



Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock) (Arachnida: Amblypygi), and its evolutionary significance

JEFFREY W. SHULTZ

Department of Entomology, University of Maryland, College Park, Maryland 20742, U.S.A.

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Skeletal muscles in the whipspider *Phrynus longipes* are surveyed and compared with those of other chelicerates to clarify the evolutionary morphology and phylogenetic relationships of the arachnids. Representatives of 115 muscle groups are described and illustrated, and their possible functions are proposed. Principal results of this analysis include new functional models for the operation of the pharyngeal and sternocoxal mechanisms in Amblypygi and a greatly expanded list of apparently unique synapomorphies supporting the monophyly of Pedipalpi (= Amblypygi, Schizomida, Thelyphonida).

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ADDITIONAL KEYWORDS:—Arthropoda – Chelicerata – Pedipalpi – morphology – muscle – phylogeny – homology – comparative anatomy.

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INTRODUCTION

This report provides an exhaustive survey of skeletal muscles in a large whipspider, *Phrynus longipes* (Pocock) (Amblypygi: Phrynidae), and explores the evolutionary, functional and phylogenetic significance of this information. This is the first such treatment of muscular anatomy in this arachnid order. The results inspired new functional models for the operation of the precerebral pharyngeal apparatus and sternocoxal complex in Amblypygi. Comparison of the data generated here with those obtained from a previous study of the whipscorpion *Mastigoproctus giganteus* (Lucas) (Thelyphonida) provides further evidence supporting the monophyly of Pedipalpi (i.e. Amblypygi, Schizomida and Thelyphonida) and against the monophyly of the Labellatae (i.e. Amblypygi and Araneae).

MATERIAL AND METHODS

Specimens

This study was based on examination of ten adult specimens (eight male and two female) of *Phrynus longipes* (Pocock) (Phrynidae) which were collected in the Dominican Republic in 1973 and maintained by the National Museum of Natural History (Smithsonian Institution). All specimens had been preserved and maintained in approximately 80% ethanol. Supplementary observations of specific structures were made on *Phrynus marginemaculatus* C.L. Koch (Phrynidae), which were collected from Torch Key, Florida, U.S.A. in 1984, and *Charon grayi* (Gervais) (Charontidae), which were collected from Guimaras Island, Philippines in 1929. These specimens were also obtained from the National Museum of Natural History (Accession No. for *C. grayi*: 99399).

Dissection

All observations and dissections were conducted using a binocular dissecting microscope with magnifications ranging from $6\times$ – $50\times$ and were recorded with drawings prepared with the aid of a camera lucida. Prior to dissection, intact specimens were examined thoroughly for external indications of muscle structure (Fig. 1). The cuticle is typically discoloured at muscle origins or differs in surface texture. The gross surface topology of the exoskeleton was also noted, as experience had shown that the exoskeletal attachments of endosternal and pharyngeal muscles are often indicated externally by depressions (Shultz, 1993). In addition to an external survey of the exoskeleton, internal cuticular structures were examined by removing soft tissue from poorly preserved specimens. Gross muscular anatomy was determined by dissection under 90% ethanol. Dissections of the prosoma typically began by exposing the dorsal musculature and proceeding ventrally through three layers, namely: (1) the dorsal exoskeleton (i.e. carapace), (2) 'endoskeletal' elements (i.e. proximal cheliceral article, carapacal doublure, endosternite), and (3) the ventral exoskeleton (i.e. sternum and coxae) (Fig. 2). Initially, a midsagittal incision was made in the carapace, and the cuticle was peeled away from one side to expose the

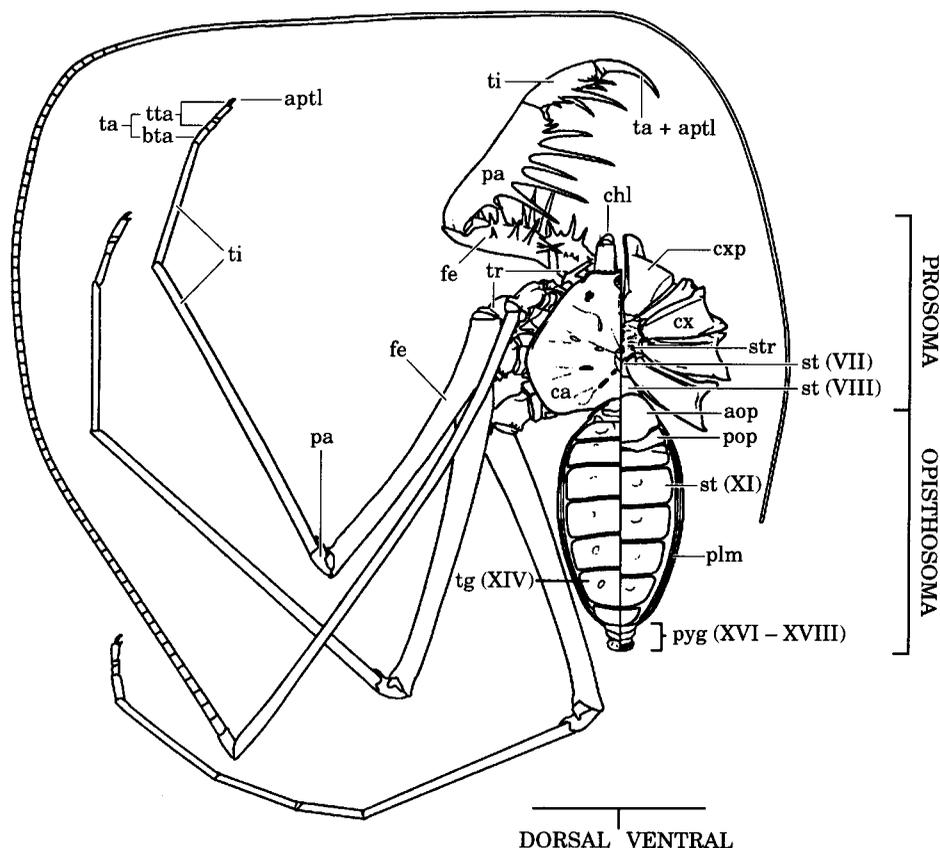


Figure 1. External anatomy of adult male *Phrynus longipes* (Pocock). Abbreviations: aop, anterior operculum; aptl, apotele; bta, basitarsus; ca, carapace; chl, chelicera; cx, pedal coxa; cxp, palpal coxa; fe, femur; pa, patella; plm, pleural membrane; pop, posterior operculum; pyg, pygidium; st, sternite; str, prosomal sternum; ta, tarsus; tg, tergite; ti, tibia; tr, trochanter; tta, telotarsus. Roman numerals indicate the postoral somite, thus 'I' indicates first postoral somite.

underlying muscles. The organization of muscular attachments was then compared to the drawings and to the cuticle of the intact side to determine how muscular attachments corresponded to the exoskeletal features noted prior to dissection. The extrinsic appendicular muscles were then traced to their insertion and removed one by one, starting anteriorly with the cheliceral muscles and moving posteriorly (Figs 4, 5, 8). The procedure was repeated on the unexposed side to confirm initial observations. The endosternite was exposed by removing the midgut caeca, coxal glands and central nervous system (Fig. 2B). The ventral layer of muscles consisted primarily of extrinsic appendicular and ventral endosternal suspensor muscles that attached to the ventral surface of the endosternite (Figs 2C, 9). These muscles were separated from the endosternite with a sharp scalpel, and the endosternite was removed to reveal the pattern of muscular attachment. Sagittal or cross sections were made in some individuals to determine relationships among the smaller or more complicated features, especially in the pharyngeal region (Fig. 3). Prosomal appendages were dissected by removing them from the body (Fig. 4) or cutting them at the coxa-trochanter joint (Figs 7, 11) and pinning them to a paraffin substrate.

