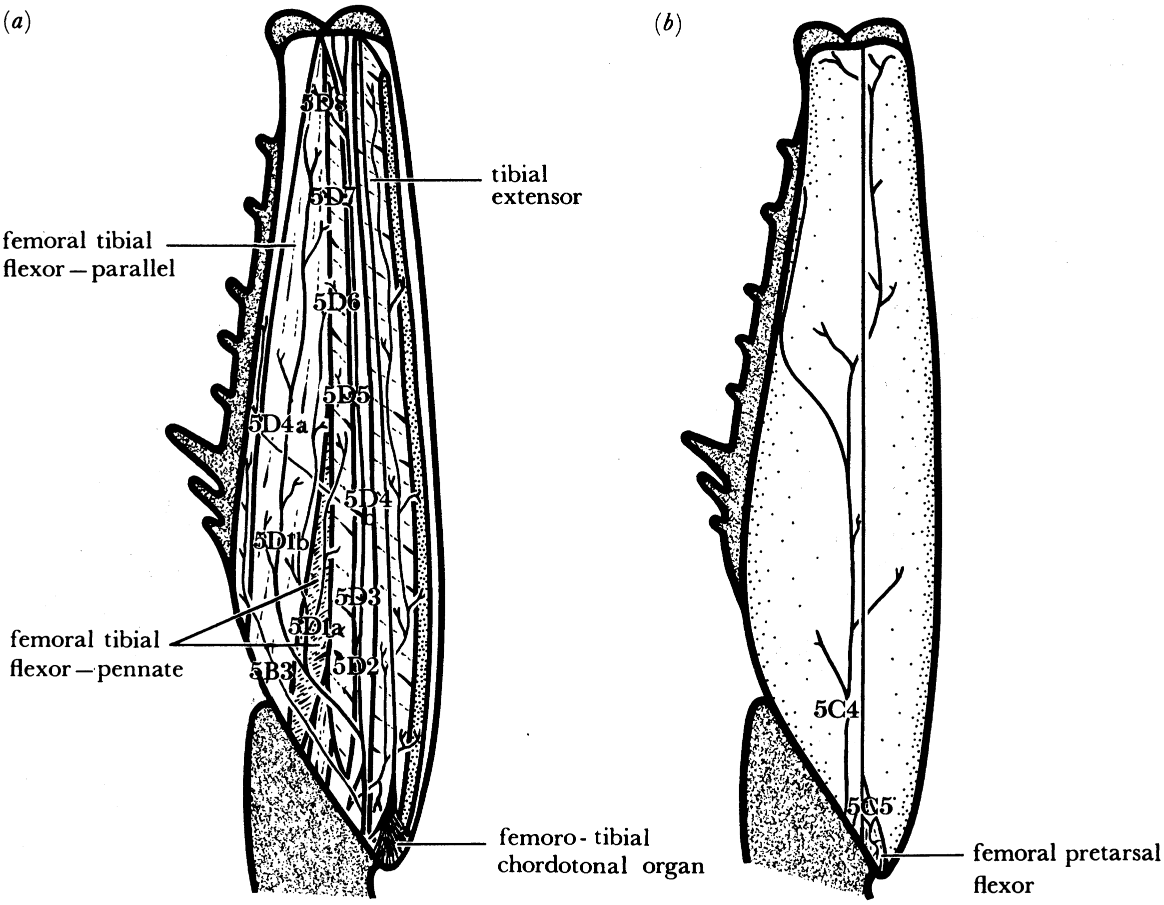

Figure 8. Muscles and nerves of the right profemur. In (*b*) the tibial flexors and extensor have been removed.

(vi) *Tibio-tarsal joint*

There is a small *tarsal extensor* (L32) which originates in the distal, dorsal region of the tibia and inserts on the dorsal, basal tarsal rim (figure 9*a*); also a *tarsal flexor* (L33) which originates in the ventral, anterior region of the tibia and inserts on the ventral, basal tarsal rim (figure 9*a*).

(vii) *Tarsal–pretarsal joint*

There are three pretarsal flexors. The *femoral pretarsal flexor* (L34c) consists of a small bundle of fibres originating on the ventral surface of the femur at its proximal tip (figure 8*b*). The *proximal tibial pretarsal flexor* (L34b) originates on the proximal, dorsal apodeme of the surface of the tibia (figure 9*a*), and the *distal tibial pretarsal flexor* (L34a) originates on the distal two thirds of the anterior surface of the tibia (figure 9*a*). All three insert on the apodeme of the unguitractor plate and together correspond to the three-part retractor unguis muscle of the locust.

