



## Skeletomuscular anatomy of the harvestman *Leiobunum aldrichi* (Weed, 1893) (Arachnida: Opiliones: Palpatores) and its evolutionary significance

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Skeletal muscles of the North American harvestman *Leiobunum aldrichi* are exhaustively surveyed and compared with other chelicerates to clarify the evolutionary morphology and phylogenetic relationships of arachnids. Representatives of 104 muscle groups are described and illustrated, and their possible functions are proposed. Comparisons of the feeding apparatus of *L. aldrichi* with that of other opilions, especially *Siro* (Cyphophthalmi) and *Acromares* (Laniatores), and two scorpion genera (*Centruroides*, *Pandinus*) indicate that the pharyngeal apparatus in *L. aldrichi* is derived and that its ability to accommodate large food particles is a secondary rather than primitive condition. Comparisons reveal several possible synapomorphies between Opiliones and Scorpiones suggesting that these orders may be sister groups. Apparently unique synapomorphies include an extrinsic cheliceral muscle that arises from the carapace and inserts on the second cheliceral article (deutomerite); an epistome divided into distal and proximal parts by a transverse sulcus; pharyngeal dilator muscles supported by a peripharyngeal skeleton formed by one dorsomedial and two ventrolateral epistomal processes, the latter also with muscular attachments to the endosternite; a specialized preoral chamber (stomotheca) derived from extensions (coxapophyses) of the coxae of the pedipalp and first two leg pairs; internal processes associated with the coxapophyses that serve, in part, as an attachment for muscles operating the coxa-trochanter joints, and lateral endosternal suspensor muscles that insert on the arthroal membrane between the leg coxae. These are the first observations providing explicit support for an Opiliones–Scorpiones clade.

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ADDITIONAL KEY WORDS:—Arthropoda – Chelicerata – Gagrellidae – morphology – muscle – phylogeny – homology – comparative anatomy.

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## INTRODUCTION

This report describes the skeletomuscular anatomy and provides an exhaustive myological survey for a common North American harvestman, *Leiobunum aldrichi* (Weed, 1893) (Palpatores: Phalangioidea: Gagrellidae), and explores the functional, evolutionary and phylogenetic significance of this information. The results provide new insights into the evolutionary morphology of the feeding apparatus of Opiliones, particularly the ability of many species to ingest large food particles, as well as a list of apparently unique synapomorphies supporting a monophyletic Opiliones–Scorpiones clade.

Opiliones have rarely held a central a role in discussions of ordinal relationships in Chelicerata, and resemblances between certain opilions and mites (Acari) were generally sufficient for many arachnologists to place these orders together (e.g. Kaestner, 1968; Savory, 1971; Weygoldt & Paulus, 1979; Shear, 1982). However, several workers have noted similarities between opilions and scorpions, especially the mouthparts, that have led some to suggest a close relationship between these two orders (e.g. Kaestner, 1931; van der Hammen, 1989; Shultz, 1990). Given that scorpions are regarded by many arachnologists to be the sister group to all other arachnids or to eurypterids (Weygoldt & Paulus, 1979; Kjellesvig-Waering, 1986; Stockwell, 1989), knowledge of skeletomuscular anatomy in Opiliones may be useful for understanding the evolutionary morphology and phylogeny of terrestrial chelicerates. In fact, preliminary descriptions of prosomal anatomy (Shultz, 1991) indicated that the arrangement of extrinsic appendicular muscles in Opiliones are very similar to that of *Limulus* (Xiphosura) and thus plesiomorphic with respect the condition found in scorpions. The present study was undertaken to clarify further the skeletomuscular features of Opiliones with the expectation that it would reveal additional insights into the evolutionary morphology of Chelicerata.

## MATERIAL AND METHODS

All observations were based on 20 adult female and five adult male *Leiobunum aldrichi* (Weed, 1893) (Palpatores: Gagrellidae) that were collected by the author in and around Columbia, Maryland, U.S.A. from June to August 1996. All specimens were killed and preserved in 95% ethanol. All observations were made using a Wild M-10 dissecting microscope (16× ocular lenses, 0.63× objective lens) at magnifications ranging from 81× to 806× using both transmitted and reflected light sources. Dissections were performed using standard techniques (Shultz, 1999) under 95% ethanol. Drawings were made with the aid of a camera lucida and were

subsequently digitized using a scanner for computerized manipulation and labeling of figures. Specific organ systems were dissected in multiple representatives of other arachnid taxa for comparison with *L. aldrichi*. These taxa were the opilions *Siro acaroides* (Ewing, 1923) (Cyphophthalmi: Sironidae) and *Acromares banksi* Goodnight & Goodnight, 1942 (Laniatores: Cosmetidae) and the scorpions *Centruroides vittatus* (Say, 1821) (Buthidae) and *Pandinus imperator* C. L. Koch, 1842 (Scorpionidae).

## RESULTS

The skeletomuscular anatomy of *Leiobunum aldrichi* is summarized below. The description provided is not intended to be complete but to provide the reader with a general understanding of skeletomuscular anatomy, especially locations of muscle attachments and features of functional or phylogenetic significance. Additional treatments of skeletomuscular anatomy in Opiliones are provided by Hansen & Sørensen (1904), Roewer (1923) and van der Hammen (1985, 1989). Numbers in the text refer to skeletal muscles listed in Table 1, where 104 muscle groups are numbered, given anatomical names, and described. Table 1 also includes comments on the function, evolution and phylogenetic significance of the muscle group and lists possible homologues described in earlier myological treatments of the whipscorpion *Mastigoproctus giganteus* (Lucas) (Uropygi) (Shultz, 1993) and whipspider *Phrynus longipes* (Pocock) (Amblypygi) (Shultz, 1999). Representatives of virtually all muscle groups are illustrated in Figures 1–8. A few muscle groups are not figured, but references are provided for relevant illustrations in other sources. Most figures are based on adult female specimens, although the description provided below is applicable to males. Aside from genitalia, adult male *Leiobunum* differ from females in being smaller, having proportionally longer legs, and a proportionally smaller opisthosoma.

### *Carapace*

The carapace comprises the dorsal elements of six postoral, appendage-bearing somites (Hansen & Sørensen, 1904; Winkler, 1957; van der Hammen, 1985, 1989) and is divided into three regions, namely, the propeltidium (prplt), mesopeltidium (msplt) and metapeltidium (mtpit) (Figs 1, 2). The propeltidium appears to correspond to tergal elements of postoral somites I–IV and bears the ozopores (ozpr) (i.e. openings to the defensive glands); optic tubercle (optbrcl); and attachments of extrinsic muscles of the chelicerae (27–33) (Figs 1, 3), pedipalps (40, 41) (Figs 1, 2) and legs (65–69) (Figs 1, 6B). The anterior margin of the propeltidium is modified to form a pair of spiny protuberances where it joins the vertical, intercheliceral frontal sclerite (frtscl) (Figs 1, 2). The margins of the carapace are scalloped, with concavities associated with the coxae of the walking legs. The mesopeltidium and metapeltidium appear to correspond to the tergites of postoral somites V and VI, respectively (Hansen & Sørensen, 1904; Winkler, 1957).

TABLE 1. Exhaustive list of skeletal muscles of the harvestman *Leiobunum aldrichi*. The Table summarizes information from 104 muscle groups. The name proposed for each muscle group is derived from anatomical characteristics (e.g. origin, insertion, fibre direction) rather than from interpretations of function. Hypotheses of muscle function are speculative and based on anatomical criteria. Comments on the evolutionary significance of muscles are generally concerned with taxonomic distribution or phylogenetic significance. An attempt is made to homologize each muscle with those of the whipscorpion *Mastigophneustes giganteus* (Uropygi) (Mgi) (Shultz, 1993) and the whipspider *Phymus longipes* (Amblypygi) (Plo) (Shultz, 1999). The abbreviation 'ncs' means 'no comparable structure'.

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
<i>Labral, epistomal and pharyngeal muscles</i>				
1	Anterior epistomal m.	Not obviously paired, small. Arises from dorsal surface of pre-sulcal region of epistome proximal to base of anterior epistomal horn; passes ventrally; inserts on labrum (Fig. 2).	Probably acts as a dorsal dilator of the preoral cavity. This muscle occurs widely in Arachnida, and its arrangement in <i>L. aldrichi</i> indicates that the labrum is a small, weakly sclerotized lobe ventral to the pre-sulcal region of the epistome. Previous workers erroneously identified the pre-sulcal epistome as the labrum (e.g. Snodgrass, 1948; van der Hammen, 1989).	Mgi: 3 Plo: 1
2	Transverse epistomal m.	Unpaired. Arises on one side of pre-sulcal region of epistome, where epistome connects firmly to medial portion of pedipalpal coxa; passes transversely; inserts on opposite side (Fig. 2).	Probably acts as an adductor of the pedipalpal coxapophyses and, thus, as a lateral compressor of the preoral cavity. Muscle 2 typically stays with the pedipalpal coxa when the pedipalp is separated from the epistome, leaving a transverse hole posterior to labrum. This muscle is widely distributed in Arachnida (Snodgrass, 1948).	Mgi: 2 Plo: Absent
3	Anterior extrinsic pharyngeal m.	Paired. Arises from dorsal and dorsolateral surfaces of pre-sulcal region of epistome; passes ventrally to posteroventrally posterior to muscle 2; inserts on dorsal surface of anterior region of pharynx (Fig. 2).	Probably acts to dilate the anterior region of the pharynx, thus opening the mouth. It is evidently an anterior continuation of the dorsal component of muscle 4.	Mgi: 4 Plo: 2
4	Dorsolateral extrinsic pharyngeal m.	Four paired components (4A-D) arise broadly from inner layer of post-sulcal region of epistome and insert on surfaces of pharynx. 4A: Arises from dorsal surface of epistome; passes ventrally; inserts on dorsal and dorsolateral surfaces of pharynx. 4B: Arises from dorsolateral surface of epistome; passes ventromedially; inserts on dorsolateral and lateral surfaces of pharynx. 4C: Arises from lateral surface of epistome; passes medially; inserts on lateral and ventrolateral surfaces of pharynx. 4D: Arises from ventrolateral surface of epistome; passes dorsomedially; inserts on ventrolateral and ventral surfaces of pharynx. Fibre bundles from muscle 4 interdigitate with those of muscle 6 (Figs 2, 8; also Snodgrass, 1948; fig. 17).	Probably acts as dilator of the pharynx. Coordinated antagonistic action of muscles 4 and 6 may produce peristalsis used in moving large food particles through the pharynx. Comparisons with extrinsic pharyngeal muscles of <i>Simo</i> (Opiliones: Cyphophthalmi) (van der Hammen, 1989; pers. obs.) and scorpions (Lankester <i>et al.</i> , 1885; pers. obs.) suggest that muscle 4 is a composite of two primitively distinct muscles (Fig. 8). Specifically, 4A and 4B appear to represent a dorsal pharyngeal dilator and 4C and 4D represent a lateral pharyngeal dilator. The complex may have evolved in association with the ability to ingest large food particles. See Discussion for details.	Mgi: 4, 6 Plo: 2, 4

5	Posterior extrinsic pharyngeal m.	Paired, thin. Arises from ventroposterior surface of frontal sclerite; passes ventrally; inserts on dorsal surface of pharynx posterior to muscle 4A. Inserts between ultimate and penultimate bands of muscle 6 (Fig. 2).	May assist dilation of the pharynx in <i>L. aldrichi</i> , but its small size indicates that this role would be minimal. It may represent a vestigial homologue of a large dorsal pharyngeal dilator muscle present in <i>Masigoproctus</i> (Shultz, 1993), <i>Phyxmus</i> (Shultz, 1999), palpigrades (Millot, 1942) and some spiders (Marples, 1983).	Mgi: 7 Plo: 3
6	Intrinsic pharyngeal m.	Paired. Series of muscular bands surrounding pharynx, attaching to pharynx at four longitudinal stiffening rods. Muscles 4 and 5 attach to pharyngeal surfaces between muscular bands (Figs 2, 8).	Probably acts as a constrictor of the pharynx. Coordinated antagonistic action of muscles 4 and 6 may produce peristalsis used in moving large food particles through the pharynx.	Mgi: 10 Plo: 5
<i>Endosternite and intersegmental tendon system</i>				
7	Endosterno-epistomal m.	Paired. Arises from anteromedial surface of anterior endosternal horns; passes medially; inserts on adjacent lateral surface of lateral layer of coxo-epistomal apodeme (Figs 6F, 8).	May function in abducting the epistomal walls thus serving to brace the epistomal skeleton against contractions of pharyngeal dilator muscles (4).	Mgi: 30? Plo: 16?
8	Anterior dorsal prosomal endosternal suspensor m.	Paired. Arises from dorsal surface of endosternite at base of anterior endosternal horn; passes anterodorsally; inserts near anterolateral margin of carapace with muscles 41 and 65 <sub>III</sub> (Figs 1, 2, 4, 6C).	May function in stabilizing the endosternite and increasing haemocoelic pressure. Probably represents the dorsal endosternal suspensor muscle of postoral somite III. This interpretation is consistent with this muscle's insertion between the tergocoxal muscles of the pedipalp and leg 1.	Mgi: 13 <sub>III</sub> Plo: 17 <sub>III</sub>
9	Posterior dorsal prosomal endosternal suspensor m.	Paired. Arises from dorsal surface of endosternite just posterior to muscle 8; passes dorsoanterolaterally; inserts on posterolateral surface of carapace within sulcus separating mesopelidium and metapelidium (Figs 1, 2, 6C).	May function in stabilizing the endosternite and increasing haemocoelic pressure. Probably represents the dorsal endosternal suspensor muscle of postoral somite VI. This interpretation is consistent with this muscle's insertion in the sulcus separating the meso- and metapelidial regions.	Mgi: 13 <sub>VI</sub> Plo: 17 <sub>VI</sub>
10	Anterior dorsal opisthosomal endosternal suspensor m.	Arises from dorsal surface of endosternite just posterior to muscle 9; passes dorsoposteriorly; inserts on anteromedial margin of first opisthosomal tergite (tergite VII) (Figs 1, 2, 6C).	May function in stabilizing the endosternite and increasing haemocoelic pressure. Probably represents the dorsal endosternal suspensor muscle of postoral somite VII. This interpretation is consistent with this muscle's insertion near the anterior margin of the first opisthosomal tergite.	Mgi: 13 <sub>VI</sub> Plo: 17 <sub>VII</sub>