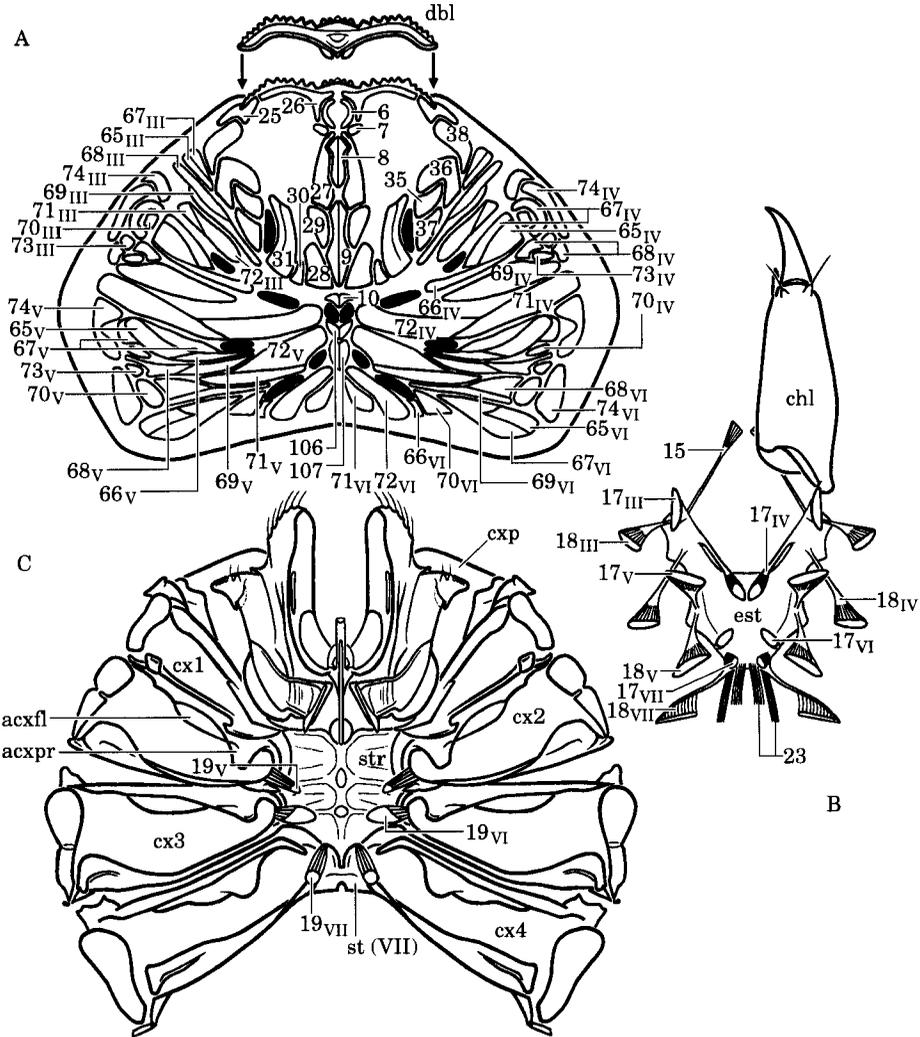


Figure 2. Skeletomuscular elements of the prosoma. A, dorsal view of the carapace with attachments of endosternal suspensor muscles in black and attachments of all other muscles indicated in white and labelled with a number. The doublure (dbl) is an anterior fold of the carapace that is depicted here as having been separated from the carapace at its marginal attachment and moved forward to show its interior dorsal surface. B, dorsal view of the right chelicera (chl) and endosternite (est). C, dorsal view of the ventral prosomal exoskeleton. Numbered muscles are described in Table 1. Abbreviations: acxfl, anterior coxal flange; acxpr, anterior coxal process; chl, chelicera; cx, pedal coxa; exp, palpal coxa; est, endosternite; st (VII), sternite of the seventh postoral somite (first opisthosomal segment) or 'metasternum'; str, prosomal sternum. Roman numerals indicate postoral somite; Arabic numerals indicate walking legs 1-4. Leg 1 corresponds to postoral somite III.

The muscles were exposed by peeling away the cuticle. Dissection of the opisthosoma was accomplished by separating it from the prosoma and by making a frontal section to expose the internal dorsal and ventral surfaces (Figs 12, 13).

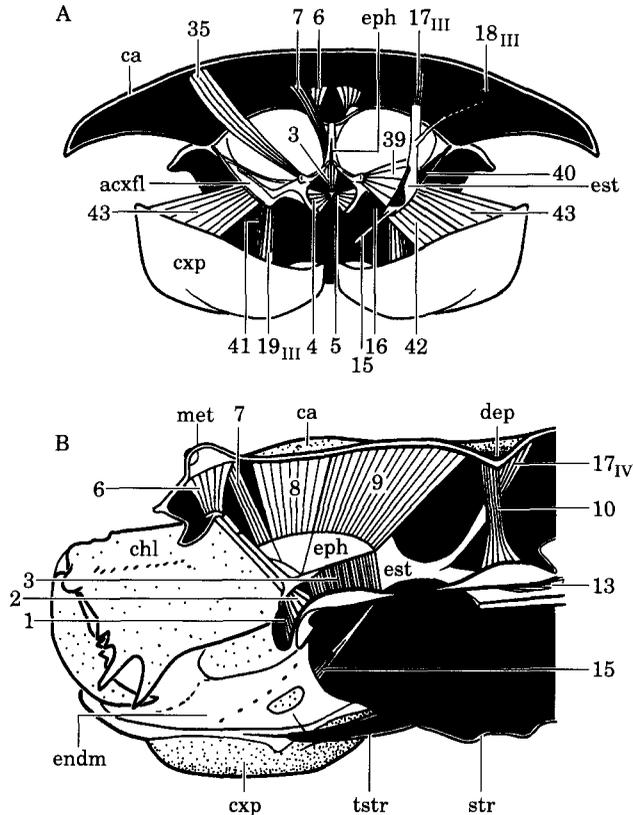


Figure 3. Skeletomuscular anatomy of the pharyngeal and epipharyngeal apparatus. A, posterior perspective of a cross section of the prosoma. The chelicerae and many muscles have been removed to show the pharyngeal and epipharyngeal structures. The anterior endosternal horn (est) is depicted on the right side, but it has been removed on the left. B, midsagittal section showing labral, epistomal, pharyngeal and epipharyngeal muscles. Numbered muscles are described in Table 1. Abbreviations: acxfl, anterior coxal flange; ca, carapace; chl, chelicera; cxp, palpal coxa; dep, central depression of the carapace; endm, enditic membrane of palpal coxa; eph, epipharyngeal sclerite; est, endosternite; met, medial eye tubercle; str, prosomal sternum; tstr, tritosternum (labium).

Homology

Working hypotheses of phylogenetic and serial homology of muscles were established using information from any and all aspects of anatomical complexity, including muscle attachment, fibre architecture, placement with respect to other muscles, etc. No class of information was regarded as having greater weight in establishing homology than others; that is, exclusive or primary reliance on 'key' criteria (e.g. ontogeny, innervation, possible function) was avoided in establishing hypotheses of homology. Consequently, the homologies proposed here should be regarded as hypotheses that are open to testing by results of future studies of development, neuroanatomy, muscle fine structure, phylogeny, etc.

The heuristic value of this minimum-assumption approach has been demonstrated in a study of the skeletomuscular system in the uropygid whipscorpion *Mastigoproctus* (Shultz, 1993). Prior to that analysis, arachnid morphologists had assumed the

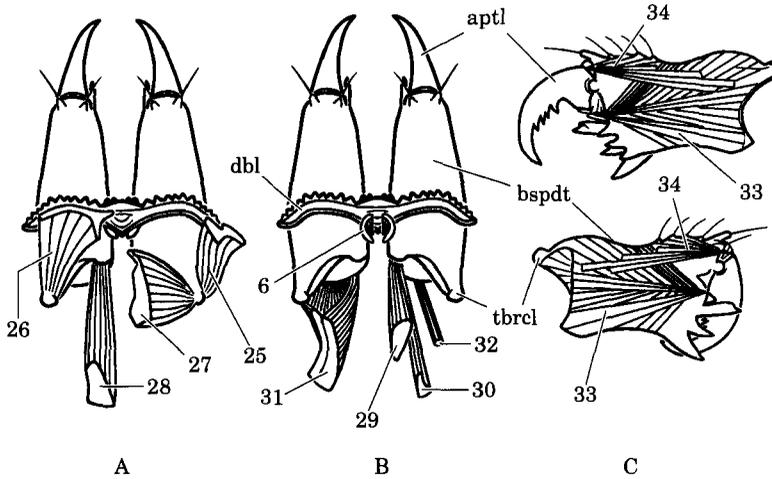


Figure 4. Skeleto-muscular anatomy of the chelicerae. A, B, dorsal views of chelicerae and carapacal doublure (dbl) showing arrangement of extrinsic muscles. C, anatomy of the left chelicera showing arrangement of intrinsic muscles. The upper figure shows a lateral view with chela open; the lower figure shows a medial view with chela closed. Numbered muscles are described in Table 1. Abbreviations: aptl, apotele; bspdt, basipodite; dbl, doublure; tbrcl, tubercle of lateral cheliceral process.

existence of two ontogenetically separate endoskeletal elements, the ectodermally derived structures containing chitin (e.g. apodemes, phragmata) and mesodermally derived tendinous structures (e.g., endosternite, intersegmental tendon system), and that ectodermally derived elements in one taxon could not be homologous with mesodermally derived elements in another (Cutler & Richards, 1974; Firstman, 1973). However, in comparing the endosternal, palpal and pharyngeal structures of spiders and whipscorpions, the simplest evolutionary scheme suggested that a series of pharyngeal, endosternal and extrinsic palpal muscles had shifted their attachment from the mesodermally derived endosternite to a cuticular process of the palpal coxa, probably via cuticularization of the endosternal tissue. If the ontogenetic criterion for establishing homology had been enforced, it would have been necessary to invoke multiple independent losses in one group of muscles and reacquisition of an equal number of anatomically similar muscles. However, by minimizing the use of evolutionary 'constraints' or 'laws' of transformation, the process of establishing homology may have been the first step in the discovery of an evolutionary process that might explain the origins of certain apodemes, phragmata and tentoria in arachnids and other arthropods.

RESULTS

Skeletal anatomy

This section provides a description of the skeletal anatomy of *Phrymus longipes*. The goal is to provide the reader with enough information to understand the descriptions of the muscles provided in Table 1 and is not intended as an exhaustive treatment.

More thorough treatments of various aspects of skeletomuscular anatomy of amblypygids can be found in Pocock (1902), Millot (1949), Weygoldt *et al.* (1972), Weygoldt (1996) and Shultz (1989).

Prosoma

The dorsal surface of the prosoma is covered by a single large sclerite, the carapace, that bears a pair of eyes on an anteromedial turret and two triads of lateral eyes (Fig. 1). The carapace doubles back anteriorly to form a doublure (Fig. 2A) which is evaginated anteroventrally to form a large conical projection (Fig. 3B). The surface topography of the carapace reflects the arrangement of the underlying musculature. Specifically, attachment sites of dorsal and dorsolateral endosternal suspensor muscles (muscle groups 17 and 18 in Table 1) are demarcated by distinct depressions, with the single central depression being the most prominent. These depressions occupy shallow 'valleys' which radiate laterally from the central depression, and these 'valleys' delimit roughly the borders of the attachment sites of the extrinsic appendicular muscles (Figs 2A, 9). The surface texture of the carapacial cuticle is rough (granular) in areas lacking muscle attachments, especially the region dorsal to the retracted chelicera and regions laterally adjacent to the central depression, where branches of the midgut caeca contact the carapace (Fig. 2A). Sites of muscular attachment tend to lack the granulation and have lighter or darker colour than the surrounding cuticle. These surface cuticular features are sufficient to identify the attachment sites of most carapacial muscles.