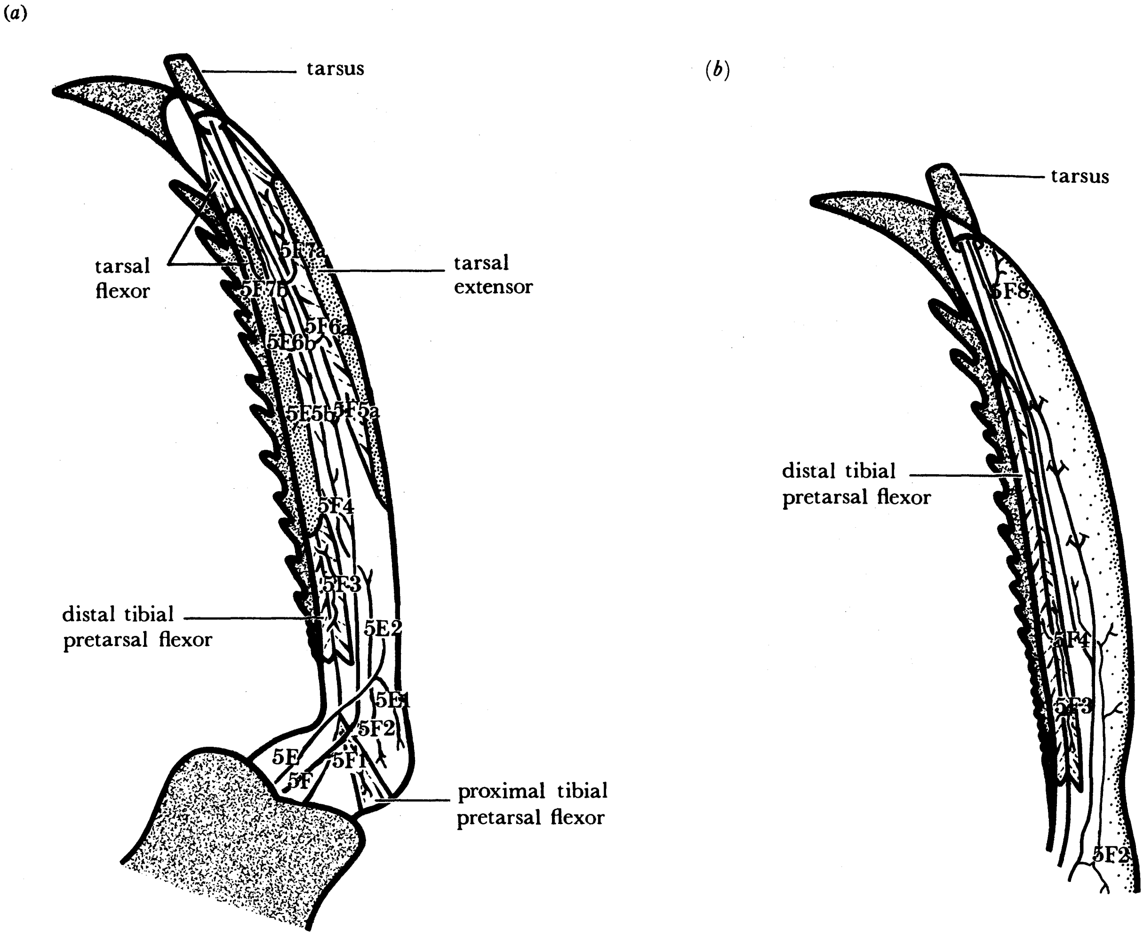

FIGURE 9. Muscles and nerves of the right protibia. In (*b*) the tarsal flexor and extensor and the proximal tibial pretarsal flexor have been removed.

No intrinsic muscles could be found in the tarsus in either cleared or dissected specimens. This is in agreement with Snodgrass (1927) and Leverault (1938).

(*b*) *Neuronal anatomy*

The prothoracic ganglion lies ventrally, immediately above and between the bases of the procoxae. Paired anterior and posterior connectives join it to the suboesophageal and mesothoracic ganglia respectively. Six pairs of nerves emanate laterally from the ganglion and a median nerve arises between the posterior connectives (figure 5).

(i) *Nerve 1*

This is a very fine nerve root which originates from the anterior surface of the ganglion, immediately lateral to the base of the anterior connective (figure 5). Within 2 mm, before giving rise to any branches, it fuses with a much larger recurrent nerve from the suboesophageal ganglion. From the fused nerve, branches run to innervate the musculature of the neck and pro-mesothoracic joints. One branch fuses with a branch of nerve 1 of the mesothoracic ganglion.

(ii) *Nerve 2*

This large nerve root, second only in size to nerve 5, arises from the antero-lateral edge of the ganglion, just posterior to nerve 1 (figure 5). Shortly after leaving the ganglion nerve 2 divides giving rise to three major branches, 2A, 2B and 2C. The first of these (2A) runs ventro-laterally and enters the coxa (figures 6*a*, 10). It continues close to the dorsal edge of the basal coxal rim and here gives rise to two small sensory branches, both of which branch repeatedly to sensory cells scattered over the cuticle and membrane of the dorsal, basal region of the coxa. Although these branches are separate they have been labelled 2A1a and 2A1b (the former being proximal) since they are small, close together and innervate the same region.