TABLE 1. *continued.*

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
11	Posterior dorsal opisthosomal endosternal suspensor m.	Paired. Arises from dorsal surface of endosternite just posterior to muscle 10; passes dorsoposteriorly parallel to muscle 10; inserts on anteromedial margin of second opisthosomal tergite (tergite VIII) medial to muscle 9 <sup>5VII</sup> (Figs 1, 2, 6C).	Probably corresponds to the dorsoventral muscle of the second opisthosomal somite (postoral somite VIII). This interpretation is consistent with this muscle's insertion on the 'intertergal' sulcus between somites VII and VIII. Scorpions are the only other arachnids examined thus far that retain an endosternal element in postoral somite VIII (Lankester <i>et al.</i> , 1885; pers. obs.), although the dorsal suspensor is often retained as a dorsoventral muscle in other arachnid taxa.	Mgi: 17 <sup>VIII</sup> Plo: 21 <sup>VIII</sup>
12	Lateral endosternal suspensor m.	Paired, three metameric elements (but see muscle 13). Arises from ventrolateral margin of endosternite; passes laterally; inserts on flexible cuticle between coxae of legs 1 and 2 (12 <sub>IV</sub> ), legs 2 and 3 (12 <sub>V</sub> ), and legs 3 and 4 (12 <sub>VI</sub> ) (Fig. 6C).	May function as lateral tensors of the endosternite or adductors of the intercoxal conjunctiva. Scorpions are the only other arachnids examined thus far with lateral intercoxal suspensors (Lankester <i>et al.</i> , 1885; Fristman, 1973). This muscle group may be homologous to the ventral endosternal suspensors found in other arachnid taxa. Although 'true' ventral suspensors appear to have had primitive sternal attachments, the prosomal sternum in opilions and scorpions has been largely replaced by the coxae and anteriorly positioned genital opening. Thus the ventral suspensors could have shifted to a lateral, intercoxal position.	Mgi: 15? Plo: 19?
13	Ventral endosternal suspensor m.	Paired. Arises narrowly from large tendinous process projecting ventrally from ventrolateral surface of endosternite; passes ventrally and posteroventrally; inserts along medial margin of pedal coxa 4 and adjacent lateral margin of genital operculum (Figs 2, 3).	Probably functions in bracing the endosternite against forces produced by other endosternal muscles and in levating the genital operculum. It may represent an enlarged fourth metameric element of muscle group 12. Its ventromedial position might be explained by the anterior migration of the ventral surface of the opisthosoma between the coxae of leg 4.	Mgi: 15 <sup>VII</sup> ? Plo: 19 <sup>VII</sup> ?

14	Posterior endosternal m.	Paired. Arises from posterior process of endosternite with muscle 15; passes ventroposteriorly; inserts on large muscle insertion plaque near anterior margin of third opisthosomal somite (sternite IX) shared with muscles 18 and 20A (Figs 1, 2, 6C).	Probably functions in bracing the endosternite against forces produced by other muscles. Firstman (1973) considered this muscle to be a true ventral suspensor, but it probably represents the endosternal attachment of the second series of ventral longitudinal muscles (20).	Mgi: 18a Plo: 23A, B
15	Anterior spiracular m.	Paired. Arises from posterior process of endosternite with muscle 14; passes posterolaterally; inserts on anterior spiracular arm (Figs 2, 6C).	Probably functions in protracting the anterior spiracular arm, thus dilating the spiracle. Probably represents the endosternal attachment of the third series of ventral longitudinal muscles (21).	Mgi: 18a Plo: 23A, B
16	Spiracular m.	Paired. Arises from anterior spiracular arm; passes posteriorly medial to primary tracheal trunk; inserts on posterior spiracular arm (Fig. 2).	Probably functions in retracting the anterior spiracular arm and protracting the posterior spiracular arm, thus constricting the spiracle. Probably represents a metameric unit of the third series of ventral longitudinal muscles (21).	Mgi: 18? Plo: 23?
17	Posterior spiracular m.	Paired. Arises from posterior spiracular arm; passes postroventrally; inserts on second muscle insertion plaque in sulcus separating sternites IX and X (Figs 1, 2).	Probably functions in retracting the posterior spiracular arm, thus dilating the spiracle. Probably represents a metameric unit of the third series of ventral longitudinal muscles (21).	Mgi: 18? Plo: 23?
18	Ventral spiracular m.	Paired, straplike. Arises from anterolateral margin of large muscle insertion plaque on anterior margin of sternite IX shared with muscles 14 and 20A; passes dorsolaterally; inserts on ventral surface of anterior spiracular arm (Figs 1, 2).	Function unclear; probably depresses and retracts the anterior spiracular arm.	Mgi: ncs Plo: ncs
19	Ventral longitudinal m., series 1	Paired, straplike. Arranged in longitudinal tract composed of two elements, 19A–B. 19A: Arises from first muscle insertion plaque in sulcus separating sternites IX and X; passes posteriorly; inserts on first muscle insertion plaque in sulcus separating sternites XI and XII. 19B: Arises from insertion of 19A; passes posteriorly; inserts on sternite XV (Figs 1, 7).	Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 19–26 may represent laterally expanded and differentiated components of the opisthosomal ventral longitudinal muscle of other arachnids.	Mgi: 18, (73–75)? Plo: 23

*continued*

TABLE 1. *continued.*

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
20	Ventral longitudinal m., series 2	Paired, straplike. Arranged in longitudinal tract composed of three elements, 20A-C. 20A: Arises from large muscle insertion plaque near anterior margin of sternite IX; passes posteriorly; inserts on first muscle insertion plaque in sulcus between sternites X and XI. 20B: Arises from insertion of 20A; passes posteriorly; inserts on medial muscle insertion plaque in sulcus separating sternites XII and XIII+XIV. 20C: Arises from insertion of 20B; passes posteriorly; inserts on sternite XV (Figs 1, 7).	Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 19-26 may represent laterally expanded and differentiated components of the opisthosomal ventral longitudinal muscle of other arachnids.	Mgi: 18, (73-75)? Plo: 23
21	Ventral longitudinal m., series 3	Paired, straplike. Arranged in longitudinal tract composed of two elements, 21A-B. 21A: Arises from second muscle insertion plaque in sulcus separating sternites IX and X; passes posteriorly; inserts on second muscle insertion plaque in sulcus separating sternites XI and XII. 21B: Arises from insertion of 21A; passes posteriorly; inserts on lateral margin of tergite XIV+XV (Figs 1, 7).	Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 19-26 may represent laterally expanded and differentiated components of the opisthosomal ventral longitudinal muscle of other arachnids.	Mgi: 18, (73-75)? Plo: 23
22	Ventral longitudinal m., series 4	Paired, thin, straplike. Arranged in longitudinal tract composed of two elements, 22A-B. 22A: Arises from medial part of pericoxal muscle insertion plaque; passes posteriorly; inserts on second muscle insertion plaque in sulcus separating sternites X and XI. 22B: Arises from insertion of 22A; passes posteriorly; inserts on lateral margin of tergite XIV+XV (Figs 1, 7).	Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 19-26 may represent laterally expanded and differentiated components of the opisthosomal ventral longitudinal muscle of other arachnids.	Mgi: 18, (73-75)? Plo: 23
23	Ventral longitudinal m., series 5	Paired, thin, straplike. Arranged in longitudinal tract composed of two elements, 23A-B. 23A: Arises from pericoxal muscle insertion plaque lateral to 22A; passes posteriorly; inserts on third muscle insertion plaque in sulcus separating sternites X and XI. 23B: Arises from insertion of 23A; passes posteriorly; inserts on lateral margin of tergite XIV+XV (Figs 1, 7).	Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 19-26 may represent laterally expanded and differentiated components of the opisthosomal ventral longitudinal muscle of other arachnids.	Mgi: 18, (73-75)? Plo: 23



24	Ventral longitudinal m., series 6	<p>Paired, straplike, thin. Arranged in longitudinal tract composed of two elements, 24A-B, 24A: Arises from pericoxal muscle insertion plaque lateral to 23A; passes posteriorly; inserts on fourth muscle insertion plaque in sulcus separating sternites X and XI. 24B: Arises from insertion of 24A; passes posteriorly; inserts on lateral margin of tergite XIV + XV (Figs 1, 7).</p>	<p>Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 19-26 may represent laterally expanded and differentiated components of the opisthosomal ventral longitudinal muscle of other arachnids.</p>	<p>Mgi: 18, (73-75)? Plo: 23</p>
25	Accessory ventral longitudinal m.	<p>Paired, thin, straplike. Not arranged sequentially in longitudinal tracts. Six elements, 25A-F, 25A: Arises from third muscle insertion plaque in sulcus separating sternites IX and X; passes posteriorly; inserts on third muscle insertion plaque in sulcus separating sternites XI and XII. 25B: Arises from sixth muscle insertion plaque in sulcus separating sternites IX and X; passes posteromedially; inserts with 25A. 25C: Arises from pericoxal muscle insertion plaque lateral to 24A; passes posteriorly; inserts on fifth muscle insertion plaque in sulcus separating sternites X and XI. 25D: Arises from small medial muscle insertion plaque in sulcus separating sternites XII and XIII + XIV; passes dorsoanteriorly; inserts on lateral margin of tergite XIV + XV. 25E: Arises from small muscle insertion plaque in sternite XIII + XIV; passes dorsoanteriorly; inserts with 25D on lateral margin of tergite XIV + XV. 25F: Arises from large muscle insertion plaque in sulcus separating sternites XII and XIII + XIV; passes posteriorly; inserts on lateral margin of tergite XIV + XV (Figs 1, 7).</p>	<p>Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 19-26 may represent laterally expanded and differentiated components of the opisthosomal ventral longitudinal muscle of other arachnids.</p>	<p>Mgi: 18, (73-75)? Plo: 23</p>
26	Lateral longitudinal m.	<p>Paired, straplike. Not arranged sequentially in longitudinal tract. Three elements, 26A-C, 26A: Arises from lateral muscle insertion plaque of somite IX; passes posteriorly; inserts on fourth muscle insertion plaque in sulcus separating sternites XI and XII. 26B: Arises with 26A; passes posteriorly; inserts on most lateral muscle insertion plaque in sulcus separating sternites XII and XIII + XIV. 26C: Arises from lateral muscle insertion plaque of somite XI; passes posteriorly; inserts on lateral margin of tergite XIV + XV (Figs 1, 7).</p>	<p>Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 19-26 may represent laterally expanded and differentiated components of the opisthosomal ventral longitudinal muscle of other arachnids.</p>	<p>Mgi: 18, (73-75)? Plo: 23</p>

*continued*

TABLE 1. *continued.*

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
<i>Cheliceral muscles</i>				
27	Cheliceral anterior ventral tergocoxal m.	Arises from spiny anterior protuberance at dorsal terminus of frontal sclerite; passes ventroposteriorly medial to other cheliceral muscles; inserts narrowly on posterior process of cheliceral coxa with muscles 28 and 29 (Figs 1, 3).	Probably functions in pivoting the cheliceral coxa against the articular process of the coxo-epistomal apodeme, thereby causing depression of the external part of the chelicera. Comparison with other opilions (e.g. <i>Ceratolasma bicantula</i> , <i>Simoacamide</i> ) indicates that muscles 27 and 28 may be subdivisions of a single muscle (personal observation).	Mgi: ncs Plo: ncs
28	Cheliceral middle ventral tergocoxal m.	Arises from carapace near anteromedian margin; passes ventroposteriorly medial to other cheliceral muscles; inserts narrowly on terminus of posterior process of cheliceral coxa with muscles 27 and 29 (Figs 1, 3).	Probably functions in pivoting the cheliceral coxa against the articular process of the coxo-epistomal apodeme, thereby causing depression of the external part of the chelicera. Comparison with other opilions (e.g. <i>Ceratolasma bicantula</i> , <i>Simoacamide</i> ) indicates that muscles 27 and 28 may be subdivisions of a single muscle.	Mgi: ncs Plo: ncs
29	Cheliceral posterior ventral tergocoxal m.	Arises from carapace posterior to eye turret in association with muscles 30 and 31; passes ventroanteriorly deep to other cheliceral muscles; inserts narrowly on terminus of posterior process of cheliceral coxa with muscles 27 and 28 (Figs 1, 3).	Probably functions in pivoting the cheliceral coxa against the articular process of the coxo-epistomal apodeme, thereby causing depression of the external part of the chelicera.	Mgi: ncs Plo: ncs
30	Cheliceral medial dorsal tergocoxal m.	Two principal slips. Arises from carapace posterior and posterolateral to eye turret; passes anteriorly to ventroanteriorly; inserts on dorsal margin of cheliceral coxa in association with muscle 31 (Figs 1, 3).	Probably functions in pivoting the cheliceral coxa against the articular process of the coxo-epistomal apodeme, thereby causing levation of the external part of the chelicera.	Mgi: ncs Plo: ncs
31	Cheliceral lateral dorsal tergocoxal m.	Two principal slips. Arises from carapace posterolateral to eye turret and muscle 30; passes anteriorly deep to 30; inserts on dorsomedial margin of cheliceral coxae in association with 30 (Figs 1, 3).	Probably functions in pivoting the cheliceral coxa against the articular process of the coxo-epistomal apodeme, thereby causing levation and adduction of the external part of the chelicera.	Mgi: ncs Plo: ncs