The ventral surface of the prosoma is formed by the prosomal sternum, the first opisthosomal sternite (metasternum), and the coxae of the palps and legs (Figs 1, 2C). The sternum is a sheet of cuticle with a complex pattern of ridges and grooves, but no muscles attach to it. It bears three heavily sclerotized protuberances along its median axis. The anterior protuberance is a large hollow process (labium or tritosternum) that projects anteriorly between the palpal coxae from the anterior margin of the sternum (Figs 1, 3B). The two other protuberances are much smaller and are located within the sternum (Figs 1, 2C). The posterior border of the sternum attaches to the more heavily sclerotized sternite of the first opisthosomal somite (metasternum), the lateral margins of which are fused to the medial margins of the coxae of the fourth leg pair (Figs 1, 2C). The sternum is attached to the proximoposterior margin of the coxa of each postcheliceral appendage via thin but heavily sclerotized bridges (Figs 1, 2C), each of which is hinged to allow movement of the coxa against the sternum.

The dorsal and ventral elements of the prosomal skeleton are joined by pliable cuticle, except for the anteromedial region between the palpal coxae and chelicerae (Figs 2C, 3B). Here the dorsomedial surfaces of the palpal coxae articulate with a complex structure formed by the consolidation of the labrum, epistome and epipharyngeal sclerite. The labrum is a small lobe of flexible cuticle that overhangs the mouth. It is attached proximally to a heavily sclerotized epistome, which is immovably fused dorsally to the epipharyngeal sclerite and has movable articulations laterally with the palpal coxae. The epipharyngeal sclerite is L-shaped in lateral perspective, with a frontal bar projecting anterodorsally between the chelicerae and an epipharyngeal process projecting posteriorly into the prosomal haemocoel. There is also a very thin vertical plate spanning the angle between the frontal bar and epipharyngeal process. The frontal bar attaches to the posterior margin of the carapacial doublure via a tough but pliable cuticular ligament.

TABLE 1. Muscles of the whipspider *Phrynus longipes*. The Table summarizes information from 115 muscle groups. The name proposed for each muscle group is derived from anatomical characteristics (for example, origin, insertion, fibre direction) rather than on 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 *Mastigoproctus giganteus* (Thelyphonida) based on information derived from an earlier study (Shultz, 1993)

No.	Name	Description	Proposed function and evolution	Proposed homologue in <i>Mastigoproctus</i>
<i>Labral, Pharyngeal and Double Muscles</i>				
1	Labral m.	Paired. Arises dorsally from lateral margin of epistome; passes ventrally; inserts on floor of labral cavity (i.e. roof of preoral chamber). Pair is separated posteriorly by muscle 2 (Figs 3, 14).	Probably functions as a dilator of the preoral chamber. May be antagonistic to cuticular elasticity or haemolymph pressure.	3
2	Anterior dorsal extrinsic precerebral pharyngeal m.	Paired. Arises dorsally from base of epipharyngeal sclerite; passes ventrally; inserts on anterior part of precerebral pharynx. Pair separated posteriorly by muscle 3 (Figs 3, 14).	Probably functions as a dorsal dilator of the anterior region of the precerebral pharynx.	4
3	Posterior dorsal extrinsic precerebral pharyngeal m.	Paired. Arises from ventral surface of posterior process of epipharyngeal sclerite; passes ventrally; inserts broadly along dorsal surface of precerebral pharynx. Its fibres interdigitate with those of muscle 5 (Figs 3, 5, 14).	Probably functions as a dorsal dilator of the precerebral pharynx.	7
4	Lateral extrinsic precerebral pharyngeal m.	Paired. Arises laterally from medial margin of palpal coxa; passes medially to posteromedially; inserts on lateral wall of precerebral pharynx. Its fibres interdigitate with those of muscle 5 (Figs 3, 5, 14).	Probably functions as a lateral dilator of the precerebral pharynx.	5, 6
5	Intrinsic precerebral pharyngeal m.	Bands of muscle fibres surrounding precerebral pharynx interdigitating dorsally with fibres of muscle 3 and laterally with fibres of muscle 4. Precerebral pharyngeal lumen is Y-shaped in cross section with two dorsal folds and one ventral fold. Muscle 5 attaches to pharynx at external apex of each fold (Fig. 3).	Probably functions as a constrictor of the precerebral pharynx.	10
6	Double m.	Paired. Arises from medial process of posteromedial margin of anterior double of carapace; passes dorsally; inserts on carapace at base of medial eye turret. Optic nerves pass between pair posteriorly (Figs 2-4).	Function unclear. May act to stabilize the anterior region of the carapace, especially the medial eye turret, against displacements of the carapace caused by action of the extrinsic pharyngeal, cheliceral, palpal and leg muscles.	11 (medial head)

7	Anterolateral tergo-epipharyngeal m.	Paired. Arises from anteromedial region of carapace posterolateral to muscle 6; passes ventromedially; inserts on anterior ventral surface of midsagittal plate of epipharyngeal sclerite (Figs 2, 3, 14).	May rotate epipharyngeal apparatus at epistome-coxa articulation. See Discussion and Fig. 14 for details.	11 (lateral head)
8	Anteromedial tergo-epipharyngeal m.	Paired. Arises dorsally from anterior midline of carapace medial to muscle 27; passes ventrally; inserts on dorsal surface of basal portion of epipharyngeal sclerite anterior to insertion of muscle 9 (Figs 2, 3, 14).	May rotate epipharyngeal apparatus at epistome-coxa articulation. See Discussion and Fig. 14 for details.	8
9	Posterior tergo-epipharyngeal m.	Paired. Arises along anterior carapace midline anterior to central carapace depression; passes anteroventrally; inserts on posterior half of midsagittal plate of epipharyngeal sclerite. Separation between carapace attachments is an asymmetrical line (Figs 2, 3, 14).	May rotate epipharyngeal apparatus at epistome-coxa articulation. See Discussion and Fig. 14 for details.	9
10	Dorsal extrinsic postcerebral pharyngeal m.	Paired. Arises from carapace along anterior transverse groove of central depression just anterior to origin of muscle 17 _{av} ; passes ventrally to ventroposteriorly; inserts on dorsal surface of postcerebral pharynx (Figs 2, 3, 5).	Probably functions as a dorsal dilator of the postcerebral pharynx.	Absent
11	Anterolateral extrinsic postcerebral pharyngeal m.	Paired. Arises from anterior endosternal horn near base of tendinous process of muscle 17 _{av} ; passes posteromedially; inserts on anterolateral walls of postcerebral pharynx (Fig. 5). Fibres interdigitate with those of muscle 14.	Probably functions as a lateral dilator of the postcerebral pharynx.	Absent
12	Posterolateral extrinsic postcerebral pharyngeal m.	Paired. Arises from dorsal surface of endosternite; passes medially; inserts on lateral walls of postcerebral pharynx posterior to muscle 11 (Fig. 5). Fibres interdigitate with those of muscle 14.	Probably functions as a lateral dilator of the postcerebral pharynx.	Absent
13	Ventral extrinsic postcerebral pharyngeal m.	paired. Arises broadly from dorsal surface of endosternite ventral and lateral to postcerebral pharynx; passes medially to anterodorsally; inserts on ventral surface of posterior part of postcerebral pharynx (Figs 3, 5).	Probably functions in the mechanical stabilization and dilation of the postcerebral pharynx. Cross section of postcerebral pharynx is X-shaped in the region where muscle 13 attaches; it is Y-shaped anteriorly.	Absent
14	Intrinsic postcerebral pharyngeal m.	Bands of muscle fibres surrounding postcerebral pharynx interdigitating with fibres of muscles 10–13. Postcerebral pharyngeal lumen is Y-shaped in cross section anteriorly and arrangement of muscle 14 is similar to that of muscle 5 of precerebral pharynx (Fig. 3). Lumen is X-shaped in cross section posteriorly, with two dorsal folds and two ventral folds. Muscle 14 attaches on pharynx at external apex of each fold. Not illustrated, but see Millot (1949: fig. 336).	Probably functions as a constrictor of the postcerebral pharynx.	Absent