In the coxa, 2A continues between the trochanteral flexor and extensor muscles. Immediately distal to the basal coxal rim, it gives rise to a further four branches in quick succession. 2A2 and 2A3 are long, sensory branches which innervate the proximal and distal halves, respectively, of the dorsal coxal surface. 2A4 innervates the proximal part of the trochanteral flexor, but the principal nerve innervating this muscle is 2A5, which itself gives rise to two major branches running the whole length of the muscle. (The exact point of branching of 2A3 is not consistent; it may arise between 2A4 and 2A5 or even distal to 2A5.) 2A6, arising nearly halfway down the coxa, also innervates a part of the trochanteral flexor muscle. The remaining branch, 2A7, continues to run between the trochanteral flexor and extensor muscles and fuses with 5A at the distal end of the coxa.

The second major branch, 2B (figures 3*a*, *b*, *c* and 10), runs dorso-anteriorly and soon divides

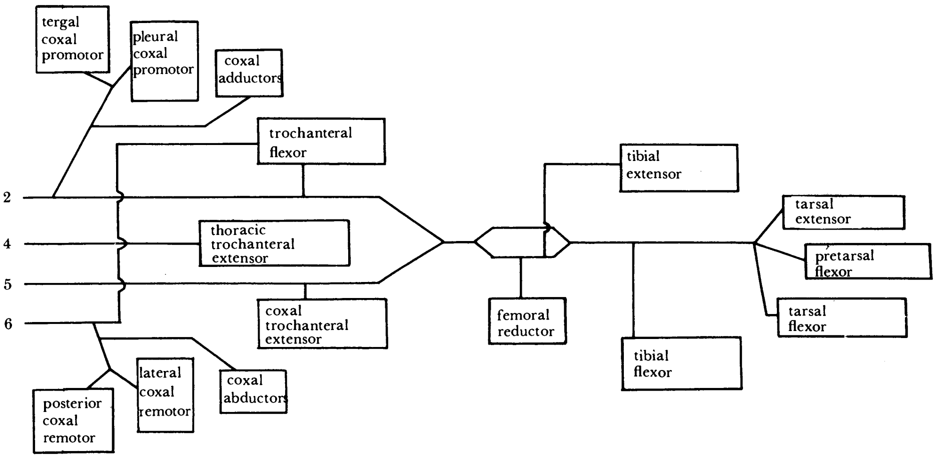

FIGURE 10. Summary diagram of the innervation of the principal prothoracic leg muscles.

into 2B1 and 2B2. 2B1 runs anteriorly along the ventro-medial side of the pleural coxal promotor, which it innervates (2B1a); it also innervates the tergal coxal promotor (2B1b). There is some variability in this branching. Either a single nerve arises from 2B1 and subsequently branches, or the two branches (a and b) arise separately. 2B1c innervates the sensory cells of the precoxal bridge. It can arise either before 2B1a or after 2B1b.

2B1 continues first anteriorly and then dorsally between the fibres of the anterior part of the tergal promotor. Here it branches again twice. The anterior branch (2B1d) innervates the sensory cells of the anterior part of the tergum, while the intermediate branch (2B1e) innervates the anterior end of the tergal promotor. The remaining part of 2B1 doubles back posteriorly between the fibres of this muscle and emerges at the posterior lateral edge of the pleural promotor. It then runs dorsally and laterally under the infolded episternum, where it branches. 2B1f innervates the pleural abductor muscle and 2B1g innervates the tergo-pleural muscle. Just before innervating the abductor, 2B1f fuses with 6B6b. The pleural abductor muscle is here defined as being innervated by 2B1f, but this does not mean that the muscle is innervated by axons from the second root and not from the sixth root.

2B2 runs posterio-laterally over the ventral edge of the anterior coxal adductor. Here it branches twice, simultaneously. The anterior branch (2B2a) runs dorsally along the lateral surface of the anterior adductor and innervates it, and also gives off a long sensory branch which runs posteriorly to innervate the medial region of the tergum. The posterior branch (2B2b) innervates the intermediate and posterior coxal adductors. The lateral branch (2B2c) innervates the sensory cells of the lateral region of the tergum, just posterior to the supracoxal infolding.

The third, and final, major branch of nerve 2 (2C) runs anteriorly without branching until it reaches the neck. Here it gives rise to three branches. 2C1 is a motor branch, innervating one of the neck muscles, while 2C2 and 2C3 are sensory branches, innervating the tergocervical and sternocervical hair plates respectively. These are the hair plates whose role in the fixation of prey was investigated by Mittlestaedt (1957).