32	Cheliceral medial tergo-coxal m.	Thin, straplike. Arises from carapace anterolateral to eye turret; passes anteroventrally along the lateral and ventral surfaces of muscles 30 and 31; inserts narrowly on medial margin of cheliceral coxa (Figs 1, 3).	Probably functions in pivoting the cheliceral coxa against the articular process of the coxo-epistomal apodeme, thereby causing rotation of the dorsal part of the chelicera ventrolaterally, thus effectively adducting the distal portions of the chelicera.	Mgi: ncs Plo: ncs
33	Cheliceral tergo-deutomerite m.	Many thin, straplike fibres. Arises primarily from carapace anterolateral to eye turret; passes anteroventrally into cheliceral coxa and runs along its internal lateral surface; inserts on ventrolateral margin of cheliceral deutomerite (Figs 1, 3).	Probably functions as a flexor of the cheliceral coxa-deutomerite joint. Scorpions are the only other arachnids known to have muscle arising from the carapace and inserting on the cheliceral deutomerite (Lankester <i>et al.</i> , 1885; Vyas, 1974).	Mgi: Absent Plo: Absent
34	Cheliceral dorsal coxa-deutomerite m.	Arises from extreme ventral and proximomedial surfaces of coxa; passes distally; inserts narrowly on dorsal rim of deutomerite (Fig. 3).	Probably functions as an extensor of the cheliceral coxa-deutomerite joint.	Mgi: Absent Plo: Absent
35	Cheliceral ventral coxa-deutomerite m.	Arises broadly from medial surface of cheliceral coxa; passes distally; inserts on ventral rim of deutomerite (Fig. 3).	Probably functions as a flexor of the cheliceral coxa-deutomerite joint.	Mgi: Absent Plo: Absent
36	Cheliceral lateral coxa-deutomerite m.	Arises from distolateral surface of cheliceral coxa; passes distally; inserts on lateral rim of deutomerite near lateral articulation with coxa (Fig. 3).	Probably functions as an adductor of the cheliceral coxa-deutomerite joint.	Mgi: Absent Plo: Absent
37	Cheliceral medial coxa-deutomerite m.	Arises from distomedial surface of cheliceral coxa; passes distally; inserts on medial rim of deutomerite near medial articulation with coxa (Fig. 3).	Probably functions as an abductor of the cheliceral coxa-deutomerite joint.	Mgi: Absent Plo: Absent
38	Cheliceral medial deutomerite-apotele m.	Large, pinnate. Fibre bundles arise in four rows on anterolateral, anteromedial, posterolateral and posteromedial surfaces of deutomerite; pass internally and distally; insert on a broad tendon that attaches to medial rim of apotele at a plagula (Fig. 3).	Probably functions as closer of the cheliceral chela.	Mgi: 59 Plo: 33
39	Cheliceral lateral deutomerite-apotele m.	Fan-shaped. Fibre bundles arise along lateral surface of deutomerite between anterolateral and posterolateral bundles of muscle 38; pass distally converging on a lateral rim of apotele; insert narrowly on lateral rim of apotele (Fig. 3).	Probably functions as opener of the cheliceral chela.	Mgi: 60 Plo: 34

*continued*

TABLE 1. *continued.*

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
<i>Pedipalpal muscles</i>				
40	Pedipalpal medial tergocoxal m.	Arises along anteromedial surface of carapace; passes anteroventrally to anteroventrolaterally; inserts on dorsal margin of pedipalpal coxa medially adjacent to muscle 41 (Figs 1, 2).	Probably functions as a levator of the pedipalpal coxa. Corresponding pedal muscles unclear, but see entries for pedal muscles 65, 66, 68 and 69.	Mgi: ncs Plo: ncs
41	Pedipalpal lateral tergocoxal m.	Arises from anterior margin of carapace in association with muscles 8 and 65 <sub>III</sub> ; passes ventrally; inserts on dorsal margin of pedipalpal coxa laterally adjacent to muscle 40 (Figs 1, 2).	Probably functions as a levator of the pedipalpal coxa. Morphology and placement with respect to muscles 8 and 65 <sub>III</sub> indicate that it probably corresponds to pedal muscle 67.	Mgi: Absent Plo: Absent
42	Pedipalpal dorsal medial endosternocoxal m.	Two slips. Arises from dorsal surface of anterior endosternal horn anteriorly adjacent to muscle 8; passes anterodorsally; inserts on small process projecting ventrally from dorsomedial margin of pedipalpal coxa (Figs 2, 4).	Function unclear. Probably corresponds to pedal muscle 70.	Mgi: Absent Plo: 40
43	Pedipalpal ventral medial endosternocoxal m.	Small. Arises on medial surface of anterior endosternal horn; passes anteriorly; inserts on pedipalpal coxa (Fig. 4)	Function unclear. Probably corresponds to pedal muscle 71.	Mgi: Absent Plo: 39
44	Pedipalpal dorsal lateral endosternocoxal m.	Arises near from dorsal surface of anterior endosternal horn anteriorly adjacent to muscle 42; passes anterodorsally; inserts on dorsolateral margin of coxa (Fig. 4).	Function unclear. Probably corresponds to pedal muscle 72.	Mgi: 31 Plo: 42
45	Pedipalpal ventral lateral endosternocoxal m.	Arises from anterior terminus of anterior endosternal horn; passes anteriorly; inserts on posterior margin of coxapophyseal sclerite that occupies posterolateral margin of coxa (Fig. 4).	Function unclear. Probably corresponds to pedal muscle 73.	Mgi: 32 Plo: 41
46	Pedipalpal medial endosterno-coxapophyseal m.	Arises from ventral surface of endosternite medial to angle of anterior endosternal horn laterally adjacent to muscle 47 and medially adjacent to muscle 75; passes anteroventrally deep to the epistome-pharyngeal complex; inserts narrowly on ventroposterior margin of coxapophyseal sclerite medially adjacent to 47 (Fig. 2).	May function as a retractor of the pedipalpal coxapophysis. Probably corresponds to pedal muscle 75.	Mgi: Absent Plo: Absent

47	Pedipalpal lateral endosterno-coxapophyseal m.	Arises from ventral surface of endosternal horn laterally adjacent to muscle 46; passes anteroventrally; inserts narrowly on posterior margin of coxapophyseal sclerite laterally adjacent to 46 (Figs 2, 4).	May function as a retractor of the pedipalpal coxapophysis. Probably corresponds to pedal muscle 76.	Mgi: Absent Plo: Absent
48	Pedipalpal long dorsal coxa-trochanter m.	Two slips. Arises from dorsolateral surface of coxo-epistomal apodeme dorsal to muscle 7; passes anterolaterally into pedipalpal coxa; inserts on dorsal margin of trochanter (Fig. 4).	Probably functions as a levator of the pedipalpal coxa-trochanter joint. Probably corresponds to pedal muscle 77C.	Mgi: Absent Plo: Absent
49	Pedipalpal medial short dorsal coxa-trochanter m.	Arises broadly from medial surface of coxa near <i>costa coxalis</i> ; passes distodorsally; inserts on dorsal margin of trochanter (Fig. 4).	Probably functions as a levator of the pedipalpal coxa-trochanter joint. Probably corresponds to pedal muscle 77A.	Mgi: 35 Plo: 44
50	Pedipalpal lateral short dorsal coxa-trochanter m.	Small. Arises narrowly from dorsolateral surface of coxapophyseal sclerite; passes distally; inserts on dorsal margin of trochanter (Fig. 4).	Probably functions as a levator of the pedipalpal coxa-trochanter joint. Probably corresponds to pedal muscle 77B.	Mgi: 35 Plo: 45
51	Pedipalpal long ventral coxa-trochanter m.	Arises broadly from inner surface of coxapophyseal sclerite; passes distodorsally; inserts on trochanteral plagula associated with ventral rim of trochanter (Fig. 4).	Probably functions as a depressor of the pedipalpal coxa-trochanter joint and may serve to levate the coxapophyseal sclerite. Probably corresponds to pedal muscle 78C. Snodgrass (1948: fig. 16F) depicted this muscle in a <i>Leioibunum</i> species as arising from the coxo-epistomal apodeme with muscle 48, but this is inconsistent with the present observations.	Mgi: ncs Plo: 47
52	Pedipalpal medial short ventral coxa-trochanter m.	Arises broadly from ventromedial surface of coxa ventral muscle 49; passes distally; inserts on trochanteral plagula associated with ventral rim of trochanter (Fig. 4).	Probably functions as a depressor of the pedipalpal coxa-trochanter joint. Probably corresponds to pedal muscle 78A.	Mgi: 36 Plo: 46
53	Pedipalpal lateral coxa-trochanter m.	Arises broadly from ventrolateral surface of coxa; passes distally; inserts on trochanteral plagula associated with ventral rim of trochanter (Fig. 4).	Probably functions as a depressor of the pedipalpal coxa-trochanter joint. Probably corresponds to pedal muscle 78B.	Mgi: 37 Plo: 48
54	Pedipalpal medial trochanter-femur m.	Arises broadly from medial surface of trochanter; passes distally; inserts on medial rim of femur (Fig. 4).	Probably functions as an adductor of the pedipalpal trochanter-femur joint. Probably corresponds to pedal muscle 79.	Mgi: 38 Plo: 50
55	Pedipalpal lateral trochanter-femur m.	Arises broadly on lateral surface of trochanter; passes distally; inserts on lateral rim of femur (Fig. 4).	Probably functions as an abductor of the pedipalpal trochanter-femur joint. Probably corresponds to pedal muscle 80.	Mgi: 39 Plo: 51, 52

continued

TABLE 1. *continued.*

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
56	Pedipalpal long femur-patella m.	Arises broadly from anterior and proximal surfaces of femur; passes distoventrally; inserts along tendon that begins half way along femur; inserts on the midventral patellar-plagula. Tendon is superficial to fibres of muscle 57 (Fig. 4).	Probably functions as a flexor of the pedipalpal femur-patella joint. Probably corresponds to the large component of pedal muscle 82.	Mgi: 41 Plo: 53
57	Pedipalpal short femur-patella m.	Arises from distodorsal surface of femur; passes distoventral; inserts along ventral margin of patella (Fig. 4).	Probably functions as a flexor of the pedipalpal femur-patella joint. May correspond to small component of pedal muscle 82.	Mgi: 42 Plo: 54 and/or 55
58	Pedipalpal long medial patella-tibia m.	Large fibre bundles. Arises broadly from dorsal and proximomedial surfaces of patella; passes distoventrally; inserts on ventromedial margin of tibia (Fig. 4).	Probably functions as an adductor/promotor and flexor of the pedipalpal patella-tibia joint. Probably corresponds to the patellar component of pedal muscle 83.	Mgi: 43 Plo: 57
59	Pedipalpal long lateral patella-tibia m.	Large fibre bundles. Arises broadly from dorsal and proximolateral surfaces of patella; passes distoventrally deep to muscle 61; inserts on ventrolateral margin of tibia (Fig. 4).	Probably functions as an abductor/retractor and flexor of the pedipalpal patella-tibia joint. No corresponding pedal muscle.	Mgi: 43 Plo: 57
60	Pedipalpal short medial patella-tibia m.	Small sheet of many small fibre bundles. Arises from dorsodistomedial surface of patella; passes distoventrally; inserts on dorsomedial margin of tibia (Fig. 4).	Probably functions as an adductor/protractor and weak flexor of the pedipalpal patella-tibial joint. Probably corresponds to pedal muscle 85.	Mgi: 44 Plo: 58
61	Pedipalpal short lateral patella-tibia m.	Sheet of many small fibre bundles. Arises broadly from distodorsolateral surface of patella; passes distoventrally; inserts on dorsolateral margin of tibia (Fig. 4).	Probably functions as an abductor/retractor and flexor of the pedipalpal patella-tibia joint. Probably corresponds to pedal muscle 86.	Mgi: 44 Plo: 59
62	Pedipalpal tibia-tarsus m.	Arises broadly from medial surface of tibia; passes distally; inserts on ventral rim of tarsus (Fig. 4).	Probably functions as a flexor of the pedipalpal tibia-tarsus joint. Probably corresponds to the tibial component of pedal muscle 87.	Mgi: (45, 46)? Plo: (61-63)?
63	Pedipalpal short tibia-apotele m.	Arises from distodorsal surface of tibia; passes distally; inserts on long, thin tendon about halfway through tarsus; tendon terminates on dorsal process of apotele (Fig. 4).	Probably functions as a levator of the pedipalpal tarsus-apotele joint. Probably corresponds to pedal muscle 89.	Mgi: Absent Plo: Absent
64	Pedipalpal long tibia-apotele m.	Arises broadly from lateral surface of tibia; passes distally; inserts on long, thick tendon near level of tibia-tarsus articulation; tendon passes through tarsus without attachment and inserts on ventral process of apotele (Fig. 4).	Probably functions as a depressor of the pedipalpal tarsus-apotele joint and, perhaps, as a flexor of the tibia-tarsus joint. Probably corresponds to pedal muscle 88.	Mgi: Absent Plo: 64

*Pedal muscles*

65	Pedal anteromedial tergocoxal m.	Legs 1–4. Arises from lateral margin of carapace, often in association with muscle 67 of anteriorly adjacent leg; passes ventrally; inserts on distoanterior margin of coxa via narrow tendon proximal to insertion of corresponding muscle 66 (Figs 1, 6B).	Probably functions in levating and, perhaps, rotating the coxa about its long axis. There is no obvious corresponding muscle in the pedipalp, although all or a portion of muscle 40 may be a serial homologue.	Mgi: 19 Plo: 65–67
66	Pedal anterolateral tergocoxal m.	Legs 1–4. Arises from carapace; passes laterally; inserts on distoanterior margin of coxa via narrow tendon distal to insertion of corresponding muscle 65 (Figs 1, 6B).	Probably functions in adducting and, perhaps, rotating the coxa about its long axis. There is no obvious corresponding muscle in the pedipalp, although all or a portion of muscle 40 may be a serial homologue.	Mgi: 20 Plo: 68, 69
67	Pedal posteromedial tergocoxal m.	Legs 1–3. Arises from lateral margin of carapace, often in association with muscle 65 of posteriorly adjacent leg; passes ventrally; inserts on distoposterior margin of coxa via narrow tendon proximal to insertion of corresponding muscle 68 (Figs 1, 6B).	Probably functions in adducting and, perhaps, rotating the coxa about its long axis. Probably corresponds to pedipalpal muscle 41.	Mgi: 21 Plo: 70
68	Pedal posterolateral tergocoxal m.	Legs 1–3. Arises from carapace; passes laterally; inserts on distoposterior margin of coxa via narrow tendon distal to insertion of muscle 67 (Figs 1, 6B).	Probably functions in levating and, perhaps, rotating the coxa about its long axis. There is no obvious corresponding muscle in the pedipalp, although all or a portion of muscle 40 may be a serial homologue.	Mgi: 22 Plo: 71–73
69	Pedal lateral tergocoxal m.	Legs 1–3. Arises from carapace; passes laterally; inserts on dorsal margin of coxa anterior to corresponding muscle 68 (Figs 1, 6B).	Probably functions in adducting and, perhaps, rotating the coxa about its long axis. There is no apparent corresponding muscle in the pedipalp, although all or a portion of muscle 40 may be a serial homologue.	Mgi: 23 Plo: 74
70	Pedal long anterior endosternocoxal m.	Legs 1–4. Two parallel slips. Arises from lateral (legs 1 and 2) or dorsal (legs 3 and 4) surfaces of endosternite; passes laterally; inserts on anterior coxal margin distal to corresponding muscle 71 (Fig. 6D).	Probably functions as an adductor and, perhaps, rotator of the pedal coxa. Probably corresponds to pedipalpal muscle 42.	Mgi: 25 Plo: 76
71	Pedal short anterior endosternocoxal m.	Legs 1–4. Arises from lateral surface of endosternite lateral and deep to corresponding muscle 70; passes laterally; inserts on anterior coxal margin proximal to 70 (Fig. 6E).	Probably functions as an adductor and, perhaps, rotator of the pedal coxa. Probably corresponds to pedipalpal muscle 43.	Mgi: 24 Plo: 75