TABLE 1. *continued*

No.	Name	Description	Proposed function and evolution	Proposed homologue in <i>Mastigoproctus</i>
<i>Intersgmental tendon system and endosternite</i>				
15	Suboral endosternal m.	Paired. Arises from end of a long, thin tendon arising from ventral surface of anterior endosternal horn near suspensor process of postoral somite III; passes anteromedially; inserts on oval suboral sclerite located in proximal region of enditic membrane of palpal coxa (Figs 2,3).	Probably invaginates the enditic membrane. The suboral endosternal muscle is present in many chelicerates, including <i>Limulus</i> , palpigrades, spiders, scorpions and <i>Mastigoproctus</i> .	12
16	Endosternopalpal m.	Paired. Arises from anterior margin of dorsal suspensor tendon of postoral somite III; passes anteriorly between muscles 39 and 40; inserts on posteromedial surface of palpal coxa (Figs 3, 5).	Probably functions as a longitudinal tensor of the endosternite. See text for an explanation of the incorporation of endosternal elements into the palpal coxa.	30?
17	Dorsal endosternal suspensor m.	Paired. Postoral somites III-VII. Arises from tendinous endosternal processes ($17_{III}-17_{VII}$), or dorsal surface of endosternite (17_{VII}); passes dorsally; inserts on carapace ($17_{III}-17_{VI}$) or tergite of first opisthosomal somite (17_{VII}). Carapacial attachments are indicated externally by depressions (Figs 1-3, 5, 12).	Probably functions in dorsoventral compression of the prosoma with consequent increase in haemocoel pressure, as in <i>Mastigoproctus</i> (Shultz, 1991). Probably corresponds to dorsoventral muscles of the opisthosoma (muscle 21).	13
18	Dorsolateral endosternal suspensor m.	Paired. Postoral somites III-V, VII. Arise from tendinous processes projecting dorsolaterally from endosternite; insert on carapace ($18_{III}-18_{V}$) or flexible cuticle posterior to coxa 4 (18_{VII}). Carapacial attachments are indicated externally by depressions (Figs 1-3, 5, 12).	Probably functions in dorsoventral compression of the prosoma with consequent rise in haemocoel pressure (Shultz, 1991). Probably corresponds to lateral muscles of the opisthosoma (muscle 22).	14
19	Ventral endosternal suspensor m.	Paired. Somites III, V-VII. Muscles 19_V to 19_{VII} arise from ventral surface of endosternite; pass ventrally; insert on posteromedial margin of coxa associated with anteriorly adjacent somite (Fig. 2). Thus ventral endosternal suspensor of somite V inserts on coxa of somite IV. Muscle 19_{III} appears to arise and insert within palpal coxa (Figs 2, 3, 6).	Probably functions in dorsoventral compression of the prosoma. A similar arrangement is present in <i>Mastigoproctus</i> , although the ventral suspensor of somite IV is present and retains a plesiomorphic sternal attachment. Coxal attachment in other ventral suspensors probably represents a synapomorphy of Pedipalpi.	15
20	Endosternotergal m.	Paired. Arises from dorsal surface of endosternite medially adjacent to tendinous processes of muscle 17_{VI} ; passes dorsoanteriorly; inserts along anterolateral margin of first opisthosomal tergite (Figs 5, 12).	Probably functions as a levator of the opisthosoma at the prosoma-opisthosoma juncture.	16
21	Dorsoventral m.	Paired. Postoral somites VIII-XIV. Arises from opisthosomal tergite; passes ventrally; inserts on ventral intersgmental tendon (21_{IX} and 21_X) or sternite (21_{XI} , 21_{XIV}) (Fig. 12).	Probably functions in dorsoventral compression of opisthosoma. Probably corresponds to muscle 17 in the prosoma.	17

22	Lateral m.	Paired. Postoral somites IX, X. Muscle 22 _{LX} arises from intersegmental tendon associated with muscle 21 ₆₅ ; passes laterally dorsal to booklung; inserts on dorsal region of pleural membrane. Muscle 22 _L arises from tendon shared with muscle 23E near anterior process of sternite X; passes laterally dorsal to booklung; inserts on dorsal region of pleural membrane (Fig. 12).	Function unclear. Probably corresponds to muscle 18 in the prosoma.	Absent
23	Ventral longitudinal m.	Paired. Spans somites VII–XVIII. Strongly muscularized in anterior region (VII–XI) and represented by a weakly muscularized tendinous sheet (aponeurosis) posteriorly to pygidial region, where it is again well muscularized (Fig. 12).	Probably functions in longitudinal compression of anterior part of opisthosoma and dorsal flexion of pygidium. Probably corresponds to the prosomal endosternite.	18 (73–75)?
24	Dorsal longitudinal m.	Paired. Spans somites VII–XVIII; strongly muscularized in anterior region (VII–XI) and represented by a weakly muscularized tendinous sheet (aponeurosis) posteriorly to pygidial region, where it becomes well muscularized again (Fig. 12).	Probably functions in longitudinal compression of anterior part of opisthosoma and ventral flexion of pygidium.	67 (70–72)?
<i>Chelicerai muscles</i>				
25	Anterolateral lateral tergocheliceral m.	Arises on anterolateral margin of carapace; passes posteriorly with medial margin passing deep to muscle 26; inserts on lateral surface of lateral cheliceral process (Figs 2, 4).	Probably functions as a protractor of the chelicera.	49
26	Anteromedial lateral tergocheliceral m.	Arises along anterior margin of carapace; passes posteriorly to posterolaterally with posterior portion passing deep to muscle 27; inserts on tubercle of lateral process of cheliceral basipodite (Figs 2, 4).	Probably functions as a protractor of the chelicera and as weak abductor of distal part of chelicera.	50
27	Posteromedial lateral tergocheliceral m.	Arises along anteromedial surface of carapace just lateral to muscle 8; passes laterally to posterolaterally; inserts on tubercle of lateral process of cheliceral basipodite (Figs 2, 4).	Probably functions in abduction of the distal part of chelicera and perhaps ventromedial rotation of dorsal part of chelicera.	51
28	Dorsal tergocheliceral m.	Arises from middle region of carapace anterior to central depression; passes anteriorly; inserts on dorsal margin of cheliceral basipodite (Figs 2, 4).	Probably functions as a retractor of the chelicera.	55
29	Anterior medial tergocheliceral m.	Arises from anteromedial surface of carapace lateral to muscle 9; curves ventrally around muscle 28; inserts along medial margin of cheliceral basipodite (Figs 2, 4).	Probably functions in depression of the distal part of the chelicera and perhaps ventrolateral rotation of the dorsal part of the chelicera.	56
30	Posterior medial tergocheliceral m.	Thin, straplike. Arises from carapace between muscles 28 and 31; passes anteromedially; inserts on medial margin of basipodite near muscle 29 (Figs 2, 4).	May function in retraction of chelicera.	54?

TABLE 1. *continued*

No.	Name	Description	Proposed function and evolution	Proposed homologue in <i>Mastigophactus</i>
31	Posterior tergocheliceral m.	Arises on carapace medial to muscle 17 <i>m</i> ; passes anteroventrally; inserts broadly along ventral margin of cheliceral basipodite. Origin on carapace appears to have two heads but is actually one head folded longitudinally. Medial part has 'dark' fibres and arises from ventral margin of cheliceral basipodite; lateral part has 'light' fibres and inserts along ventral margin of cheliceral process (Figs 2, 4).	May function in retraction of chelicera and depression of distal tip. Other functions possible.	57 (52+53)?
32	Endosterno-cheliceral m.	Thin, straplike. Arises from anterior margin of tendinous process of first endosternal suspensor muscle (17 <i>m</i>); passes anteriorly; inserts on ventral margin of cheliceral basipodite in association with tendinous insertion of muscle 31 (Fig. 4).	Probably functions in retraction of chelicera.	58
33	Ventral cheliceral basipodite-apotele m.	Arises broadly from cheliceral basipodite; inserts on ventral plagula of apotele (Fig. 4).	Closes cheliceral chela.	59
34	Dorsal cheliceral basipodite-apotele m.	Arises from distodorsal and proximodorsal surfaces of cheliceral basipodite; inserts on dorsal margin of apotele (Fig. 4).	Opens cheliceral chela.	60
<i>Palpal muscles</i>				
35	Palpal anteromedial tergocoxal m.	Arises from anterolateral region of carapace between muscles 36 and 37; passes ventromedially; attaches to anterior coxal process via stout tendon (Figs 2, 3, 5, 14).	May function in abducting the inner (pharyngeal) portion of the palpal coxae and adducting the outer (enditic) portion, thereby assisting in dilation of the precerebral pharynx (Fig. 14). Probably corresponds to pedal muscles 65-67.	Absent
36	Palpal anterolateral tergocoxal m.	Arises from anterolateral region of carapace; passes anteroventrally; inserts on distoanterior margin of palpal coxa (Figs 2, 5).	May function in levation of palpal coxa. Probably corresponds to pedal muscles 68-69.	28
37	Palpal posterolateral tergocoxal m.	Arises from carapace lateral to muscle 17 <i>m</i> ; passes anteroventrolaterally; inserts on distoposterior margin of palpal coxa (Figs 2, 5).	May function in levation of palpal coxa and abduction of enditic portion of palpal coxa. Probably corresponds to pedal muscles 71-73.	Absent
38	Palpal lateral tergocoxal m.	Arises from anterolateral surface of carapace; passes ventrally; inserts on inner distoposterior surface of palpal coxa (Figs 2, 5, 14).	May function in levation of palpal coxae and in abduction of the enditic processes (Fig. 14). Probably corresponds to pedal muscle 74.	29
39	Palpal anteromedial endosternocoxal m.	Arises from anterior surface of tendinous process of first dorsal endosternal suspensor muscle (17 <i>m</i>); passes anteriorly to anterolaterally; inserts on posteromedial surface of palpal coxa medial to muscle 16 (Figs 3, 5).	May function in abducting the pharyngeal part of the palpal coxa and adducting the enditic part. Probably corresponds to pedal muscle 75.	Absent