(iii) *Nerve 3*

Nerve 3 branches out from the ganglion just posterior to nerve 2 but a short way in from the lateral edge of the ganglion, on the ventral surface (figure 5). The nerve is fine and almost immediately gives rise to anterior and posterior branches, both of which are sensory. The anterior branch (3A) innervates sensory cells underlying the basisternite while the posterior branch (3B) innervates cells of the intersegmental membrane between the furcal apophysis and the basal coxal rim.

(iv) *Nerve 4*

Posterior to nerve 3 and right on the lateral edge, nerve 4 emerges from the ganglion and runs ventro-laterally into the base of the leg (figure 5). Before reaching the base of the leg it splits into two. The smaller branch (4A) runs anteriorly and immediately branches again. 4A1 continues forwards and innervates a neck muscle (Leverault's (1938) muscle 4), which inserts on the trochantin. 4A2 runs ventro-laterally to innervate the anterior coxal rotator. The larger part of the root (4B) (figure 10) forms three branches at the base of the coxa. 4B1 turns dorsally and innervates the proximal parts of the tergal trochanteral extensor muscles. 4B2 branches, giving rise to 4B2a, which innervates the distal parts of the tergal trochanteral extensors, and

4B2b, which branches again to innervate the proximal and distal parts of the sternal coxal adductor muscle, respectively. In one preparation the proximal part of this muscle was innervated instead by a branch from 4B1. 4B3 innervates the pleural trochanteral extensor.

(v) *Nerve 5*

This is the largest nerve of the prothoracic ganglion and is the main nerve of the fore legs. The nerve arises from the ganglion immediately posterior to nerve 4 and runs ventro-laterally into the coxa (figures 5, 6 and 10). As it enters the coxa a sensory branch (5A1) (figure 6*a*) arises and innervates sensory cells underlying the proximal, ventral part of the coxal cuticle. Just distal to this, another small branch (5A2) leaves the main trunk and innervates the proximal part of the coxal trochanteral extensor. The nerve next branches about a third of the way along the coxa, and 5A3 runs in among the fibres of the coxal trochanteral extensor, branching twice. 5A3a is a small branch running proximally to innervate the coxal trochanteral extensor. The major branch (5A3b) runs distally, giving off many small branches which innervate the same muscle, and then runs in among the fibres of the posterior accessory trochanteral extensor which it also innervates (figure 6*b*). The third branch (5A3c) runs the length of the coxal trochanteral extensor, branching to innervate its anterior fibres, and at the distal end of the coxa it innervates the small anterior accessory trochanteral extensor muscle.

After giving rise to 5A3, 5A runs without branching to the coxo-trochanteral (C–T) joint, just before which it fuses with 2A7 (figure 6). It then splits into two branches, 5B and 5C (figures 7 and 8). This branching may well be a specialization to overcome the problems of passing a thick nerve through a highly mobile joint, as the two branches rejoin after passing the joint. Such an adaptation was not, however, observed at the C–T joint of *P. americana* (Nijenhuis & Dresden 1955*a*, *b*), of *Dissosteira carolina* (Schmitt 1959) or of *Locusta migratoria* (Campbell 1961).

5B gives rise only to sensory branches. The first (5B1) innervates the sensory cells of the cuticle of the anterior face of the trochanter and of the anterior side of the C–T joint; 5B2 innervates the femoro-tibial chordotonal organ; 5B3 innervates the sense organs of the proximal part of the femur.

The other half of the divided leg nerve (5C) has both sensory and motor branches. 5C1 is a sensory branch innervating the sense organs of the posterior wall of the trochanter and of the posterior side of the C–T joint. 5C2 runs along the anterior side of the femoral reductor muscle, sending numerous fine branches in among its fibres and innervating them. 5C3 is another motor branch; it is rather slender and innervates the small trochanteral tibial flexor muscle (figures 3 and 8*a*). The next branch (5C4) is a very long, sensory branch which innervates the sense organs of the posterior surface of the femur. About halfway along the femur it branches and 5C4a innervates the sensory cells of the middle part of the ventral cuticle of the femur, while 5C4b continues down the femur, innervating the posterior cuticle and terminating in sensory endings around the proximal side of the femoro-tibial (F–T) joint.

The last two branches of 5C are both motor nerves and they originate close together. 5C5 is a fine branch innervating the femoral pretarsal flexor, while 5C6 runs down the ventral side of the tibial extensor sending small branches in among its fibres.

Immediately distal to the trochantero-femoral (T–F) joint the remaining parts of 5B and 5C rejoin forming nerve 5D (figures 7*b* and 8*a*). This runs the length of the femur until just before the F–T joint, where it again splits into two. A number of branches emanate from this nerve in the femur. 5D1 is a large branch which originates immediately after the rejoining of 5B and 5C (occasionally it originates from 5C, that is, proximal to the join) and it runs ventrally and distally in among the fibres of the tibial flexor muscles, where it gives rise to two main branches. The anterior of these (5D1a) divides again, one part innervating the parallel-fibred tibial flexor while the other part innervates the proximal region of the pennate-fibred tibial flexor. The posterior branch (5D1b) innervates only fibres of the parallel-fibred tibial flexor.