*continued*

TABLE 1. *continued.*

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
72	Pedal long posterior endosternocoxal m.	Legs 1-4. Two parallel slips. Arises from lateral endosternal surface (legs 1 and 2), dorsal endosternal surface (leg 3) or posterolateral endosternal margin (leg 4); passes laterally; inserts on posterior coxal margin distal to corresponding muscle 73 (Fig. 6D).	Probably functions as an adductor and, perhaps, rotator of the pedal coxa. Probably corresponds to pedipalpal muscle 44.	Mgi: 27 Plo: 78
73	Pedal short posterior endosternocoxal m.	Legs 1-4. Arises from lateral surface of endosternite lateral and deep to corresponding muscle 72; passes laterally; inserts on posterior coxal margin proximal to 72 (Fig. 6E).	Probably functions as an adductor and, perhaps, rotator of the pedal coxa. Probably corresponds to pedipalpal muscle 43.	Mgi: 26 Plo: 77
74	Pedal diagonal endosternocoxal m.	Legs 2-4. Arises on ventrolateral margin of endosternite, often near corresponding muscle 12; passes posterolaterally; inserts on proximoposterior margin of coxa (Fig. 6F).	Function unclear. No corresponding pedipalpal muscle. The muscle is unique among the arachnids examined thus far, although its posterior coxal attachment is similar to that of the intracoxal muscles of <i>Mastigoproctus</i> and <i>Phrynus</i> .	Mgi: 34? Plo: 79?
75	Pedal anterior endosternocoxapophyseal m.	Leg 1. Large muscle with two principal slips. Arises from anteroventral surface of endosternite; passes anteroventrally deep to and in parallel with pedipalpal muscle 47; inserts on anterior rim of coxapophysis (Fig. 2).	Probably functions as a levator and/or adductor of the coxapophysis. Probably corresponds to pedipalpal muscle 46. A similar muscle has been described on the fourth leg of the xiphosurans <i>Limulus</i> (Lankester <i>et al.</i> , 1885) and <i>Carcinoscopius</i> (Manton, 1964).	Mgi: Absent Plo: Absent
76	Pedal posterior endosternocoxapophyseal m.	Legs 1-2. Arises from ventrolateral (inner) surface of endosternite; passes ventrally to ventroanteriorly; inserts on dorsal flange of coxapophyseal sclerite (Fig. 2).	Probably functions as a depressor of the coxapophysis. Probably corresponds to pedipalpal muscle 47. A similar muscle has been described on the fourth leg of the xiphosurans <i>Limulus</i> (Lankester <i>et al.</i> , 1885) and <i>Carcinoscopius</i> (Manton, 1964).	Mgi: Absent Plo: Absent
77	Pedal dorsal coxa-trochanter m.	Legs 1-4. Three heads arising from anterior (77A), posterior (77B), and proximocentral (77C) surfaces of coxae. Inserts on dorsal rim of trochanter. In legs 1-2, 77C arises from inner surface of flange of coxapophyseal sclerite (Fig. 5).	Probably functions as levator of the coxa-trochanter joint. Component 77A probably corresponds to pedipalpal muscle 49; 77B to 50 and 77C to 48.	Mgi: 36, 37 Plo: 82-84



78	Pedal ventral coxa-trochanter m.	Legs 1–4. Three heads arising from anterior (78A), posterior (78B) and proximocentral (78C) surfaces of coxae. Inserts on ventral rim of trochanter. In legs 1–2, 78C arises from inner surface of flange of coxapophyseal sclerite (Fig. 5).	Probably functions as depressor of the coxa-trochanter joint. Component 78A probably corresponds to pedipalpal muscle 52; 78B to 53 and 77C to 51.	Mgi: 35 Plo: 81, 82
79	Pedal anterior trochanter-femur m.	Legs 1–4. Arises broadly from anterior surface of trochanter; passes distally; inserts on anterior margin of femur (Fig. 5).	Probably functions as protractor of the trochanter-femur joint. Probably corresponds to pedipalpal muscle 54.	Mgi: 38 Plo: 86, 87
80	Pedal posterior trochanter-femur m.	Legs 1–4. Arises broadly from posterior surface of trochanter; passes distally; inserts on posterior margin of femur (Fig. 5).	Probably functions as retractor of the trochanter-femur joint. Probably corresponds to pedipalpal muscle 55.	Mgi: 39 Plo: 89, 90
81	Pedal dorsal trochanter-femur m.	Arises from mid-dorsal trochanteral apodeme fans distally; inserts along anterior and posterior margins of femur deep to insertions of muscles 79 and 80, except in areas adjacent to ventral condyle of trochanter femur joint, where pedal nerves and tracheae pass from trochanter to femur (Fig. 5).	Probably functions in leg autotomy by breaking a line of weakness at the base of the femur and retracting their attachments to close off the joint. There is no corresponding muscle in the pedipalp. This muscle may be homologous with the pedal diagonal trochanter-femur muscle of other chelicerates, as it arises from the trochanter near a condyle of the trochanter-femur joint and inserts on the femur without cuticular tendons. Shultz (1989, 1993) has hypothesized that this muscle is a vestige of an undifferentiated basifemur-telofemur joint in other chelicerates.	Mgi: 40? Plo: 92?
82	Pedal femur-patella m.	Legs 1–4. Two components, one large and one small. Large component (82A): Pinnate, composed of large fibre bundles. Arises broadly from surfaces of femur; passes distoventrally; inserts on long tendon that terminates on mid-ventral patellar plagula. Small component (82B): Composed of small fibre bundles. Arises from distoventral surfaces of femur; fibres converge on borders of patellar plagula, where they insert (Fig. 5).	Probably functions as a flexor of the femur-patella joint. Probably corresponds to pedipalpal muscles 56 and 57.	Mgi: 41, 42 Plo: 93–95
83	Pedal femoropatella-tibia m.	Legs 1–4. Arises narrowly from extreme distoanterior surface of femur and broadly from anterior surface of patella; inserts on anterior margin of tibia (Fig. 5).	Probably functions as a flexor/protractor of the patella-tibia joint. The patellar component may correspond to pedipalpal muscle 58.	Mgi: 43 Plo: 96

continued

TABLE 1. *continued.*

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
84	Pedal femur-tibia m.	Legs 1-4. Arises from tendon projecting distally from distodorsal process of femur; passes distally into patella without attachment, where it divides into two components, 84A-B. 84A inserts deep to muscle 86 on dorsal margin of tibia posteriorly adjacent to anterodorsal patella-tibia condyle. 84B inserts on posterior margin of tibia deep to 86 on dorsoposterior margin of tibia anteriorly adjacent to ventroposterior patella-tibia condyle (Fig. 5).	Both heads probably function in extension at the femur-patella joint and extension/retraction at the patella-tibia joint. However, low mechanical advantage of both heads at the patella-tibia joint suggests that extension of the femur-patella joint is its principal function. 84A appears to be the only component present in certain <i>Laniatores</i> (Shultz, 1989). The muscle has two tibial tendons in scorpions (Couzijn, 1976; van der Hammen, 1989) that may correspond to the two components in <i>L. aldrichi</i> .	Mgi: Absent Plo: Absent
85	Pedal anterior patella-tibia m.	Legs 1-4. Arises from anterodorsal surface of patella; passes distoventrally; inserts on dorsal half of anterior margin of tibia (Fig. 5).	Probably functions as a flexor/protractor of the patella-tibia joint. Probably corresponds to pedipalpal muscle 60.	Mgi: 44a Plo: 97
86	Pedal posterior patella-tibia m.	Legs 1-4. Arises from dorsal and dorsoposterior surfaces of patella; passes posteroventrally; inserts on dorsoposterior margin of tibia (Fig. 5).	Probably functions as an extensor/retractor of the patella-tibia joint. Probably corresponds to pedipalpal muscle 61.	Mgi: 44b Plo: 98
87	Pedal patellotibia-tarsus m.	Legs 1-4. Arises narrowly from dorsal surface of patella and broadly from surfaces of tibia; passes distally; inserts on long tendon that terminates on midventral tarsal plagula (Fig. 5).	Probably functions as flexor of the tibia-basitarsus joint. Probably corresponds to the tibial component of pedipalpal muscle 62.	Mgi: 46 Plo: 99
88	Pedal patellotibia-apotele m.	Legs 1-4. Arises from dorsal surface of patella and distodorsal surface of tibia; inserts on long tendon that passes dorsal to tendon of muscle 87 in tibia; tendon terminates on ventral process of apotele (Fig. 5).	Probably functions as a depressor of the telotarsus-apotele joint. Probably corresponds to pedipalpal muscle 64	Mgi: 47 Plo: 100
89	Pedal tarsus-apotele m.	Legs 1-4. Arises from proximodorsal surface of tarsus; passes distally; inserts on long tendon that terminates on dorsal process of apotele (Fig. 5).	Probably functions as levator of the telotarsus-apotele joint. Probably corresponds to pedipalpal muscle 63	Mgi: 48 Plo: 101
90	<i>Opisthosomal muscles</i> Medial tergo-carapacial m.	Paired. Arises from anteromedial margin of mesopeltidial tergal region; passes posteriorly; inserts on anteromedial margin of first opisthosomal tergite (tergite VII) (Figs 1, 7A).	Probably functions in longitudinal compression or stiffening of the mesopeltidial and metapeltidial region of the carapace and the prosoma-opisthosoma juncture.	Mgi: 65 Plo: 106

91	Lateral tergo-carapacial m.	<p>Paired. Arises from carapace at sulcus associated with origins of pedal tergo-coxal muscles 66<sub>v</sub>, 66<sub>v</sub> and 69<sub>v</sub>; passes posteromedially; inserts on anteromedial margin of first opisthosomal tergite (tergite VII) lateral to muscle 90 (Figs 1, 7A).</p> <p>Three metameric elements, 92A–C. 92A: Three bundles; one median, two lateral. Arises from three dorsal muscle insertion plaques within sulcus separating tergites XI and XII; passes posteriorly; inserts on muscle insertion plaque separating tergites XII and XIII. 92B: Unpaired muscle sheet. Arises from insertion of 92A; passes posteriorly; inserts on muscle insertion plaque separating tergites XIII and XIV + XV. 92C: Arises from insertion of 92B; passes posteriorly; inserts on anterior margin of anal operculum (Figs 1, 7).</p>	<p>Probably functions in longitudinal compression or stiffening of the mesopeltidial and metapeltidial region of the carapace and the prosoma-opisthosoma juncture.</p>	<p>Mgi: 66 Plo: 107</p>
92	Intertergal m.	<p>Paired. Somites VII to XIV and/or XV. Several slips. Slips arise from lateral series of small tergal muscle insertion plaques; pass ventrally to posteroventrally; insert on lateral muscle insertion plaque with corresponding muscles 94 and 95 (Figs 1, 7).</p>	<p>Probably functions in compressing or stiffening the posterior tergal region of the opisthosoma.</p>	<p>Mgi: 64 Plo: 105</p>
93	Short lateral opisthosomal m.	<p>Paired. Somites VII–XIII. Several slips. Slips arise from dorsolateral series of muscle insertion plaques of anteriorly adjacent intertergal sulcus lateral to insertion plaques of muscle 95 associated with anteriorly adjacent somite; pass ventrally; insert on lateral muscle insertion plaque with corresponding muscles 93 and 95 (Figs 1, 7).</p>	<p>Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 93–95 form a box-truss configuration reminiscent of the intersegmental tendon system of <i>Triarthrus</i> (Trilobita) (Cisne, 1981), cephalocarid and other crustaceans (Hessler, 1964) and other arthropods (Boudreaux, 1979).</p>	<p>Mgi: ncs Plo: ncs</p>
94	Long anterior lateral opisthosomal m.	<p>Paired. Somites VIII–XII. Several slips. Slips arise from dorsal series of muscle insertion plaques of posteriorly adjacent intertergal sulcus medial to insertion plaques of muscle 94 associated with posteriorly adjacent somite; pass ventrally to anteroventrally; insert on lateral muscle insertion plaque with corresponding muscles 93 and 94 (Figs 1, 7).</p>	<p>Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 93–95 form a box-truss configuration reminiscent of the intersegmental tendon system of <i>Triarthrus</i> (Trilobita) (Cisne, 1981), cephalocarid and other crustaceans (Hessler, 1964) and other arthropods (Boudreaux, 1979).</p>	<p>Mgi: ncs Plo: 22?</p>
95	Long posterior lateral opisthosomal m.	<p>Paired. Somites VIII–XII. Several slips. Slips arise from dorsal series of muscle insertion plaques of posteriorly adjacent intertergal sulcus medial to insertion plaques of muscle 94 associated with posteriorly adjacent somite; pass ventrally to anteroventrally; insert on lateral muscle insertion plaque with corresponding muscles 93 and 94 (Figs 1, 7).</p>	<p>Probably functions in regulating opisthosomal volume and haemocoelic pressure. Muscles 93–95 form a box-truss configuration reminiscent of the intersegmental tendon system of <i>Triarthrus</i> (Trilobita) (Cisne, 1981), cephalocarid and other crustaceans (Hessler, 1964) and other arthropods (Boudreaux, 1979).</p>	<p>Mgi: ncs Plo: ncs</p>