40	Palpal anterolateral endosternocoxal m.	Arises from anterolateral surface of tendinous process of first dorsal endosternal suspensor muscle (17 _{III}); passes anterolaterally; inserts broadly on dorsal surface of anterior coxal flange medial to muscle 36 (Figs 3, 5). Arises from dorsoproximal surface of coxa proximal to coxa-femur muscle (49); passes ventrally; inserts on posteromedial margin of coxa near 19 _{III} and medial flange (Figs 3, 6).	Function unclear. Probably corresponds to pedal muscle 76.	Absent
41	Palpal medial coxal m.	Arises from ventral surface of endosternite at first tendinous process; passes ventrolaterally; inserts along posterior margin of coxa proximal to muscle 43 (Figs 3, 6). Arises from dorsoposterior surface of palpal coxa near muscle 44; passes posteriorly to posterolaterally; inserts on posterior margin of coxa distally adjacent to muscle 37 (Figs 3, 6).	Function unclear. Probably corresponds to pedal muscle 77.	32
42	Palpal posterior endosternocoxal m.	Arises from ventral surface of endosternite at first tendinous process; passes ventrolaterally; inserts along posterior margin of coxa proximal to muscle 43 (Figs 3, 6). Arises from dorsoposterior surface of palpal coxa near muscle 44; passes posteriorly to posterolaterally; inserts on posterior margin of coxa distally adjacent to muscle 37 (Figs 3, 6).	Function unclear. Probably corresponds to pedal muscle 78.	31
43	Palpal intracoxal m.	Arises from dorsoposterior surface of coxa and inferior surface of anterior coxal flange; passes distally; inserts on dorsal margin of trochanter (Fig. 6). Arises broadly from posterior surface of palpal coxa; passes distally deep to muscle 44; inserts on dorsal margin of trochanter (Fig. 6).	Function unclear. The homologue of this muscle in <i>Mastigophictus</i> was mistakenly regarded as a modified endosternocoxal muscle (Shultz, 1993), but it is apparently a serial homologue of the intracoxal muscle of the legs (<i>i.e.</i> pedal muscle 79 in <i>Phytinus</i>).	33
44	Palpal anterior dorsal coxa-trochanter m.	Arises broadly from dorsoposterior surface of coxa and inferior surface of anterior coxal flange; passes distally; inserts on dorsal margin of trochanter (Fig. 6). Arises broadly from posterior surface of palpal coxa; passes distally deep to muscle 44; inserts on dorsal margin of trochanter (Fig. 6).	Probably functions as a levator/abductor of the coxa-trochanter joint. Probably corresponds to pedal muscle 80.	35
45	Palpal posterior dorsal coxa-trochanter m.	Arises broadly from posterior surface of palpal coxa; passes distally deep to muscle 44; inserts on dorsal margin of trochanter (Fig. 6).	Probably functions as a levator/abductor of the coxa-trochanter joint. Probably corresponds to pedal muscle 81.	35
46	Palpal anterior ventral coxa-trochanter m.	Four principal heads. Arises broadly from enditic (46A), dorsal (46B-C) and ventral (46D) surfaces of coxa; inserts on anteroventral process of trochanter (Fig. 6). Two principal heads. Arises from dorsal (47A) and midventral (47B) surfaces of trochanter; inserts on midventral rim of trochanter (Fig. 6).	Probably functions as an adductor/depressor of the coxa-trochanter joint. Probably corresponds to pedal muscle 82.	36
47	Palpal middle ventral coxa-trochanter m.	Two principal heads. Arises from dorsal (47A) and midventral (47B) surfaces of trochanter; inserts on midventral rim of trochanter (Fig. 6).	Probably functions as a depressor/adductor of the coxa-trochanter joint. Probably corresponds to pedal muscle 83.	?
48	Palpal posterior ventral coxa-trochanter m.	Arises broadly from ventroposterior surface of coxa; passes distally; inserts on ventroposterior margin of trochanter (Fig. 6).	Probably functions as a depressor/adductor of the coxa-trochanter joint. Probably corresponds to pedal muscle 84.	37
49	Palpal coxa-femur m.	Arises broadly along anterior phragma of coxa; passes distally through trochanter without attachment; inserts on posterior dorsal margin of femur (Figs 6, 7). Arises broadly on dorsoanterior surface of trochanter; passes distally; inserts along dorsal margin of femur (Fig. 6).	Probably functions as a levator of the trochanter-femur joint. Probably corresponds to pedal muscle 85.	38 (coxal head)
50	Palpal dorsal trochanter-femur m.	Arises broadly on dorsoanterior surface of trochanter; passes distally; inserts along dorsal margin of femur (Fig. 6).	Probably functions as a levator of the trochanter-femur joint. Probably corresponds to pedal muscle 86.	38 (trochanteral head)
51	Palpal small ventral trochanter-femur m.	Arises from distoanterior surface of trochanter just proximal to anterior trochanter-femur condyle; inserts on immediately adjacent ventral margin of femur (Fig. 7).	Probably functions as a minor depressor of the trochanter-femur muscle. Probably corresponds to pedal muscle 89.	39?

continued

TABLE 1. *continued*

No.	Name	Description	Proposed function and evolution	Proposed homologue in <i>Mastigoproctus</i>
52	Palpal large ventral trochanter-femur m.	Arises broadly from morphologically ventral and anteroventral surfaces of trochanter; passes distally; inserts broadly along morphologically ventral margin of femur. Not illustrated, but similar to pedal muscle 90 (Fig. 11).	Probably functions as a depressor of the trochanter-femur joint. Probably corresponds to pedal muscle 90.	39
53	Palpal long femur-patella m.	Arises from two principal heads along morphologically posterior margin of femur; passes distally; inserts on a tendon that terminates on patellar plagula (Fig. 7).	Probably functions as a flexor of femur-patella joint. Probably corresponds to femoral heads of pedal muscle 93.	41 (femoral heads)
54	Palpal anterior femur-patella m.	Arises broadly on morphologically anterior surface of femur; passes distally; inserts on morphologically anteroventral margin of patella (Fig. 7).	Probably functions as a flexor of the femur-patella joint. Probably corresponds to pedal muscle 94.	42a
55	Palpal posterior femur-patella m.	Arises on morphologically distoposterior surface of femur; passes distally; inserts on morphologically posteroventral margin of patella (Fig. 7).	Probably functions as a flexor of the femur-patella joint. Probably corresponds to pedal muscle 95.	42b
56	Palpal femur-tibia m.	Long, straplike. Symmetrically paired about palpal nerve. Arises from morphologically distodorsal surface of femur; passes distally along morphologically ventral surface of patella; inserts on tibial rim on either side of tibial plagula (Fig. 7).	Probably functions as a flexor of the patella-tibia joint. Morphologically anterior head (56A) probably corresponds to pedal muscle 96.	43 (femoral heads)
57	Palpal long patella-tibia m.	Symmetrically paired about palpal nerve. Arises broadly from morphologically anterior, posterior and dorsal surfaces of patella; passes distally; insert on tibial plagula via long tendon (Fig. 7).	Probably functions as a flexor of the patella-tibia joint. May correspond to pedal muscles 97 and 98.	43 (patellar heads)
58	Palpal anterior patella-tibia m.	Arises from morphologically distoanterior surface of patella; inserts broadly on morphologically anterior margin of tibia (Fig. 7).	Probably functions as a flexor of the patella-tibia joint. No apparent corresponding pedal muscle.	44a
59	Palpal posterior patella-tibia m.	Arises from morphologically distoposterior surface of patella; inserts broadly on morphologically posterior margin of tibia (Fig. 7).	Probably functions as a flexor of the patella-tibia joint. No apparent corresponding pedal muscle.	44b
60	Palpal patella-tarsus m.	Straplike. Symmetrically paired about palpal nerve. Arises from morphologically distodorsal surface of patella; passes distally along morphologically ventral surface of tibia; inserts ventrally on tarsal rim (Fig. 7).	Probably functions as a flexor of the tibia-tarsus joint. No apparent corresponding pedal muscle.	45 (patellar heads)
61	Palpal long tibia-tarsus m.	Arises from morphologically proximoposterior and dorsal surfaces of tibia; passes distally; inserts on long tendon that attaches to tarsal plagula (Fig. 7).	Probably functions as a flexor of the tibia-tarsus joint. Probably corresponds to pedal muscle 99.	45 (tibial heads)

62	Palpal anterior tibia-tarsus m.	Arises from morphologically disoanterior surface of tibia; inserts on morphologically anterior margin of terminal article (tarso-apotele) (Fig. 7).	Probably functions as a flexor of the tibia-tarsus joint. No corresponding pedal muscle.	46a
63	Palpal posterior tibia-tarsus m.	Arises from morphologically distoposterior surface of tibia; inserts on morphologically posterior margin of terminal article (tarso-apotele) (Fig. 7).	Probably functions as a flexor of the tibia-tarsus joint. No corresponding pedal muscle.	46b
64	Palpal tibia-apotele m.	Arises from morphologically distoposterior surface of tibia; passes distally; inserts on heavily sclerotized tendon that attaches distally along morphologically ventral surface of terminal article (tarso-apotele) (Fig. 7).	Probably functions as a flexor of the tibia-tarsus joint. Probably corresponds to pedal muscle 100.	Absent
<i>Pedal muscles</i>				
65	Lateral anteromedial tergocoxal m.	Legs 1-4. Arises from lateral surface of carapace; passes medially; inserts on apex of anterior coxal process via narrow tendon (Figs 2, 8, 15). Composed of 'light' fibres.	'Light' fibres and high mechanical advantage at sternocoxal articulation suggest function in rapid, powerful coxal depression (Fig. 15). Muscles 65-67 appear to be autapomorphic functional specializations of a single primitive muscle, the anteromedial tergocoxal muscle (Shultz, 1991). Probably corresponds to palpal muscle 35.	19
66	Medial anteromedial tergocoxal m.	Legs 2-4. Arises from carapace medial to origin of corresponding muscle 67; passes ventrolaterally; inserts on medial margin of anterior coxal process. (Figs 2, 8, 15). Composed of 'light' fibres.	'Light' fibres and high mechanical advantage at sternocoxal articulation indicate function in rapid, powerful coxal depression (Fig. 15). Muscles 65-67 appear to be autapomorphic functional specializations of a single primitive muscle, the anteromedial tergocoxal muscle (Shultz, 1991). Probably corresponds to palpal muscle 35.	19
67	Anterior anteromedial tergocoxal m.	Legs 1-4. Arises from carapace adjacent to origin of corresponding lateral anteromedial tergocoxal muscle; passes ventromedially; inserts broadly on anterior face of anterior coxal process (Figs 2, 8, 15). Composed of 'dark' fibres.	Probably functions as a levator of the sternocoxal joint. Muscles 65-67 appear to be autapomorphic functional specializations of a single primitive muscle, the anteromedial tergocoxal muscle (Shultz, 1991). Probably corresponds to palpal muscle 35.	19
68	Lateral anterolateral tergocoxal m.	Legs 1-4. Arises from lateral region of carapace; inserts narrowly on disoanterior margin of coxa (Figs 2, 8, 15). Composed of 'light' fibres.	'Light' fibres and high mechanical advantage at sternocoxal joint suggest function in rapid, powerful coxal levation/rotation (Fig. 15). Muscles 68 and 69 appear to be autapomorphic functional specializations of a single primitive muscle, the anterolateral tergocoxal muscle (Shultz, 1991). Probably corresponds to palpal muscle 36.	20
69	Medial anterolateral tergocoxal m.	Legs 1-4. Arises broadly along carapace; passes ventrolaterally; inserts broadly on anterior margin and anterior surface of coxa (Figs 2, 8, 15). Composed of 'dark' fibres.	Probably functions in levation/rotation of sternocoxal joint (Fig. 15). Muscles 68 and 69 appear to be autapomorphic functional specializations of a single primitive muscle, the anterolateral tergocoxal muscle (Shultz, 1991). Probably corresponds to palpal muscle 36.	20