In addition, all along the length of 5D, small branches (about six in all) arise and run ventrally in among the fibres of the pennate-fibred tibial flexor; these are named 5D2, 3, 6, 7, etc. Two other branches (5D4 and 5D5) arise about halfway along the femur. 5D4 is sensory and immediately divides again. 5D4a runs ventrally, through the posterior part of the flexor muscles, and innervates sensory cells on the ventral surface of the femur, while 5D4b innervates the sense organs of the distal anterior surface. 5D5 innervates fibres of the parallel-fibred tibial flexor.

At the distal end of the femur, before the F–T joint, 5D branches to form the two major nerves of the tibia, 5E and 5F (figure 9). The anterior of these (5E) is sensory and branches again past the joint. 5E1 innervates the proximal dorsal surface and 5E2 the anterior surface of the tibia. The posterior branch (5F1) originates as 5F passes through the F–T joint, and is a fine branch which innervates the proximal tibial pretarsal flexor. 5F2 is a sensory nerve which leaves 5F immediately after the joint and innervates the whole of the posterior surface of the tibia. About a quarter of the distance along the tibia 5F3 arises as a fine branch running ventrally and posteriorly to innervate the distal tibial pretarsal flexor. 5F4 occurs immediately distal to this and runs down the posterior surface of the tibia and into the tarsus. The destination of this nerve in the tarsus has not been investigated, but as there are no muscles in the tarsus it can be assumed that it is sensory.

The distal half of 5F gives rise to three pairs of branches (5F5a; 5F6a, b; 5F7a, b). In each pair the ‘a’ branch runs dorsally and innervates fibres of the tarsal extensor and the ‘b’ branch runs ventrally and innervates fibres of the tarsal flexor. Just before the tibio-tarsal (T–T) joint 5F gives rise to 5F8, a sensory branch innervating the distal anterior part of the tibia and the T–T joint. The remaining part of the nerve (5F9) enters the tarsus and, like 5F4, is presumably sensory.

(vi) *Nerve 6*

About midway between nerve 5 and the posterior connective, nerve 6 emerges from the lateral edge of the ganglion and it immediately branches into two (6A and 6B) (figures 3, 5, 6*b* and 10). 6A runs ventro-laterally towards the coxa. Almost at once it gives off a branch (6A1) which runs dorsally to innervate the sternal posterior rotator of the coxa. When nerve 6A reaches the coxal base it runs dorsally, between the sternal trochanteral extensors and the exoskeleton, until it reaches the dorsal side of the basal rim. Halfway across its traverse of the coxal base, a small sensory branch (6A2) arises to innervate the membranes of the posterior side of the thoracic–coxal (T–C) joint (figure 6*b*).

The main branch of 6A turns and runs between the trochanteral extensors and flexor, giving rise to numerous small branches which innervate the fibres of the flexor muscle. These are collectively called 6A3. At the distal end of the coxa the final branch of this nerve (6A4) arises and innervates the accessory trochanteral flexor. As 6A4 runs across the coxa to this muscle it passes close to 5A and, in some preparations, a fine strand was seen joining the two. This may be either connective tissue or a nerve branch. Pipa & Cook (1959) observed such a connection in the meso- and metathorax of *P. americana*, though not in the prothorax, so this may be a genuine fusion of nerves.

The other branch of nerve 6 (6B) runs dorso-posteriorly from the ganglion between the posterior rotator and the posterior remotor, and there branches several times in quick succession (figure 3). 6B1 runs anteriorly to innervate the lateral coxal remotor, 6B2 innervates the posterior coxal remotor, 6B3 innervates the tergal posterior coxal rotator, and 6B4 innervates the posterior medial coxal abductor. 6B5 runs laterally between the tergal posterior coxal rotator and the posterior medial coxal abductor, giving rise to a posterior branch (6B5a), which innervates the anterior region of the posterior medial coxal abductor, and an anterior branch (6B5b), which innervates the intermediate and posterior lateral abductors. The final branch (6B6) runs anteriorly along the medial surface of the tergal posterior coxal rotator and past the lateral side of the tergopleural muscle. Here it gives rise to 6B6a, a very fine branch which innervates the anterior coxal abductor, and 6B6b, which fuses with 2B1f and hence possibly innervates the pleural abductor. A homologous fusion between nerves of the third (corresponds to the second root in *Hierodula*, see table 1) and sixth roots has been observed in *P. americana* (Nijenhuis & Dresden 1955*a*, *b*).