*continued*

TABLE 1. *continued.*

No.	Name	Description	Function, serial homology, evolution, etc.	Proposed homology
96	Anterior short intersternal m.	Paired. Arises from muscle insertion plaques separating sternites IX and X; passes anteriorly to anterolaterally; inserts along pericoxal muscle insertion plaque (Figs 1, 7).	Probably functions in regulation of opisthosomal volume and haemocoelic pressure.	Mgi: 68 Plo: 108
97	Ventral anal operculum m.	Paired. Arises from posterior margin of sternite XII; passes dorsoanteriorly medial to muscle 102; inserts on dorsolateral margin of anal operculum with muscle 98 (Fig. 7).	Probably functions in closing the anal operculum.	Mgi: ncs Plo: ncs
98	Anterior anal operculum m.	Paired. Several loosely associated slips. Arises narrowly from lateral margin of tergite XVI+XV; passes posteriorly; inserts on dorsolateral margin of anal operculum with muscle 97 (Fig. 7).	Probably functions in closing the anal operculum.	Mgi: ncs Plo: ncs
99	Dorsal rectal m.	Unpaired. Arises from anterior margin of tergite XIV+XV; passes internally; inserts on dorsal surface of rectum at same level as muscle 100 (Figs 1, 7).	Probably functions in dilating the rectum.	Mgi: ncs Plo: ncs
100	Ventral rectal m.	Unpaired. Arises from sternite XV; passes internally; inserts on ventral surface of rectum at same level as muscle 99 (not illustrated).	Probably functions in dilating the rectum.	Mgi: ncs Plo: ncs
101	Anterior extrinsic genital m.	Paired. Both sexes. Female: Arises from sternite laterally adjacent to genital operculum and medially adjacent to medial margin of coxa 4; passes medially, fanning anteriorly and posteriorly; inserts on medially adjacent region of outer sheath of ovipositor. Male: Arises from posterolateral surface of genital operculum. Small bundle of fibres passes anteriorly; inserts along subterminal surface of ventral stiffening rod of outer sheath of penis. Large bundle of fibres passes posteromedially; inserts along posterior half of ventral stiffening rod (Figs 1, 7).	Probably functions in dilating the outer sheath of the ovipositor and in protracting the penis. The functional morphology of ovipositor protraction and retraction is discussed in Martens <i>et al.</i> (1981, especially fig. 41).	Mgi: ncs Plo: ncs

102	Posterior extrinsic genital m.	Paired. Both sexes. Arises from tergite XIV + XV; passes anteriorly; inserts on extreme posterolateral margin of ovipositor and penis (Figs 1, 7).	Probably functions in retracing the ovipositor and penis. The functional morphology of ovipositor protraction and retraction is discussed in Martens <i>et al.</i> (1981, especially figs 16, 41). This muscle may represent a medial component of the ventral longitudinal muscles (muscles 20-26, Fig. 7A, B).	Mgi: 18, (73-75)? Plo: 23?
103	Intrinsic ovipositor m.	Not obviously paired. Thin sheet of muscle fibres lining inner surface of ovipositor shaft. Attaches at proximal margin of each annular sclerite. Not illustrated but see Martens <i>et al.</i> (1981: fig. 43g).	Probably functions in stiffening and/or shortening the ovipositor or portions of the ovipositor. Coordinated interaction between the muscle and elasticity or haemolymph pressure may produce peristaltic movement of ovipositor through soil.	Mgi: ncs Plo: ncs
104	Intrinsic penial m.	Bipinnate. Arises from inner surfaces of penial shaft proximal to lateral bulbs; passes distomedially; inserts on long central tendon that terminates at base of glans (Fig. 7C).	Probably functions in flexing glans against shaft and is probably antagonistic to cuticular elasticity.	Mgi: ncs Plo: ncs



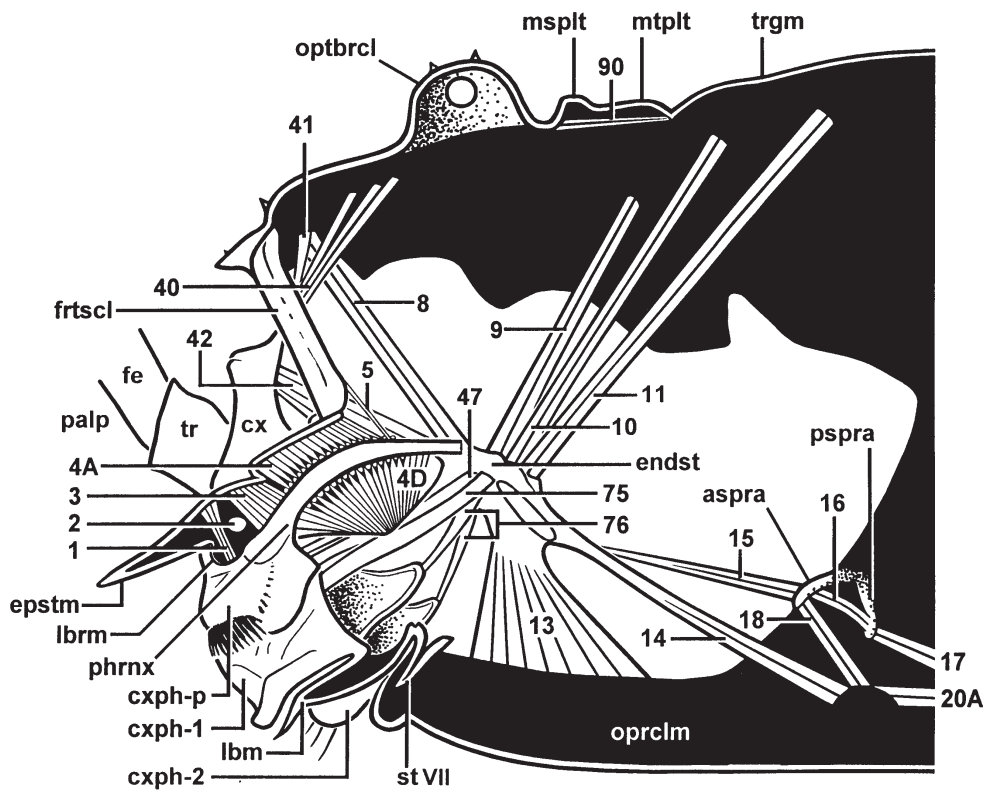


Figure 2. Prosoma of adult female divided midsagittally to show arrangement of the stomotheca (feeding apparatus) and endosternite (endst). The chelicera, leg coxae and ovipositor have been removed. Arabic numerals indicate muscles listed in Table 1. Abbreviations: aspra, anterior spiracular arm; cx, coxa; cxph-1, coxapophysis of leg 1; cxph-2, coxapophysis of leg 2; cxph-p, coxapophysis of pedipalp; epstm, epistome; endst, endosternite; fe, femur; frtscl, frontal sclerite; lbrm, labium; lbrm, labrum; mspit, mesopeltidium; mtplt, metapeltidium; oprclm, genital operculum; optbrcl, optic tubercle; phrnx, pharynx; pspra, posterior spiracular arm; st VII, sternite of seventh postoral somite; tr, trochanter; trgm, tergum of opisthosoma.

### *Endosternite*

The endosternite (endst) is a procurved, horseshoe-shaped sheet of stiff connective tissue that occupies the ventral portion of the prosomal haemocoel (Figs 2, 6). The

Figure 1. External anatomy of adult female *Leiobumum aldrichi* from dorsal, ventral and lateral perspectives. Inset above dorsal perspective is an enlarged view of three groups of muscle insertions (a, b, c) on the prosomal carapace. Arabic numerals indicate muscles listed in Table 1. Roman numerals indicate the postoral somite with which the indicated muscle or sclerite is associated. Abbreviations: aop, anal operculum; aptl, apotele or apotelic claw; chl, chelicera; cx, pedal coxa; cyp, pedipalpal coxa; cxph-1, coxapophysis of leg 1; cxph-2, coxapophysis of leg 2; cxph-p, coxapophysis of pedipalp; epstm, epistome; fe, femur; lbrm, labium; lmip, lateral muscle insertion plaque; mspit, mesopeltidium; mtplt, metapeltidium; oprclm, genital operculum; optbrcl, optic tubercle; ozpr, ozopore; pa, patella; pcmip, pericoxal muscle insertion plaque; pcs, pericardial suspensors; st, sternite; ta, tarsus; tg, tergite; ti, tibia; trgm, opisthosomal tergum.

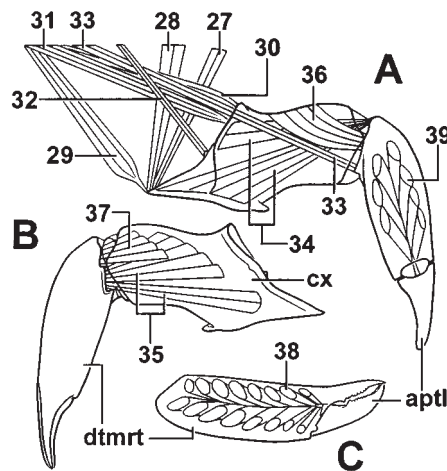


Figure 3. Skeletomuscular anatomy of the left chelicera of adult female. A, medial perspective showing arrangement of intrinsic and extrinsic muscles (compare with Fig. 1: dorsal). B, lateral perspective. C, anterior perspective of deutomerite and apotele. Arabic numerals indicate muscles listed in Table 1. Abbreviations: aptle, apotele; cx, coxa; dtmrt, deutomerite.

anterior projections of the endosternite are called anterior horns. The endosternite is suspended in the haemocoel dorsally by four pairs of muscles (8–11) that insert on the carapace and opisthosomal tergum (trgm) (Figs 2, 6), laterally by three muscle pairs (12) that insert on the arthrodial membranes between the pedal coxae (cx) (Fig. 6C), ventrally by a large muscle (13) that attaches to the lateral margin of the genital operculum (oprclm) and medial margin of pedal coxa 4 (Fig. 2), and posteriorly by two muscles (14, 15) that attach to an opisthosomal sternite (st) and anterior spiracular arm (aspra), respectively (Figs 2, 6C). The endosternite also has a muscular attachment to the coxo-epistomal apodeme (ceap) (7) (Fig. 6F) and serves as an attachment for extrinsic muscles of the pedipalpal (42–47) (Figs 2, 4) and pedal coxae (70–74) (Figs 2, 6D–F).

#### *Stomotheca and pharynx*

The preoral chamber, or stomotheca, is formed dorsoanteriorly by the epistome (epstm), laterally by coxapophyses of the pedipalpal coxae (cxph-p) and postero-ventrally by coxapophyses of leg 1 (cxph-1) and an associated sclerite, the labium (lbm) (Figs 1, 2). The labium is probably a sternal element associated with postoral somite III (Winkler, 1957) and is supported posteriorly by coxapophyses of leg 2 (cxph-2). The mouth is located near the ventral surface of the epistome and opens into a well-muscularized pharynx (phrnx) (Fig. 2). The walls of the pharynx have two pairs of longitudinal sclerotized rods that serve as sites of muscle attachment. Pharyngeal dilator muscles (3, 4) arise from the inner surfaces of the epistome (Fig. 2).

The dorsal surface of the epistome is divided transversely by a deep sulcus (epsul), or infolding of the cuticle (Figs 2, 6F), and is manifested internally as a collarlike ridge which appears to strengthen the epistome against deformation by the pharyngeal



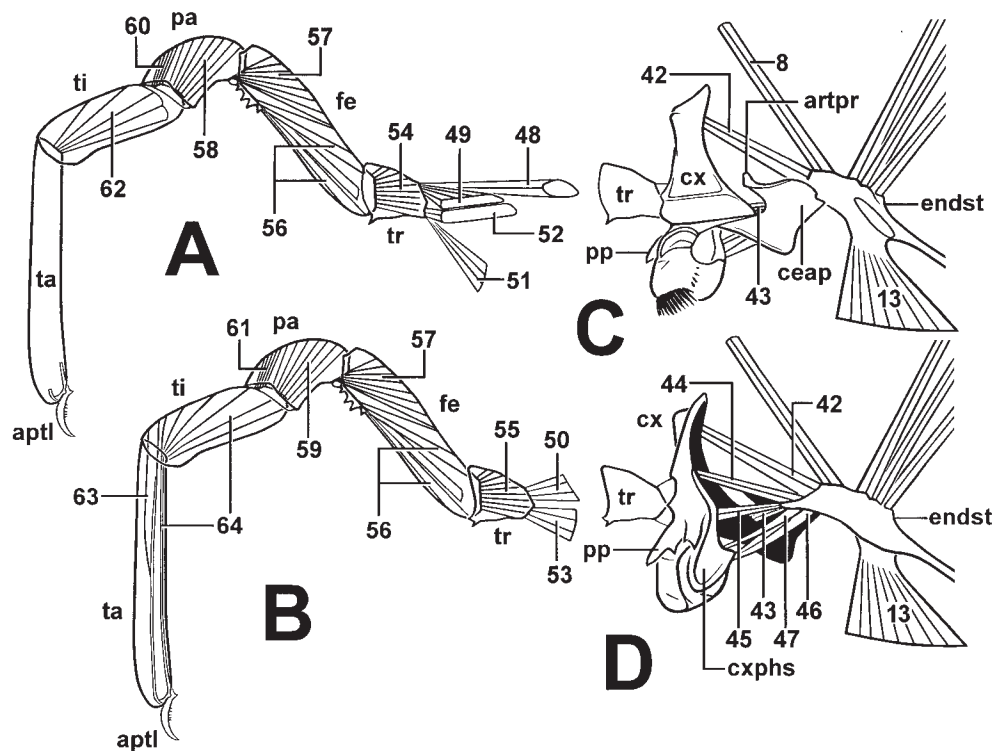


Figure 4. Skeletomuscular anatomy of the pedipalpal complex of adult female and its relationship to the endosternite. A, medial view of the right pedipalp showing arrangement of intrinsic muscles. The pedipalp is drawn as if the trochanter has been separated from the coxa, but the coxa-trochanter muscles have retained their 'intact' orientation (compare to Fig. 4C). B, lateral view of left pedipalp showing arrangement of intrinsic muscles. The pedipalp is drawn as if the trochanter has been separated from the coxa, but the coxa-trochanter muscles have retained their 'intact' orientation (compare with Fig. 4D). C, medial view of right pedipalpal coxa showing its relationship to the endosternite and the arrangement of the endosternocoxal muscles. The epistome has been removed from the coxa by severing the pre-epistomal connection and the ventral and posterior margins of the coxo-epistomal fold. Thus the medial surface of the outer layer of the coxo-epistomal fold is seen (compare to Figs 2, 4D, 6F). D, lateral view of left pedipalpal coxa showing its relationship to the endosternite and the arrangement of the endosternocoxal muscles (compare to Figs 2, 4C, 6F). Arabic numerals indicate muscles listed in Table 1. Abbreviations: aptl, apotele; artpr, articular process where the chelicera pivots against the coxo-epistomal apodeme (compare to Fig. 6F); cx, coxa; ceap, coxo-epistomal apodeme; cxphs, coxapophyseal sclerite; endst, endosternite; fe, femur; pa, patella; pp, pedipalpal coxal process; ta, tarsus; ti, tibia; tr, trochanter.