TABLE 1. *continued*

No.	Name	Description	Proposed function and evolution	Proposed homolog in <i>Mastigoproctus</i>
70	Posteromedial tergocoxal m.	Legs 1-2. Arises from lateral surface of carapace, typically in association with tergocoxal muscles from posteriorly adjacent leg; passes ventroanteriorly; inserts narrowly on posterior margin of coxa (Figs 2, 8). Composed of 'light' fibres.	'Light' fibres and orientation suggest that this muscle functions as rapid rotator of the sternocoxal joint. No apparent corresponding muscle in palp.	21
71	Lateral posterolateral tergocoxal m.	Legs 1-4. Arises from lateral region of carapace; inserts narrowly on distoposterior margin of coxa (Figs 2, 8). Composed of 'light' fibres.	'Light' fibres and high mechanical advantage at sternocoxal joint indicate function in rapid levation/rotation of the sternocoxal joint; probably antagonistic to muscles 65 and 66. Muscles 71, 72 and 73 appear to be autapomorphic functional specializations of a single muscle, the posterolateral tergocoxal muscle (Shultz, 1991). Probably corresponds to palpal muscle 37.	22
72	Medial posterolateral tergocoxal m.	Legs 1-4. Arises broadly along the carapace; passes ventrolaterally; inserts broadly on posterior margin and posterior surface of coxa (Figs 2, 8). Composed of 'dark' fibres.	Probably functions as a levator/rotator of the sternocoxal joint. Muscles 71, 72 and 73 appear to be autapomorphic functional specializations of a single muscle, the posterolateral tergocoxal (Shultz, 1991). Probably corresponds to palpal muscle 37.	22
73	Posterior posterolateral tergocoxal m.	Legs 1-4. Arises from lateral surface of carapace; passes anteroventrally; inserts on posterolateral margin of coxa near muscle 71 (Figs 2, 8). Composed of 'light' fibres.	Probably functions as a rotator of the sternocoxal joint. Muscles 71, 72 and 73 appear to be autapomorphic functional specializations of a single muscle, the posterolateral tergocoxal (Shultz, 1991). Probably corresponds to palpal muscle 37.	22
74	Lateral tergocoxal m.	Legs 1-4. Arises from lateral region of carapace; passes posteroventrally; inserts narrowly on posterolateral surface of coxa (Figs 2, 8). Composed primarily of 'dark' fibres.	Probably corresponds to palpal muscle 37. Probably functions as a levator/rotator of the sternocoxal joint. Apparently homologous to the pleurotergal muscle of <i>Mastigoproctus</i> and the <i>musculi laterales</i> of spiders, both of which insert on the pleural membrane adjacent to coxa rather than on coxa directly. Probably corresponds to palpal muscle 38.	23
75	Anteromedial endosternocoxal m.	Legs 1-4. Arises from ventral surface of endosternite; passes ventrally or ventrolaterally; inserts on anteromedial coxal margin medial to muscle 76 (Fig. 9).	Function uncertain. Probably corresponds to palpal muscle 39.	24
76	Anterolateral endosternocoxal m.	Legs 1-4. Arises from ventral surface of endosternite; passes dorsolaterally; inserts broadly on medial margin anterior coxal process (Fig. 9).	Function uncertain. Probably corresponds to palpal muscle 40.	25

77	Posteromedial endosternocoxal m.	Legs 1-4. Arises from ventral surface of endosternite; passes ventrally or ventrolaterally; inserts on medial or posteromedial coxal margin medial to muscle 78 (Fig. 9). Legs 1-4. Arises from the ventral surface of endosternite; passes laterally; inserts on posterior coxal margin at posterior attachment of muscle 79 (Fig. 9). Legs 2-4. Sheet of parallel fibres. Arises from posterior surface of anterior coxal process; passes posteriorly to posterodistally; inserts on proximal posterior margin of coxa in association with attachment of corresponding muscle 78 (Fig. 9).	Function uncertain. Probably corresponds to palpal muscle 41.	26
78	Posterolateral endosternocoxal m.	Legs 1-4. Arises from the ventral surface of endosternite; passes laterally; inserts on posterior coxal margin at posterior attachment of muscle 79 (Fig. 9).	Function uncertain. Probably corresponds to palpal muscle 42.	26
79	Intracoxal m.	Legs 2-4. Sheet of parallel fibres. Arises from posterior surface of anterior coxal process; passes posteriorly to posterodistally; inserts on proximal posterior margin of coxa in association with attachment of corresponding muscle 78 (Fig. 9).	Function of this muscle is unclear, but it may provide facultative rigidity to the anterior coxal process. This muscle may be synapomorphic for Pedipalpi, as it has yet to be observed in other arachnids. Probably corresponds to palpal muscle 43.	34
80	Anterior dorsal coxa-trochanter m.	Legs 1-4. Arises by one or two heads from proximoanterior surface of coxa at base of anterior process; passes distally; inserts on anterior dorsal margin of trochanter (Fig. 10).	Probably functions as a levator/promotor of the coxa-trochanter joint. Probably corresponds to palpal muscle 44.	35
81	Posterior dorsal coxa-trochanter m.	Legs 1-4. Arises from posterior surface of coxa near margin; passes distally; inserts on dorsal margin of trochanter posterior to muscle 80 (Fig. 10).	Probably functions as a levator of the coxa-trochanter joint. Probably corresponds to palpal muscle 45.	35
82	Anterior ventral coxa-trochanter m.	Legs 1-4. Arises broadly from ventroanterior surface of coxa; passes distally; inserts on apex on subcondylar process of trochanter (Fig. 10).	Probably functions as a promotor/depressor of the coxa-trochanter joint. Probably corresponds to palpal muscle 46.	36
83	Middle ventral coxa-trochanter m.	Legs 1-4. Arises broadly from ventral surface of coxa; passes distally; inserts on ventral plagula of trochanter (Fig. 10).	Probably functions as a depressor of the coxa-trochanter joint. Probably corresponds to palpal muscle 47.	?
84	Posterior ventral coxa-trochanter m.	Legs 1-4. Arises broadly from the posterior surface of coxa; passes distally; inserts on posterior margin of trochanter (Fig. 10).	Probably functions as a remotor/depressor of the coxa-trochanter joint. Probably corresponds to palpal muscle 48.	37
85	Coxa-femur m.	Legs 1-4. Arises broadly along anterior phragma of coxa; passes distally through trochanter without attachment; inserts on morphologically posterior dorsal margin of femur (Fig. 11).	Probably functions as a levator of the trochanter-femur joint. Probably corresponds to palpal muscle 49.	38 (coxal head)
86	Anterior dorsal trochanter-femur m.	Legs 1-4. Arises on morphologically dorsoanterior surface of trochanter; passes distally; inserts on morphologically anterior part of dorsal margin of the femur (Fig. 11).	Probably functions as a levator of the trochanter-femur joint. Probably corresponds to palpal muscle 50.	38 (trochanteral head)
87	Posterior dorsal trochanter-femur m.	Legs 1-4. Arises on morphologically anterior surface of trochanter; passes distally; inserts on morphologically posterior part of the dorsal margin of femur with muscle 85 (Fig. 11).	Probably functions as a levator of trochanter-femur joint. Probably corresponds to palpal muscle 50.	38 (trochanteral head)

continued

TABLE 1. *continued*

No.	Name	Description	Proposed function and evolution	Proposed homologue in <i>Mastigoproctus</i>
88	Long dorsal trochanter-femur m.	Legs 2-4. Arises from morphologically proximal anterior surface of trochanter between muscles 86 and 87; passes distally; inserts without tendons on morphologically dorsal surface of proximal one-fourth of femur (Fig. 11).	Probably functions as a levator of the trochanter-femur joint. Shultz (1989) has suggested that this muscle is associated with the apomorphically undifferentiated basifemur-telofemur joint. No corresponding palpal muscle.	Absent
89	Anterior ventral trochanter-femur m.	Legs 1-4. Arises on morphologically anterior surface of trochanter just proximal to origin of muscle 92; passes transversely across trochanteral haemocoel; inserts on inner surface of posterior subcondylar flange via cuticular tendon (Fig. 11).	Function uncertain. Probably corresponds to palpal muscle 51.	39?
90	Posterior ventral trochanter-femur m.	Legs 1-4. Arises broadly from morphologically ventral and posteroventral surfaces of trochanter; passes distally; inserts on margins of posterior subcondylar flange on morphologically posteroventral margin of femur (Fig. 11).	Probably functions as a depressor of the trochanter-femur joint. Probably corresponds to palpal muscle 52.	39
91	Long transverse trochanter-femur m.	Legs 2-4. Arises on morphologically anteroventral surface of trochanter; passes distoposteriorly, arching over trochanteral head of muscle 93; inserts broadly along morphologically posterior surface of femur (Fig. 11).	Function uncertain. Because the muscle acts near the level of the condyles and arches over the trochanteral head of muscle 93, it may function in adjusting orientation of this muscle with respect to the condylar axis. No corresponding palpal muscle.	Absent
92	Short transverse trochanter-femur m.	Legs 1-4. Arises on morphologically disoanterior surface of trochanter near anterior trochanter-femur condyle; passes distoposteriorly, arching over muscle 91 (where present) and trochanteral head of muscle 93; inserts on morphologically proximal posterior surface of femur near posterior trochanter-femur condyle (Fig. 11).	Function uncertain. Because the muscle acts at the level of the condyles and arches over trochanteral head of muscle 93, it may function in adjusting orientation of 93 with respect to the condylar axis. No corresponding palpal muscle.	40
93	Trochanterofemur-patella m.	Legs 1-4. Trochanteral head (93A) arises from distally; inserts along proximal third of a stout tendon that terminates distally on patellar plagula. Femoral heads (93B) arise from proximal and morphologically posterior surfaces of femur; insert distally along tendon shared with trochanteral head (Fig. 11).	Probably functions as a depressor of the trochanter-femur joint and flexor of femur-patella joint. May function in forming an internal mechanical linkage that coordinates movement at these two joints (Shultz, 1992). Probably corresponds to palpal muscle 53.	41
94	Anterior femur-patella m.	Legs 1-4. Arises from elongate oval region on morphologically anterodorsal surface of distal fourth of femur (visible externally); passes distally; inserts on patellar plagula (Fig. 11).	Probably functions as a flexor of the femur-patella joint. Probably corresponds to palpal muscle 54.	42a