(*c*) *Anatomy of motor neuron somata*

The somata of motor neurons innervating some of the proximal muscles of the leg were identified by the use of cobalt chloride backstaining. Figure 11 shows the positions of all the cell bodies identified by this technique. In all preparations in which the nerve to the coxal trochanteral extensor was stained, two axons could be seen to stain in the main leg nerve. However, only one cell body, CTrE(i) (figure 11), was ever stained. The cells that innervate the anterior and posterior coxal promotors are shown as separate groups on either side of the diagram. However, it can be seen that the positions occupied by some of these cells are very similar, and there is no way of determining from the data available whether these are distinct cells, or single cells that innervate both muscles.

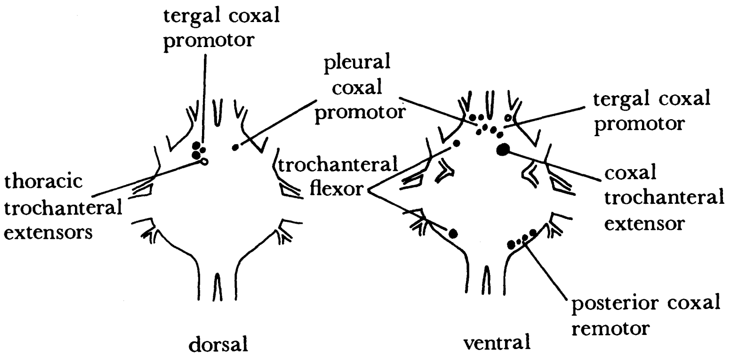

FIGURE 11. Identified motor neuron somata of the prothorax. All of the somata are ipsilateral; both sides of the ganglion are used for convenience in presentation.

4. DISCUSSION

There have been a number of previous morphological studies of the thoracic nervous system of members of the orthopteroid orders. Comparing these with the results of the present study

TABLE 1. THE INNERVATION OF THE PRINCIPAL LEG MUSCLES OF FOUR ORTHOPTEROID INSECTS. PROTHORACIC LEG OF *HIERODULA MEMBRANACEA*, *PERIPLANETA AMERICANA* AND *ACATHACRIS RUFICORNIS*; MESOTHORACIC LEG OF *P. AMERICANA* AND *LOCUSTA MIGRATORIA*

	Hierodula membranacea prothoracic leg		*Periplaneta americana* prothoracic leg (Pipa & Cook 1959)		*Periplaneta americana* mesothoracic leg (Nijenhuis & Dresden 1955*a*)		*Acanthacris ruficornis* prothoracic leg (Ewer 1957)		*Locusta migratoria* mesothoracic leg (Cambell 1961)
nerve	muscle	nerve	muscle	nerve	muscle	nerve	muscle	nerve	muscle
2B	coxal promotor (M) tergal coxal adductor (I)	3A	74, 75 (I) 70, 71, 72, 73 (M)	3A	126 (I), 127 (I) 118, 119, 120 (M)	IIζ IIγ	68 (I) 62 (M)	3A	94, 95, 96 (I) 89 (M)
2A	tibial extensor (6) femoral reductor (6) trochanteral flexor	3B	sensory nerve to coxa (2)	3B	142 (tibial extensor) 141 (femoral reductor) 138, 139c (2) (trochanteral flexors)	IIη	sensory nerve to coxa no motor branches	3B	sensory nerve to coxa
	fuses with the main leg nerve distally		fuses with the main leg nerve distally		fuses with the main leg nerve distally		no fusion with the main leg nerve		fuses with the main leg nerve distally
4	tergal and pleural trochanteral extensors	4	85 (a, b, c, d) (tergal and pleural trochanteral extensors)	4	135a, b, c (tergal and pleural trochanteral extensors)	IIε	71 (trochanteral extensor, all parts)	3C	103 (b, c, d) (tergal and pleural trochanteral extensors)
	anterior rotator (K) sternal adductor (N)		MX1 (K), (3) 82 (N)		105 (K) 132 (N)		anterior rotator (K) (4) 69 (N)	4B	92 (K) 100, 101 (N)
5	main leg nerve no innervation to the trochanteral flexor	5	main leg nerve no innervation to muscles 88, 89 (trochanteral flexor)	5	main leg nerve no innervation to muscles 138, 139, 140, 142 (trochanteral flexors)	III	main leg nerve no innervation to muscles 70, 71 (trochanteral flexor and extensor)	5	main leg nerve no innervation to muscle 102 (trochanteral flexor)

6A	trochanteral flexor	6B	88, 89 (2) (trochanteral flexor)	6B	139a, b, 140 (2) (trochanteral flexors)	IV A	70 (trochanteral flexor)	4A	102 (trochanteral flexor)
	sternal posterior rotator (L)		83 (L)		133, 134 (L)				
	possibly fuses with main leg nerve distally				possibly fuses with main leg nerve distally (5)	IV C	66, 67 (L)	4C	93 (L)
6B	coxal remotors coxal abductors (J)	6A	76, 77 78, 79, 80, 81 (J)	6A	129, 130, 131 (J)	IV D	63, 64, 65 (J)	4D	90, 91 (J)

The names and numbers of the nerves and muscles are as described by the original authors. Pipa & Cook (1959) and Nijhenuis & Dresden (1955*a*) both used the muscle numbering system of Carbonell (1947); Ewer (1957) and Campbell (1961) used that of Snodgrass (1929). Names in brackets after muscle numbers give functional descriptions; letters in brackets refer to the muscle group to which a basal coxal muscle has been ascribed.