dilators (3, 4). The pre-sulcal portion of the epistome is drawn out anteriorly into a process or 'horn'. Some workers consider the pre-sulcal epistome to be homologous with the labrum of other arachnids (e.g. Hansen & Sørensen, 1904; Snodgrass, 1948; Kaestner, 1968; van der Hammen, 1985), but this interpretation does not appear to be correct. The labrum in chelicerates is generally a membranous structure and, in the cases examined thus far, a muscle (1) arises from the anterior region of the epistome, passes ventrally and inserts on the ventral labral surface (Fig. 2) (Snodgrass, 1948; Shultz, 1993, 1999). Using these criteria, the labrum (lbrm) in *L. aldrichi* would appear to be a small membranous lobe lying ventral to the pre-sulcal

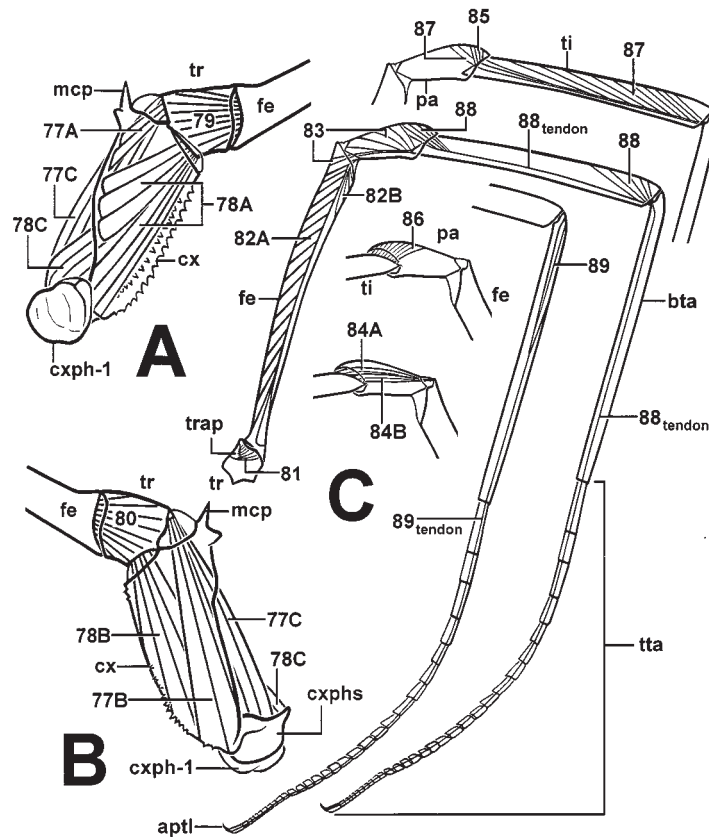


Figure 5. Skeletomuscular anatomy of the left member of the first leg pair of an adult female. A, proximal portion of leg 1 in anteromedial perspective, as indicated by the arrow in Fig. 6D. B, proximal portion of leg 1 in posterolateral perspective; C, distal portion of leg 1 in anteromedial perspective. Small insets show posterolateral perspectives of the femur (fe), patella (pa) and tibia (ti). Arabic numerals indicate muscles listed in Table 1. Abbreviations: aptl, apotele; bta, basitarsus; cx, coxa; cxph-1, coxapophysis of leg 1; cxphs, coxapophysial sclerite; fe, femur; mcp, medial coxal process; pa, patella; ti, tibia; tr, trochanter; trap, trochanteral apodeme; tta, telotarsus.

epistome and anterior to the mouth (Fig. 2). The pre-sulcal epistome fuses laterally to the medial surface of each pedipalpal coxa (Fig. 4). A transverse muscle (2) passes from one side of the pre-sulcal epistome to the other, attaching at the points where the epistome fuses to the pedipalpal coxae (Fig. 2).

The epistome is essentially an external sclerite, but the ventrolateral portions are hidden from external view within a deep cuticular fold formed between the epistome and the pedipalpal coxae (Fig. 6). The potential space formed by this coxo-epistomal fold is essentially non-existent; the two sides of the fold are so closely associated that they superficially appear to be one layer. The posterior epistomal margin is folded anteriorly to form a dorsal bilayered rim, the anterior edge of which is continuous with the outer layer of the coxo-epistomal fold (Figs 6F, 8). The medial edge of posterior marginal rim attaches to the base of the frontal sclerite (Fig. 2), which leaves a semicircular notch in the dorsoposterior margin of the epistome when it is removed. The anteromedial edge of the posterior marginal rim bears a pronounced

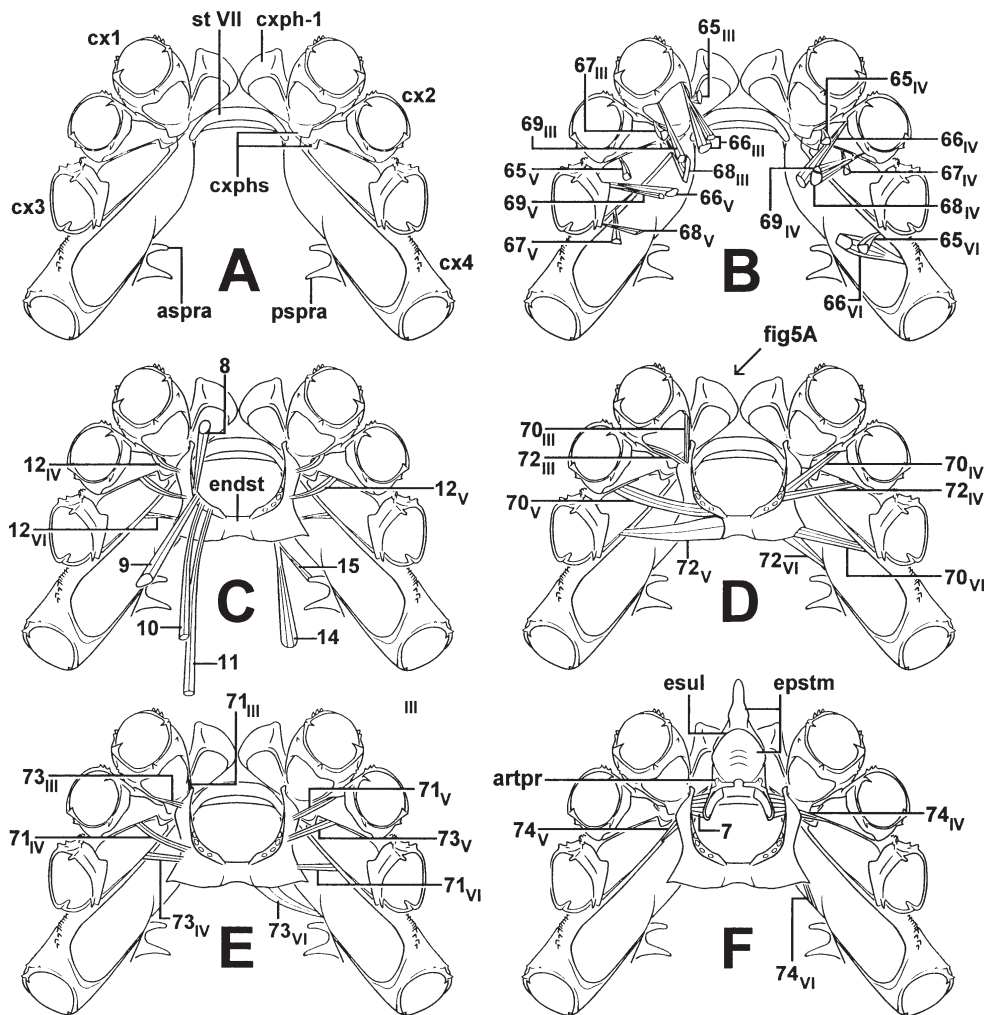


Figure 6. Skeletomuscular anatomy of the leg coxae of an adult female from a dorsal perspective. A, skeletal anatomy of the sternocoxal complex. B, arrangement of the tergocoxal muscles (compare to Fig. 1). C, arrangement of the endosternite and endosternal suspensor muscles relative to the pedal coxae. D, arrangement of endosternocoxal muscles and perspective of Fig. 5A. E, arrangement of endosternocoxal muscles. F, arrangement of endosternocoxal muscles and placement of the epistome with respect to the endosternite and sternocoxal complex. Arabic numerals indicate muscles listed in Table 1. Roman numerals indicate the postoral somite with which the indicated muscle or sclerite is associated. Abbreviations: artpr, articular process; aspra, anterior spiracular arm; cx, coxa; cxph-1, coxapophysis of leg 1; cxphs, coxapophysial sclerites of legs 1 and 2; endst, endosternite; epstm, epistome; esul, epistomal sulcus; pspra, posterior spiracular arm; st, sternum.

tubercle (artpr) that serves as a pivot for the cheliceral coxa. The posterior marginal fold is much broader laterally and received fibres from a muscle (7) that arises on the anterior horns of the endosternite (Figs 6F, 8). The anterior margin of this region is also continuous with the outer layer of the coxo-epistomal fold, the ventral part of which is more well sclerotized than the rest and forms a 'bridge' connecting the ventrolateral margin of the epistome to the ventromedial margin of the pedipalpal

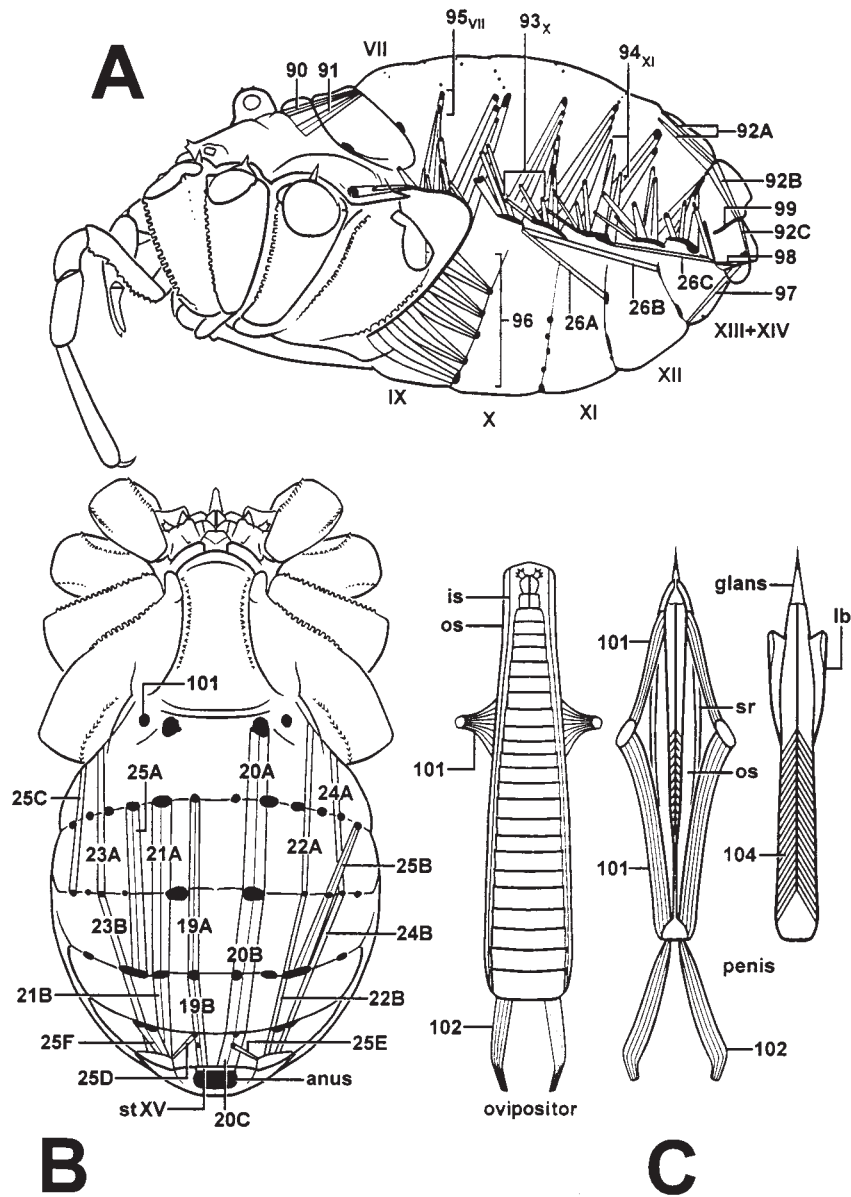


Figure 7. Skeleto-muscular anatomy of the opisthosoma. A, lateral perspective of adult female. B, ventral perspective of adult female with anal operculum removed to show sternite XV. C, ventral perspective of genitalia of adult female (*ovipositor*) and male (*penis*). Compare to Fig. 1. Arabic numerals indicate muscles listed in Table 1. Roman numerals indicate the postoral somite with which the indicated muscle or sclerite is associated. Abbreviation: is, inner sheath of ovipositor; lb, lateral bulb of penis; os, outer sheath of ovipositor or penis; sr, ventral stiffening rod of outer sheath of penis; st, sternite.

coxa (Fig. 4). The complex formed by the epistome, coxo-epistomal fold and bridge sclerite is here termed the coxo-epistomal apodeme (*ceap*) (Figs 4, 6F, 8).