95	Posterior femur-patella m.	Legs 1-4. Arises from two elongate oval regions on morphologically disoposterior surface of femur (visible externally); passes distally; inserts on morphologically ventral and posterior margins of patella (Fig. 11). Legs 1-4. Arises from extreme distodorsal surface of femur; passes distally deep to 97 in close association with main pedal nerve; inserts via narrow tendon on morphologically proximoanterior rim of tibia (Fig. 11).	Probably functions as a flexor of the femur-patella joint. Probably corresponds to palpal muscle 55.	42b
96	Femur-tibia m.	Legs 1-4. Arises broadly from morphologically posterior and distodorsal surface of patella; inserts on tibial 'plagula' (Fig. 11).	Functions with muscles 97 and 98 to break ventral tibial rim during autotomy (Weygoldt, 1984). Probably functions as a flexor of the patella-tibia joint in leg 1. Probably corresponds to palpal muscle 56A.	43 (femoral head)
97	Anterior patella-tibia m.	Legs 1-4. Arises broadly from morphologically anterior surface of patella; inserts on tibial 'plagula' (Fig. 11).	Functions with muscles 96 and 98 to break ventral tibial rim during autotomy (Weygoldt, 1984). Probably functions as a flexor of the patella-tibia joint in leg 1. Probably corresponds to palpal muscle 57A.	44a
98	Posterior patella-tibia m.	Legs 1-4. Arises broadly from morphologically anterior surface of patella; inserts on tibial 'plagula' (Fig. 11).	Functions with muscles 96 and 97 to break ventral tibial rim during autotomy (Weygoldt, 1984). Probably functions as a flexor of the patella-tibia joint in leg 1. Probably corresponds to palpal muscle 57B.	44b
99	Tibia-tarsus m.	Legs 1-4. Leg 1: Arises from distal tibiomerres; passes distally; inserts on morphologically ventral rim of first tarsomere. Legs 2-4: Arises primarily along morphologically ventral surface of distal half of tibia; passes distally to insert on long tendon; tendon inserts on inferior rim of tarsus (Fig. 11). Legs 2-4. Arises from proximal one-half of tibia; passes distally; inserts on long tendon that extends distally to insert on the lower margin of the apotele. Tendon is free in tibial haemocoel but is constrained to morphologically ventral surface of tarsus (Fig. 11). Legs 2-4. Arises broadly from surfaces of basitarsus and extreme distal surface of tibia; passes distally; fibres insert on tendon that attaches to the superior surface of apotele. Muscle fibres do not extend much beyond the basitarsus-telotarsus	Probably functions as a flexor of the tibia-tarsus joint and, perhaps, the intratibial joints. Probably corresponds to palpal muscle 61.	46
100	Tibia-apotele m.	Legs 2-4. Arises from proximal one-half of tibia; passes distally; inserts on long tendon that extends distally to insert on the lower margin of the apotele. Tendon is free in tibial haemocoel but is constrained to morphologically ventral surface of tarsus (Fig. 11). Legs 2-4. Arises broadly from surfaces of basitarsus and extreme distal surface of tibia; passes distally; fibres insert on tendon that attaches to the superior surface of apotele. Muscle fibres do not extend much beyond the basitarsus-telotarsus	Probably functions as a depressor of tarsus-apotele joint and, perhaps, as a flexor of the intratibia, tibia-tarsus, and intratarsus joints. Probably corresponds to palpal muscle 64.	47 (tibial head)
100	Tibiotarsus-apotele m.	Legs 2-4. Arises broadly from surfaces of basitarsus and extreme distal surface of tibia; passes distally; fibres insert on tendon that attaches to the superior surface of apotele. Muscle fibres do not extend much beyond the basitarsus-telotarsus	Probably functions as a levator of the tarsus-apotele joint. No corresponding palpal muscle.	48
<i>Opisthosomal muscles</i>				
102	Dorsal pleural m.	Paired, sheetlike, somites VIII-XV. Arises from lateral surface of tergite; passes ventrolaterally; inserts on adjacent pleural fold (Fig. 12). Fibres arising near anterolateral corner of tergite are especially well developed and form a discrete bundle.	Probably regulates opisthosomal volume and expansion of pleural membranes.	61

TABLE 1. *continued*

No.	Name	Description	Proposed function and evolution	Proposed homologue in <i>Mastigoproctus</i>
103	Middle pleural m.	Paired, sheathlike, somites VIII–XV. Arises from one pleural fold; inserts on adjacent pleural fold (Fig. 12).	Probably regulates opisthosomal volume and expansion of pleural membranes.	62
104	Ventral pleural m.	Paired, sheathlike, somites VIII–XV. Arises from lateral surface of sternite; passes dorsolaterally; inserts on adjacent pleural fold (Fig. 12). Fibres arising near anterolateral corner of sternite are especially well developed and form a discrete bundle.	Probably regulates opisthosomal volume and expansion of pleural membranes.	63
105	Intergeral m.	Unpaired (except where divided by pericardium), sheathlike, somites VIII–XVIII. Superficial to muscle 24. Arises broadly along anterior margin of tergite or intertergal fold; passes anteriorly; inserts on anteriorly adjacent tergite (Fig. 12).	Probably regulates opisthosomal volume and expansion of intertergal membranes.	64
106	Anterior carapacotergal m.	Paired. Arises from posterior margin of central depression of carapace; passes posteriorly deep to muscle 107; inserts near anterior margin of first opisthosomal tergite (Figs 2, 12).	Probably functions in levating the opisthosoma at the prosoma-opisthosoma juncture.	65
107	Posterior carapacotergal m.	Paired. Arises from carapacial midline just posterior to origin of muscle 106; passes posteriorly superficial to muscle 106; inserts near anterior margin of first opisthosomal tergite (Figs 2, 12).	Probably functions in levating the opisthosoma at the prosoma-opisthosoma juncture.	66
108	Intersternal m.	Unpaired (except where associated with sternite VIII), sheathlike, somites VIII–XVIII. Superficial to muscle 23. Arises broadly along anterior margin of sternite or intersternal fold; passes anteriorly; inserts on anteriorly adjacent sternite (Fig. 12).	Probably regulates opisthosomal volume and expansion of intersternal membranes.	68
109	Intrinsic pygidial m.	Paired. Arises anteriorly from lateral surface of second pygidial ring (somite XVIII); passes distally; inserts on lateral margins of anal operculum (tergite XVIII) (Fig. 12).	Probably functions in closing the anal operculum (tergite XVIII).	76?
110	Venopericardiac m.	Paired. Segmental distribution not determined. Arises from ventrolateral surface of pericardium; passes ventrolaterally; inserts on pulmonary sinus or lateral sternal surface. Not illustrated.	Probably functions as a dilator of pericardium and pulmonary sinuses.	69
111	Anterior extrinsic opercular m.	Paired. Anterior (genital) operculum only. Arises from sternite VIII; passes ventrally; inserts on anteromedial surface of anterior operculum (Fig. 13).	Probably functions in levating the anterior operculum.	82

112	Posterior extrinsic opercular m.	Paired. Anterior and posterior opercula. Muscle 112_{iii} arises from intersegmental tendon associated with muscle 21_{iv} ; passes ventromedially; inserts on anterior (genital) operculum between gonopod and booklung (Figs 12, 13). Muscle 112_{iv} arises from ventral surface of anterior sternal process associated with muscle 21_{x} ; passes ventroanteriorly; inserts on medial region of posterior operculum (Fig. 12).	Muscle 112_{iii} probably functions in levating the operculum. Function of muscle 112_{iv} is unclear.	83
113	Anterior extrinsic telopodial m.	Paired. Male only. Arises from sternite VIII; passes ventroposteriorly; inserts on posterior midventral region of telopodite (gonopod) (Fig. 13).	Probably functions in retracting and depressing the distal part of telopodite (gonopod). Probably corresponds to a retractor muscle of the ventral eversible sacs of postoral somite IX in the amblypygid <i>Charon grayi</i> (see Results).	86
114	Posterior extrinsic telopodial m.	Paired. Male only. Arises broadly along anterolateral surface of anterior operculum anterior to book lung; passes dorsally and medially; inserts along ventrolateral margin of telopodite (gonopod) (Fig. 13).	Probably functions in retracting and levating the distal part of the telopodite (gonopod). Probably corresponds to a retractor muscle of the ventral eversible sacs of postoral somite IX in the amblypygid <i>Charon grayi</i> (see Results).	87, 88
115	Intrinsic telopodial m.	Paired. Both sexes. Arises from internal surfaces of telopodite (gonopod); inserts on walls of spermatophore-forming chamber in male and clawlike sclerite in female. Not illustrated but see Weygoldt, Weisemann & Weisemann (1972).	Functions in forming the spermatophore in male and in opening the spermatophore in female (Weygoldt <i>et al.</i> , 1972).	Absent

Appendages

The terminological conventions used by Couzijn (1976) and Shultz (1989) were devised to facilitate comparisons among arachnids and are used here to describe the skeletomuscular system of the palps and legs. According to this convention, the postcheliceraral appendages of the hypothetical primitive chelicerate are envisioned as projecting laterally from the body, with the joints arranged so that the principal intrinsic movements occur within a vertical plane. This model is approximated in several arachnid taxa (e.g. most spiders), but in most arachnids, the appendages or elements of the appendages have undergone some degree of torsion about their long axis. In amblypygids, for example, the hypothetical 'primitive' anterior face of the palp and legs corresponds to the anatomical dorsal or anterodorsal face due to proximal torsion during evolution. Consequently, throughout this paper, the term 'morphologically anterior surface' refers to the anatomy of the model organism, while the term 'anatomically anterior surface' refers to a direct description of the animal. It is hoped that this convention will avoid confusion when comparing homologous appendicular structures within an organism and between organisms.