Numbers in brackets indicate:

(1) Muscle 126 is a sternal coxal promotor. This muscle might be a homologue of the tergal or pleural coxal promotors or of the anterior rotator (which runs from the sternum to the anterior part of the coxal base) of the prothorax of *H. membranacea*. The anatomical evidence is in favour of the former, as muscle 126 of the mesothorax in *P. americana* is innervated from the same nerve root as the prothoracic coxal promotors of both species, while the prothoracic anterior rotator in both is innervated from a different root (root 4).

(2) The trochanteral flexor muscles of the metathoracic leg of *P. americana* innervated from nerve 3B are different muscles from those innervated by nerve 6B in this leg. Pipa & Cook (1959) pointed out that, in the prothoracic leg of *P. americana* there is no innervation of trochanteral flexors by nerve 3B, as the homologues of muscles 138 and 139c in the mesothoracic leg are missing from the prothoracic leg. Muscles 88 and 89, the homologues of muscles 139 and 140, are present and are innervated by nerve 6B.

(3) MX1 is a very fine anterior rotator of the prothoracic leg in *P. americana*. It was first described by Pipa & Cook (1959) and hence does not have a Carbonell (1947) number.

(4) The anterior rotator of the prothoracic leg of *A. ruficornis* is the name given to that muscle by Ewer (1957). Snodgrass (1929) did not describe a homologue to this muscle in *Dissosteira carolina*.

(5) Pipa & Cook (1959) observed a branch of nerve 6B merging distally with the main leg nerve in the meso- and metathorax of *P. americana*, although this was not observed by Nijhenuis & Dresden (1955*a*).

(6) Based on electrophysiological evidence.

should prove fruitful, first, in enabling a deeper understanding of the mantid nervous system and, second, in helping to elucidate some of the common features of the innervation of insect legs.

Nesbitt (1941) suggested that, in the orthopteroid orders, the nerves innervating basal leg muscles could be regarded as falling into an anterior and a posterior group. The anterior group innervates the tergal promotors, the anterior rotators and the pleural abductors (Nesbitt presumably did not mean sternal abductors); while the posterior group innervates the tergal remotors, the posterior rotators and the sternal adductors. Nesbitt's (1941) study did not deal with the peripheral nerves and it is useful to consider his thesis by comparing the innervation pattern of the leg muscles.

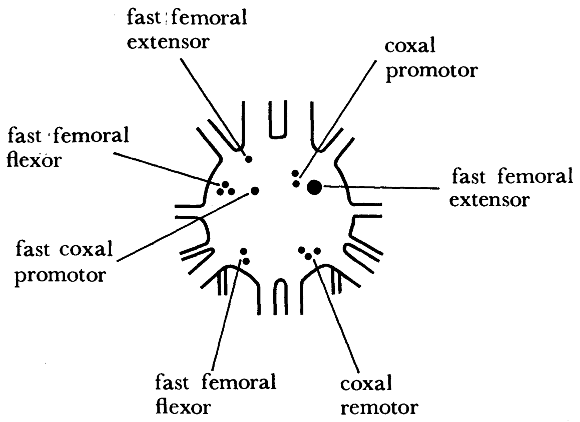

FIGURE 12. Some identified motor neuron somata of the cockroach metathoracic ganglion (Fourtner & Pearson 1977) and of the locust mesothoracic ganglion (Bentley 1970). All of the somata are ipsilateral; both sides of the ganglion are used for convenience in presentation. The outline of the ganglion is that of a cockroach metathoracic ganglion (after Pearson & Fourtner 1977). Data from the locust metathoracic ganglion is not comparable as it includes fused abdominal ganglia.

In *H. membranacea* there are six main nerves which between them innervate all the basal and intrinsic muscles of the legs. In table 1 the closest equivalent nerve branches in another dictyopteran (*Periplaneta americana* (Nijenhuis & Dresden 1955*a*, *b*; Pipa & Cook 1959)) and two orthopterans (*Acanthacaris ruficornis* (Ewer 1957) and *Locusta migratoria* (Campbell 1961)) are listed. The reasons for regarding some of the basal leg muscles of the mantid and the cockroach as arising from groups of muscles with functions other than those which they now serve have been discussed above. Hence, for comparative purposes, table 1 also indicates, for the basal leg musculature, the Snodgrass (1935) muscle group (figure 2) from which each muscle is thought to have arisen.