The pedipalpal coxapophysis is membranous along its anterior and medial surfaces

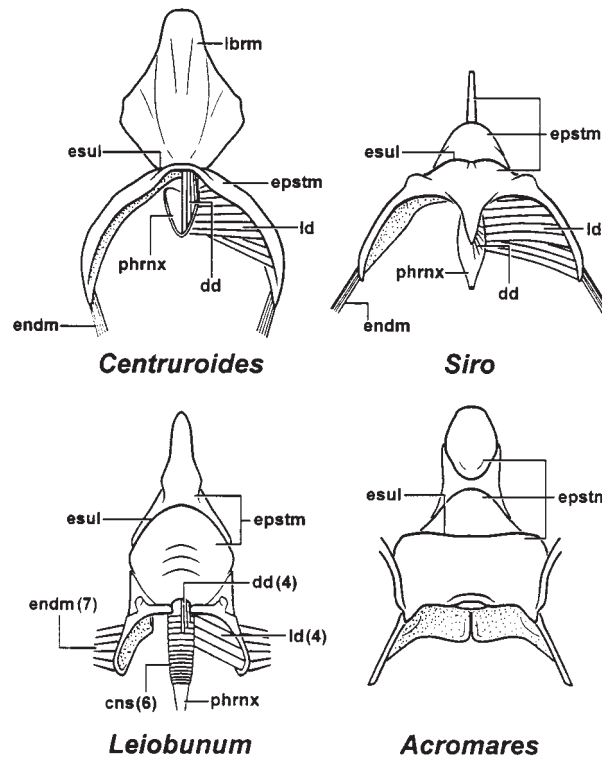


Figure 8. Dorsal view of the epistome-pharynx complex in four arachnids, including the scorpion *Centruroides vittatus* (Buthidae) and the opilions *Siro acaroides* (Cyphophthalmi: Sironidae), *Leiobunum aldrichi* (Palpatores: Gagrellidae) and *Acromares banksi* (Laniatores: Cosmetidae). The dilator muscles have been removed from the left side to show the ventral structures of the epistome, which are shaded. The entire pharyngeal apparatus has been removed from *Acromares* to show that the lateral epistomal processes encircle the pharynx. The pharyngeal apparatus in *Acromares* is otherwise similar to that of *Leiobunum*. The labrum is large in scorpions but is a ventral lobe in the opilions. A transverse epistomal sulcus is present in all representative taxa shown here, but the pre-epistomal region in *Centruroides* is hidden in dorsal perspective by the anteriorly reflected dorsal process associated with the dorsal dilator muscle. Arabic numerals indicate muscles listed in Table 1. Abbreviations: cns, constrictor muscle of pharynx; dd, dorsal dilator of pharynx; endm, muscular connection between epistome and endosternite; epstm, epistome; esul, epistomal sulcus; lbrm, labrum; ld, lateral dilator muscle of pharynx; phrn, pharynx.

(Figs 2, 4) but is more well sclerotized along its posterolateral surface, where it abuts the membranous anteromedial surface of the coxapophysis of leg 1 (Fig. 4D). The posterior margin of the sclerotized region of the coxapophysis, the coxapophyseal sclerite (cxphs), is associated with three muscles, a depressor of the pedipalpal coxa-trochanter joint (51) (Fig. 4) and two muscles that attach to the endosternite (46, 47). The coxapophysis of leg 1 is similar to that of the pedipalp in having a membranous portion associated with the preoral chamber, but the coxapophyseal sclerite projects into the prosomal haemocoel as a broad flange. The coxapophysis of leg 1 is also associated with coxa-trochanter muscles (77, 78) (Fig. 5) and two muscles attaching to the endosternite (75, 76) (Fig. 2). The coxapophyses of leg 1 are separated from those of leg 2 by the labium, which projects anteroventrally from the base of coxa 1. The organization of the coxapophysis of leg 2 is very

similar to that of leg 1, except that it lacks a membranous component and has only one muscle (76) associated with its coxapophyseal sclerite (Fig. 2).

### *Appendages*

Each chelicera (chl) is composed of three articles, namely coxa (cx), deutomerite (dtmrt) and apotele (aptl) (Fig. 3). The ventral surface of the cheliceral coxa pivots on a process of the coxo-epistomal apodeme (Figs 2, 4, 6F) and movement is regulated by six tergo-coxal muscles (27–32). The coxa-deutomerite joint has a loose bicondylar articulation that allows flexion, extension and some rotation under the influence of five muscles, four arising in the coxa (34–37) and one on the carapace (33). The deutomerite and apotele form the chela of the chelicera. The deutomerite-apotele joint is a strong bicondylar articulation operated by antagonistic muscles (38, 39) (Fig. 3).

The pedipalp is composed of seven articles, namely, coxa (cx), trochanter (tr), femur (fe), patella (pa), tibia (ti), tarsus (ta) and apotele or apotelic claw (ap) (Fig. 4). The coxa is laterally compressed and has a large ventromedial extension (coxapophysis) that is closely associated with the epistome (Figs 2, 3). The coxa can be moved against the prosoma through the action of two tergo-coxal (40, 41) and six endosternocoxal muscles (42–45). The coxa joins the trochanter at a transverse bicondylar articulation that undergoes levation and depression under the influence of six muscles (48–53) (Fig. 4). The trochanter-femur joint has a vertical bicondylar articulation that undergoes adduction and abduction under the control of two muscle (54, 55). The femur-patella joint as a dorsal hinge articulation that undergoes flexion and extension. The joint is operated by two muscles (56, 57) that appear to act as flexors; there is no apparent extensor muscle (Fig. 4). The patella joins the tibia at a near vertical bicondylar articulation that undergoes adduction and abduction under the influence of four symmetrically arranged muscles (58–61). The tibia-tarsus joint has a dorsal hinge articulation that undergoes flexion and extension. There is one muscle (62) that appears to act as a flexor; there is no apparent extensor muscle. The tarsus-apotele joint has a strong transverse bicondylar articulation that undergoes levation and depression under the influence of two antagonistic muscles (63, 64) (Fig. 4). These muscles also traverse the tibia-tarsus joint and may influence movement there (Fig. 4).

Each leg is composed of seven principal articles, namely coxa (cx), trochanter (tr), femur (fe), patella (pa), tibia (ti), tarsus (ta) and apotele (ap) (Figs 1, 5, 6). The tarsus is divided into a proximal basitarsus (bta) and distal telotarsus (tta), and the telotarsus is subdivided into a many tarsomeres. The coxae of legs 1–3 are attached to the prosoma by flexible arthrodial membranes. However, each is equipped dorsomedially with a vertical spikelike process that contacts the carapace at its marginal concavities (Fig. 1). The process apparently serves as a pivot point that allows rotation of the coxa about its long axis. These coxae are also equipped with five tergo-coxal muscles (65–69) (Figs 1, 6D) and five to seven endosternocoxal muscles (70–76), depending on the leg (Figs 2, 6D–F). Some of the endosternocoxal muscles (75, 76) of legs 1 and 2 have been described above in the discussion of the stomotheca. The coxa of leg 4 is larger than the others and its mobility appears to be more limited. It attaches to the carapace along a broad hinge that is operated by two tergo-coxal muscles (65<sub>VI</sub>, 66<sub>VI</sub>) (Figs 1, 6B) and five endosternocoxal muscles (70<sub>VI</sub>–74<sub>VI</sub>) (Figs 1, 6D–F).

The coxa of each leg joins the trochanter at a transverse bicondylar articulation that undergoes levation and depression under the influence of two muscle groups (77, 78), each with three principal heads (Fig. 5). The trochanter joins the femur at a vertical bicondylar joint that undergoes protraction and retraction. These movements are apparently accomplished by two symmetrically arranged antagonistic muscles (79, 80). The trochanter-femur joint is the site of leg autotomy. A circumferential line of weakness at the base of the femur is apparently broken by contraction of muscle (81), which arises from a dorsal apodeme in the trochanter (trap) (Fig. 5). Contraction of this muscle, perhaps in association with contraction of muscles 79 and 80, apparently pulls the proximal margin of the femur and the arthrodial membranes of the trochanter-femur joint into the trochanter.

The femur joins the patella at a transverse bicondylar joint that undergoes flexion and extension (Fig. 5). The joint is traversed by three muscles (82–84), including an apparent flexor (82) and extensor (84). The patella-tibia joint has a bicondylar articulation with one anterodorsal condyle and one posteroventral condyle. It undergoes movements intermediate between flexion-protraction and extension-retraction brought about by four muscles (83–86), although elements of two other muscles also traverse the joint (87, 88). The tibia-tarsus joint has a dorsal hinge that undergoes flexion and extension. The joint is supplied with a flexor (87) but no apparent extensor muscle (Fig. 5). Extension may be accomplished by an elastic sclerite that spans the dorsal region of the arthrodial membrane and/or by haemolymph pressure. The intratarsal joints are loosely hinged and can undergo a range of movements, but there are no muscles intrinsic to the tarsus that might operate them. The apotele-tarsus joint is operated by two muscles (88, 89) via long tendons (Fig. 5). These muscles probably also serve to move the intratarsal joints.

### *Opisthosoma*

The opisthosoma in members of Opiliones is thought to be composed to nine complete somites representing postoral somites VII–XV (Figs 1, 7) (Hansen & Sørensen, 1904; Winkler, 1957; van der Hammen, 1989). This may represent a reduction of posterior elements from the 12-segmented condition that appears to be primitive for Chelicerata (Shultz, 1990). The segmental boundaries are delimited dorsally by muscle insertion sites (10, 11, 92, 94, 95, 97–99) (Figs 1, 7) and cuticular or subcuticular coloration. There appear to be no cuticular structures corresponding to tergal margins, and, consequently apparent segmental boundaries may reflect primary rather than secondary segmentation (Snodgrass, 1935). The last apparent tergite is generally interpreted as a fusion of tergites XIV and XV (Figs 1, 7) (Hansen & Sørensen, 1904; Winkler, 1957; van der Hammen, 1985, 1989), but, given that tergal boundaries are distinguished largely by patterns of muscle attachment, this ‘fusion’ may actually represent the loss of most of the relevant ‘intertergal’ muscles. Indeed, one possible ‘intertergal’ muscle (102) appears to remain (Figs 1, 7). Some workers consider the anal operculum (aop) to represent tergite XVI, the last ontogenetically pre-anal somite (i.e. somite XVI) (Hansen & Sørensen, 1904; Winkler, 1957). However, given the apparent absence of a corresponding sternite and presence of dorsally articulated post-anal structures in other chelicerate taxa (e.g. Xiphosura, Eurypterida, Scorpiones, Palpigradi, Uropygi), it is possible that the anal operculum is a post-anal structure.

The segmental boundaries of the ventral surface of the opisthosoma are more difficult to appreciate, especially in the anterior region. The interpretation presented here follows the system proposed by Hansen & Sørensen (1904). Deviations from this system (e.g. Winkler, 1957; van der Hammen, 1989) are not concordant with observations of the present study. The first opisthosomal sternite (postoral somite VII) is largely hidden from external view by the genital operculum (compare Figs 1, 2). Hansen & Sørensen referred to sternite VII as the '*arculi genitales*', because it forms the anterior and lateral margins of the pregenital opening in many opilionid taxa. Sternite VII in *L. aldrichi* is well-developed anteriorly (Figs 2, 6), but the lateral portion appears to be present as a thin strip of cuticle between the genital operculum and the coxa of leg 4. The second opisthosomal sternite (postoral somite VIII) appears to be represented laterally by a triangular region posteriorly adjacent to the coxa of leg 4 (Fig. 1) and is associated with the tracheal spiracle and the anterior extrinsic genital muscle in the female (101). The boundaries between the remaining 'sternites' are similar to those between the 'tergites' in being indicated largely by rows of muscle insertion sites (Figs 1, 7) and probably reflect primary rather than secondary segmentation. Similarly, there appears to have been a 'fusion' of sternites XIII and XIV, but, again, this may be attributed to a loss of most of the relevant muscles. However, external indication of the boundary may have been preserved by the insertion of one paired muscle (25E) (Figs 1, 7). The most posterior sternite, sternite XV, is a small transverse sclerite that is typically hidden from external view by the anal operculum (compare Figs 1, 7B).

The lateral or pleural margins of sternites are also indicated externally by sites of muscle attachment, the lateral muscle insertion plaques (lmip) (Figs 1, 7), associated with four muscle groups (26, 93–95). These plaques are best observed in gravid females or any animal with an expanded opisthosoma. In unexpanded individuals, the plaques can be obscured by an overhanging fold formed by the lateral 'tergal' region. However, the pleural region of the pre-anal somites is often folded even in a partially expanded opisthosoma such that the lateral margin of tergite XIV + XV is essentially 'internalized' (compare Figs 1, 7B). The pleural muscle insertion plaques associated with somites VII and VIII and most of those between sternites VIII and IX are arranged in a single series posteriorly adjacent to pedal coxa 4 and is here termed the pericoxal muscle insertion plaque (pcmip) (Figs 1, 7). The pericoxal plaque is associated with ventral longitudinal muscles (22–25) and intersternal muscles (96) (Figs 1, 7).

The principal openings to the tracheal system, the spiracles, are just posterior to the coxae of leg 4. The base of each of the two primary tracheal trunks is embraced by two cuticular arms, one anterior and one posterior (Figs 2, 6). The spiracular arms are supplied with muscles (15–18) which appear to constrict and dilate the bases of the tracheal trunks.

#### *Genital structures*

The ovipositor is a long, tapered, dorsoventrally flattened cylinder composed of numerous cuticular annulations and ends in a pair of fingerlike processes equipped with terminal sensory organs (Fig. 7C). There is a thin sheet of muscle (103) that attaches to the annuli and shortens the ovipositor or regions of the ovipositor. The ovipositor is ensheathed by two layers. The inner sheath (is) is a thin, translucent,



highly elastic membrane that attaches to the ovipositor at its base and is free distally. The outer sheath (os) also attaches to the base of the ovipositor, but its anterior end attaches at the anterior margin of the genital operculum and the adjacent body wall. The potential space between the outer sheath and ovipositor plus inner sheath is the pregenital chamber. The anterior end of the pregenital chamber appears to be dilated by a pair of muscles (101) (Figs 2, 7). The ovipositor is apparently protracted by haemolymph pressure and retracted by a pair of muscles (102) (Figs 2, 7). The ovipositor complex is protected ventrally by the genital operculum (Figs 1, 2, 7) and the opening to the pregenital chamber is protected anteriorly by sternite VII (Fig. 2). Martens, Hoheisel & Götze (1981) have provided a detailed anatomical and functional analysis of the ovipositor.