The data in table 1 indicates that there is a considerable degree of similarity in the general plan of innervation of the legs in the four species considered. The general pattern of motor innervation in *H. membranacea* is almost identical to that of the pro- and mesothoracic legs of *P. americana*, the only major differences being: (i) that 3B in the prothorax of *P. americana* does not innervate the trochanteral flexor; and (ii) where it does so, in the mesothorax, the parts of the muscle innervated by it are distinct from those innervated by 6B. This latter distinction cannot easily be made in *H. membranacea*, suggesting that the homologues of the separate muscles in the cockroach mesothorax had merged in the mantid leg as the coxa lengthened. However, recent work suggests that three parts (two pennate and one parallel-fibred) of this muscle can be distinguished having distinct innervation (Davis-Tomlins 1982).

There is a greater number of differences from the orthopterans, but these are explained mainly by the smaller number of nerve trunks leaving the ganglion in orthopterans. For example, nerves that leave the ganglion in two roots (second and fourth in the mantid, third and fourth in the cockroach) all arise from one nerve root (second) in *A. ruficornis* (Ewer 1957).

However, some of the differences are more significant, particularly those concerning the innervation of the intrinsic leg musculature of *A. ruficornis*. The trochanteral extensor (TrE) in this species is innervated by axons from only one nerve root (2), while in the others the tergal and pleural parts of the muscle receive innervation from root 4 (in Dictyoptera) or root 3C (in *L. migratoria*), while the coxal parts are innervated by root 5. The nerve branch innervating TrE in *A. ruficornis* appears to be the homologue of a branch of the fourth nerve root of the mantids, which innervates only the tergal and pleural parts of the muscle. The cobalt staining studies have shown that the nerves to the two parts of the muscle carry axons from two quite distinct groups of nerve cell somata in the ganglion. Whether the situation in *A. ruficornis* represents a reduction in the amount of innervation of the extensor muscles or the bringing together of both sets of axons in one branch is unknown.

Though undoubtedly there are differences, the innervation of the leg muscles of all the insects shown in table 1 clearly shares many common features. In addition, in all the prothoracic ganglia there is a first nerve root which fuses with a recurrent nerve from the suboesophageal ganglion and innervates the muscles of the neck and pro-mesothoracic joint. There is also a median nerve arising on the dorsal side of the ganglion and this nerve, having fused with a branch from the mesothoracic ganglion, innervates the muscles of the first spiracles.

The above basic pattern of innervation extends beyond the orthopteroid orders. The prothoracic ganglion of the alder fly, *Chauliodes formosanus* (Neuroptera) gives rise to three pairs of lateral roots and a median nerve (Maki 1936). The first root and the median nerve correspond closely to the pattern described above, while the second and third roots each have three major motor branches which together correspond to the six major leg motor branches described in *H. membranacea*. The same basic pattern can also be seen in *Agulla adnixa* (Neuroptera) (Matsuda 1956).

These observations make it possible to comment on Nesbitt's (1941) characterization of an anterior and a posterior group of leg motor nerves. Firstly it must be said that in only one of the four orthopteroid insects considered, the locust, is the sternal adductor innervated from the posterior group, which Nesbitt described as the typical situation. However, it is clear that these basic groupings do exist, not only among the orthopteroid orders but also in at least one other order, the Neuroptera. Indeed, it is possible to go further than this and to say that in orthopteroid insects the motor nerves of certain muscle groups tend to be associated. These are (i) the tergal promotor and pleural abductor (where these have not assumed a modified function); (ii) the trochanteral flexor (when innervated from the anterior group) and certain distal leg muscles (see table 1); (iii) the trochanteral extensors of the thorax, the anterior rotator and the sternal adductor; (iv) the posterior rotator and the trochanteral flexor; (v) the remotors of the coxa and (vi) the majority of the intrinsic muscles of the leg. In addition these groupings appear to hold true, in general, in the Neuroptera.

Furthermore, such interspecific similarities go beyond the level of nerve branching. There have so far been few studies in other species of the positions of the somata of neurons innervating muscles homologous to those studied here. However, comparison of those that are known in the cockroach metathoracic ganglion (Fourtner & Pearson 1977) and in the locust mesothoracic ganglion (Bentley 1970) with those of mantids (figure 12) shows a striking coincidence of position. The positions of many motor neuron somata in the locust metathoracic ganglion are known (for example, Burrows 1973), but as this ganglion is a fusion of the last thoracic ganglion with abdominal ganglia valid comparisons of position are difficult to make.

It can be concluded that, while there are many important similarities between the limb muscles and their patterns of innervation among orthopteroid insects, much more information from comparable studies on other groups is required before detailed inferences can be drawn with regard to evolutionary relationships. Furthermore, comparative detailed analyses of the locations of the motor neuron somata and dendritic fields in a wide range of species should provide further insight into such relationships, while at the same time providing a useful basis for comparative neurophysiological studies.

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