The penis is a long cuticular cylinder that tapers rapidly at its anterior terminus (Fig. 7C). The terminus (glans) is more heavily sclerotized than the shaft and can be flexed against the shaft by an intrinsic bipinnate muscle (104) (Fig. 7C). The distal portion of penial shaft bears a pair of cuticular bulbs (lb), each with an anterior opening. When the penis is retracted, the openings to the bulbs are engaged by hook-shaped, cuticular ducts that project from the roof of the pregenital chamber. The penis is enclosed with a cuticular sheath (os) that appears to correspond to outer sheath of the ovipositor. The cuticular sheath attaches to the penis at its base, but the sheath is incomplete on the ventral surface. The sheath has four longitudinal stiffening rods (sr), two well-developed ventrolateral and two less-developed dorsal rods, with extrinsic penial muscles (101) attaching to the ventrolateral rods (Fig. 7C). Like the ovipositor, the penis complex is protected ventrally by the genital operculum and anteriorly by sternite VII.

## DISCUSSION

### *Evolution of the epistome-pharynx complex in Opiliones*

Many opilions, including *Leiobunum*, are unusual among extant arachnids in being able to ingest solid particles (Weygoldt & Paulus, 1979), including small arthropods and entire appendages of larger arthropods (personal observations), but arachnologists have not determined whether this ability is primitive or has evolved secondarily. Most arachnids macerate and digest prey externally and ingest the liquefied material through a well-muscularized pharynx (Snodgrass, 1948). Because xiphosurans and morphologically primitive members of many other arthropod lineages ingest particulate matter, it is generally thought that extraintestinal digestion and fluid feeding by arachnids is a derived feature (Weygoldt & Paulus, 1979; Shultz, 1990). If ingestion of large particles by *L. aldrichi* and its relatives was a primitive trait, an understanding of their feeding apparatus might shed light on the evolutionary transition from intra- to extraintestinal digestion. However, observations of the skeletomuscular morphology of the epistome, pharynx and pharyngeal dilator muscles in opilions and other arachnids suggest that the feeding apparatus in *L. aldrichi* is derived. Specifically, the epistome is an elongate, subcylindrical sclerite that nearly encircles the pharynx, except for the midventral region (Figs 2, 6F, 8), thus allowing the pharyngeal dilators to expand the pharyngeal lumen circumferentially. In contrast, the pharynx in most fluid-feeding arachnids generally has a narrow inlet

and outlet and a system of muscles arranged in transverse and/or dorsoventral planes. This system allows passage of fluids and expansion of the pharyngeal lumen but does not maximize circumferential dilation that would allow the passage of large solid particles via peristalsis.

In an attempt to understand the evolution of the circumferential pharyngeal dilators, the epistome-pharynx complex of *L. aldrichi* (Suborder Palpatores) was compared to that of representatives from the other two opilionid suborders, *Siro acaroides* (Suborder Cyphophthalmi) and *Acromares banksi* (Suborder Laniatores), and two scorpions, *Centruroides vittatus* (Buthidae) and *Pandinus imperator* (Scorpionidae) (Fig. 8). The epistome-pharynx complex in scorpions has an organization similar to that of certain Opiliones (Fig. 8), and it seems justifiable to regard scorpions as an outgroup for use in polarizing features in the epistome-pharynx complex of Opiliones.

The epistome of scorpions is a recurved, crescent-shaped sclerite (Fig. 8) that projects ventroposteriorly into the prosomal haemocoel from its lateral attachment to the pedipalpal coxae. The anteromedial margin of the epistome has a transverse sulcus that divides the epistome into a small pre-sulcal sclerite associated with the large membranous labrum and a much larger post-sulcal region. The pre-sulcal epistome is extremely small in *Centruroides* (Fig. 8) but is larger in other scorpion species (e.g. *Pandinus imperator*). The dorsoposterior margin of the post-sulcal epistome is drawn out into a process that is reflected anteriorly and bears dorsal pharyngeal dilator muscles on its posterior surface. Lateral pharyngeal dilator muscles arise from the medial surfaces of the lateral epistomal arms and insert on the lateral surfaces of the pharynx. The dorsoventral and transverse orientations of the pharyngeal dilator muscles are typical of fluid-feeding arachnids.

The epistome-pharynx complex in the cyphophthalmid opilion *Siro* is very similar to that of scorpions and is thus probably more primitive than that of the other opilions examined here (Fig. 8). The epistome is crescent-shaped and bears lateral pharyngeal dilators on the epistomal arms and dorsal pharyngeal dilators from a mid-dorsal epistomal process. It differs from scorpions in having a pair of knoblike protuberances against which the chelicera can pivot, a more well-developed epistomal sulcus, a larger pre-sulcal epistome and a dorsoposteriorly projecting dorsal process. The near-orthogonal arrangement of pharyngeal dilators in *Siro* is typical of many fluid-feeding arachnids, but the feeding behaviour of this animal has yet to be documented.

The condition of the epistome-pharynx complex in *L. aldrichi* has been described in detail above in Results. Rather than the three-branched framework of scorpions and *Siro*, the epistome in *L. aldrichi* is more cylindrical and nearly envelops the pharynx. This evolutionary transformation apparently occurred through rearward expansion of the dorsomedial positions of the epistome rather than through cuticularization or 'filling in' of the spaces between the three epistomal processes. The rearward expansion hypothesis is supported by the orientation of the cheliceral pivots. In *Siro acaroides* the pivots are located anteriorly, but they are posterior structures in *L. aldrichi*. In addition to the rearward expansion of the dorsal epistomal elements, the lateral epistomal margins in *L. aldrichi* have assumed a more ventral placement with respect to the pharynx. These two evolutionary modifications have permitted the development of a near-continuous ring of dilator muscles radiating from the surfaces of the pharynx. The arrangement in the laniatorid *Acromares banksi* is similar to that of *L. aldrichi*, but exceeds *L. aldrichi* in the development of the circumferential dilation mechanism. Here the lateral margins of the epistome meet

midventrally below the pharynx to form a complete box around the pharynx (Fig. 8).

Phylogenetic implications of diversity in the epistome-pharynx complex are inconsistent with a recent cladistic analysis of relationships within Opiliones (Martens, 1980, 1986; Martens *et al.*, 1981). Based on their analyses of genitalic characters, Martens and his coworkers have suggested that Cyphophthalmi be placed among the Palpatores and that Laniatores be regarded as the sister group to all other Opiliones. In contrast, the present analysis indicates that Palpatores (e.g. *Leiobunum*) and Laniatores (e.g. *Acromares*) form a monophyletic group united by circumferential pharyngeal dilators and associated epistomal modifications. However, this result is consistent with a recent quantitative parsimony analysis of opilion phylogeny using genitalic and non-genitalic characters (Shultz, 1998) and molecular sequence data (Giribet *et al.*, 1999; Shultz & Regier, unpublished observations).

#### *Phylogenetic implications at the ordinal level*

The phylogenetic position of Opiliones within Arachnida is controversial. Arachnologists have tended place this order near Acari and/or Ricinulei (Kaestner, 1968; Savory, 1971; Yoshikura, 1975; Weygoldt & Paulus, 1979; Shear, 1982), but few compelling synapomorphies among these groups have been identified (Shultz, 1990). However, in a quantitative cladistic analysis of ordinal relationships in Arachnida, Shultz (1990) proposed a clade (Dromopoda) in which Opiliones was the sister group to Scorpiones, Pseudoscorpiones and Solifugae. The proposed synapomorphies included a pedal femur-patella extensors, reduction in the number of endosternal suspensors, differentiation of the meso- and metapeltidial elements of the carapace, loss of the coxal gland orifice associated with leg 1, and several other characters. The present analysis yielded additional possible synapomorphies, including absence of anterior doublure, tergo-pharyngeal and sterno-pharyngeal muscles in all four orders and presence of elastic arthrodistal sclerites spanning the tibia-tarsus joints in Opiliones, Scorpiones and Solifugae (pers. obs.). In contrast, present observations failed to support the hypothesis that Scorpiones is more closely related to Haplcnemata (i.e. Pseudoscorpiones + Solifugae) than to Opiliones, and revealed several apparently unique synapomorphies supporting an Opiliones-Scorpiones clade. These potential synapomorphies are summarized below. A more rigorous, quantitative phylogenetic analysis must await comparable information from a larger sample of arachnid taxa.

#### *Cheliceral tergo-deutomerite muscle*

The chelicerae of Opiliones and other Chelicerata are primitively composed of three articles, namely coxa, deutomerite and apotele (Fig. 3). Scorpiones (Lankester, Benham & Beck, 1885; Vyas, 1974) and Opiliones (Fig. 3) appear to be unique among Chelicerata in having a muscle (33) that arises from the carapace and inserts on the proximal margin of the deutomerite. This muscle is absent in *Limulus* (Xiphosura) (pers. obs.) and *Eukoeneria* (Palpigradi) (Roewer, 1934; pers. obs.) and has yet to be recorded in pycnogonids and mites, which are the only extant chelicerates with three-segmented chelicerae. Members of the other extant chelicerate orders have only two articles and appear to lack the coxa-deutomerite joint.

*Three-branched epistomal skeleton supporting the pharyngeal dilator muscles*

As noted above in the discussion of the epistome-pharynx complex, Opiliones and Scorpiones appear to share a unique system for supporting the extrinsic pharyngeal muscles. Specifically, the epistome has three processes, one median and two lateral, which serve as the skeletal framework to which the pharyngeal dilator muscles attach. In addition, the epistome is divided transversely by a sulcus and each lateral epistomal process has a posterior attachment to the endosternite or its evolutionary derivatives. Similarities are most pronounced between scorpions and *Siro* (Cyphophthalmi) (Fig. 8). Although highly modified, the same elements are also present in Palpatores and Laniatores.

*Intercostal endosternal suspensor muscles*

Intercostal suspensor muscles may represent a unique synapomorphy of Opiliones and Scorpiones. In his model of the ancestral arachnid endosternite, Firstman (1973) envisioned a horizontal sheet of connective tissue suspended within the haemocoel by a metameric series of muscles. Each metameric unit was viewed as having a pair of dorsal and transverse suspensors attaching to the carapace and a pair of ventral suspensors attaching to the sternum. However, in a notable departure from his model, Firstman (following Lankester *et al.*, 1885) indicated that the 'transverse' suspensors of scorpions attached to the flexible intercoxal membrane rather than the carapace. Firstman apparently did not observe the similar 'transverse' suspensors of *Leiobunum* (Fig. 6B). It is unclear whether these 'transverse suspensors' are novel structures, true transverse suspensors that have shifted to a new insertion, or ventral suspensors that have shifted laterally due to displacement of the ventral prosomal elements by anterior migration of the pregenital and genital regions of the opisthosoma.

*Stomotheca*

Scorpions and opilions are unique among arachnids in having a preoral chamber (stomotheca) formed laterally by the pedipalpal coxae and ventrally by extensions of the first and, to a lesser extent, second pedal coxae (Kaestner, 1931; van der Hammen, 1989; Shultz, 1990). Many workers refer to the coxal extensions as 'endites', and thereby implicitly homologize them with the mobile coxal endites of xiphosurans. However, there is little evidence other than similarity of position to support this view, and, even here, the coxal gnathobases or 'sessile endites' of xiphosurans seem more well suited as possible homologues. Each mobile endite in xiphosurans joins the medial surface of the coxa at a distinct articulation operated by a single muscle arising within the coxa (*Limulus*: pers. obs.; *Tachypleus*: Manton, 1964). In contrast, there is no such joint in opilions or scorpions, and the limited independent movement of each 'endite', when present at all, is regulated indirectly by endosternocoxal muscles (46, 47, 75, 76) (Figs 2, 4), coxa-trochanter muscles (77C, 78C) (Fig. 5A, B) and by extrinsic coxal muscles that move the entire coxa (40–47, 65–64) (Figs 2, 4, 6). Given the morphological novelty and uncertain homology of these structures, the theoretically neutral term 'coxapophysis' (van der Hammen, 1989) has been used here to denote these coxal extensions in opilions and scorpions.

Similarities between the stomotheca of *L. aldrichi* and other opilions with that of scorpions are also present in their internal structure. The proximoposterior margins

of coxae 1 and 2 (coxapophyseal sclerites) are modified into cuticular flanges that project dorsoposteriorly into the prosomal haemocoel (Figs 2, 5A, B, 6A). These flanges are very large in scorpions (Lankester *et al.*, 1885; Snodgrass, 1948; Shultz, 1991), where they extend almost to the carapace, but they are smaller in *L. aldrichi* and occupy a space ventral to the endosternite (Fig. 2). Despite the differences in relative proportion, the posterior coxal flanges of both arachnid groups serve as attachment sites for muscles that operate the coxa-trochanter joints (77C, 78C) (Fig. 5A, B) (Lankester *et al.*, 1885; pers. obs.). Furthermore, the coxapophyses of leg 2 have a posterior articulation with a ventral sclerite that is interpreted here as the sternite of the first opisthosomal somite (Fig. 6A; pers. obs.). These features are undoubtedly derived and do not occur elsewhere among extant Chelicerata.

In a previous treatment of arachnid ordinal relationships, Shultz (1990) hypothesized that presence of a stomotheca is synapomorphic for all dromopodan arachnids (i.e. Opiliones, Scorpiones, Pseudoscorpiones and Solifugae) based on evidence of a 'reduced' stomotheca in Pseudoscorpiones and Solifugae. This evidence consisted of the observation that the preoral chamber in the two orders is formed laterally by 'enditic' elements of the pedipalpal coxae. However, this feature is present in most arachnids and, perhaps, even eurypterids (Selden, 1981) and, thus, does not reflect the former existence of a stomotheca nor does it represent a synapomorphy for Dromopoda. Indeed, there is no evidence for the existence of coxapophyses or associated skeletomusculature on legs 1 and 2 in Pseudoscorpiones and Solifugae. Thus, the stomotheca is probably best regarded as a potential synapomorphy of Opiliones and Scorpiones only.

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