Each walking leg consists of seven podomeres, namely the coxa, trochanter, femur, patella, tibia, tarsus (divided into a proximal basitarsus and distal telotarsus), and apotele (Figs 1, 11). The proximoanterior margin of each coxa extends dorsally and forms an anterior coxal process, which is relatively small in leg 1 but very large in the remaining legs (Fig. 2C). A shelf-like anterior coxal flange projects dorsoposteriorly along the distoanterior coxal margin and intersects the distal edge of the anterior coxal process (Fig. 2C). The coxae of legs 1–3 attach to the prosomal sternum by means of a sclerotized bridge; the coxa of leg 4 is fused with the first opisthosomal sternite (Fig. 2C). The coxa-trochanter joint is fairly complex. The anterior rim of the trochanter pivots against a coxal process, and the joint is formed posteriorly by a two sclerites that interact in a complicated manner to allow a variety of movements.

The joints of the more distal podomeres are simpler (Fig. 11). The trochanter-femur joint in all legs and tarsus-apotele joint in legs 2–4 have bicondylar hinges equipped with antagonistic muscles (Figs 10, 11). The femur-patella, tibia-tarsus, intratibial and intratarsal joints have dorsal hinge articulations (Fig. 11). The femur-patella and tibia-tarsus joints are operated by flexor muscles, but the intratibial and intratarsal joints have no muscles of their own, although the tendons of muscles associated with more distal joints may span them (Fig. 11). The patella-tibia joint (Fig. 11) is essentially immobile and is specialized for autotomy (Weygoldt, 1984). The skeletal anatomy of leg 1 differs from the others in being antenniform, having many intratibial and intratarsal joints, and lacking the apotele (Fig. 1).

The palps are specialized for prey capture, and their coxae are an important component of the feeding apparatus. Although highly modified, the palpal coxae have the same basic organization as the pedal coxae (Figs 2C, 5, 6). An anterior coxal process arises from the anterior margin of the coxa in association with a well-developed anterior coxal flange (Figs 2C, 5B, 6). However, rather than projecting dorsally into the prosomal haemocoel, as in the legs, the anterior process of the palp is folded over the dorsal surface of the coxa such that its distal end is positioned medially, where it is strongly attached to the medial part of the coxa just dorsal to the origin of the lateral pharyngeal dilator muscles (muscle 4 in Table 1). Consequently, the true dorsal surface of the coxa can only be observed by removing the thin anterior coxal process (Fig. 5B). The process is connected strongly to the coxa only at its proximal and distal ends such that a narrow space exists between the ventral surface of the process and dorsal surface of the coxa.

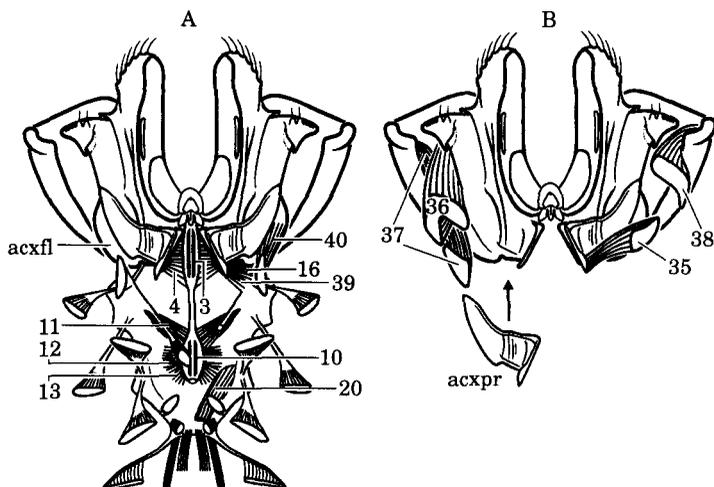


Figure 5. Dorsal view of the pharyngeal and palpal regions. The epipharyngeal apparatus has been cut away at its connection to the epistome (cf. Fig. 2C). A, dorsal view of the arrangement of the precerebral pharynx and postcerebral pharynx. The dorsal dilators (muscles 3 and 10) have been removed, though their attachments on the dorsal pharyngeal surface are depicted. B, dorsal view of the palpal coxae, tergocoxal muscles and labrum. The anterior coxal process (acxpr) has been removed from the left coxa. In the intact condition, the process arises along the proximal margin of the anterior coxal flange (acxfl) and is folded over the dorsal surface of the coxa. It is attached secondarily to the medial surface of the coxa. Numbered muscles are described in Table 1. Abbreviations: acxfl, anterior coxal flange; acxpr, anterior coxal process.

This space opens to the external environment ventral to the chelicerae and tends to collect and trap dirt and debris.

The distal part of the palp is formed by the trochanter, femur, tibia and a composite tarsus + apotele and is equipped with an elaborate arrangement of spines (Figs 1, 7). The arrangement of the coxa-trochanter joint is similar to that of the legs (Fig. 6). The trochanter-femur joint has a bicondylar hinge operated by antagonistic muscles, and the remaining joints have hinge articulations operated by flexor muscles (Fig. 7).

Each chelicera is composed of two articles, the distal apotele (fang) and proximal basipodite (Figs 2B, 4). The joint between these articles has a bicondylar hinge operated by antagonistic muscles (Fig. 4). The lateral margin of the basipodite projects posteriorly into the prosomal haemocoel farther than the dorsal, medial or ventral margins and thus forms a cheliceral process. There is a sclerotized tubercle or knob near the terminus of this process that serves as an attachment site for extrinsic muscles. The chelicera lacks a sclerotized attachment to the body but is connected by a sleeve of pliable cuticle that permits a range of motions, primarily protraction-retraction and levation-depression. Physical constraints imposed by the carapacial doublure, palpal coxae and frontal bar of the epipharyngeal sclerite appear to limit the amount of rotation the chelicera can undergo.

Opisthosoma

The opisthosoma is composed of 12 somites, representing postoral somites VII to XVIII, each with a dorsal tergite and ventral sternite (Figs 1, 12). The tergites and sternites are joined laterally by a pleural membrane with longitudinal folds.

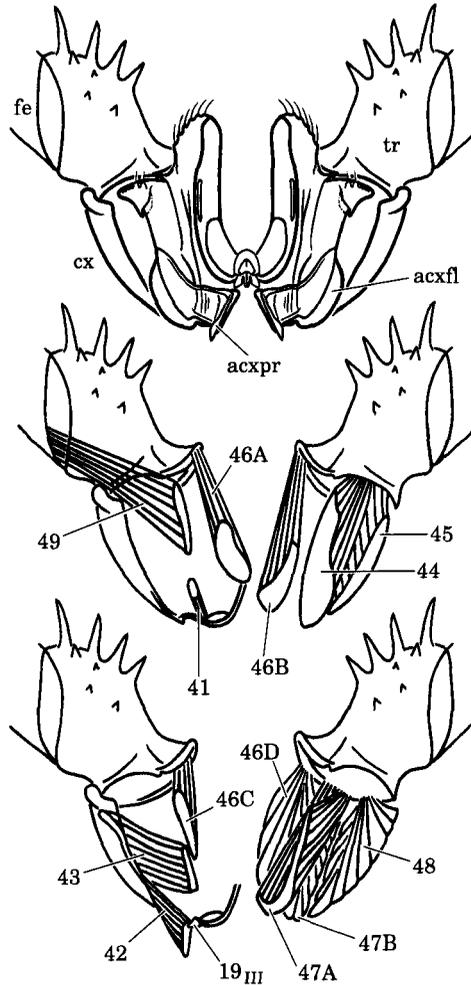


Figure 6. Dorsal view of the skeletomuscular anatomy of the palpal trochanters and coxae. Numbered muscles are described in Table 1. Abbreviations: acxfl, anterior coxal flange; acxpr, anterior coxal process; cx, coxa; fe, femur; tr, trochanter.

The last three somites are narrow in comparison with the rest of the opisthosoma, forming a pygidium. The anus opens at the terminus of the pygidium.

The first tergite is narrower than the posteriorly adjacent tergites, and its posterior margin fits within the modified anterior margin of the second tergite. It is possible that by locking and unlocking this arrangement, the animal can decrease or increase flexibility in this region. The remaining tergites are relatively simple sclerotized plates.

The ventral surface of the opisthosoma is formed by two opercula (postoral somites VIII and IX) and 12 sternites (postoral somites VII–XVIII) (Figs 1, 12B). The anterior and posterior opercula are large plates that form the anterior ventral surface of the opisthosoma (Figs 1, 12, 13). Results from previous work on the whipscorpion *Mastigoproctus* (Shultz, 1993) indicated that these two sclerites are modified appendages of postoral somites VIII and IX. The anterior (genital operculum) is the larger and bears a pair of booklungs on its posterolateral margins (Figs 1, 12B, 13). A pair of gonopods is located between the booklungs in both sexes (Fig.

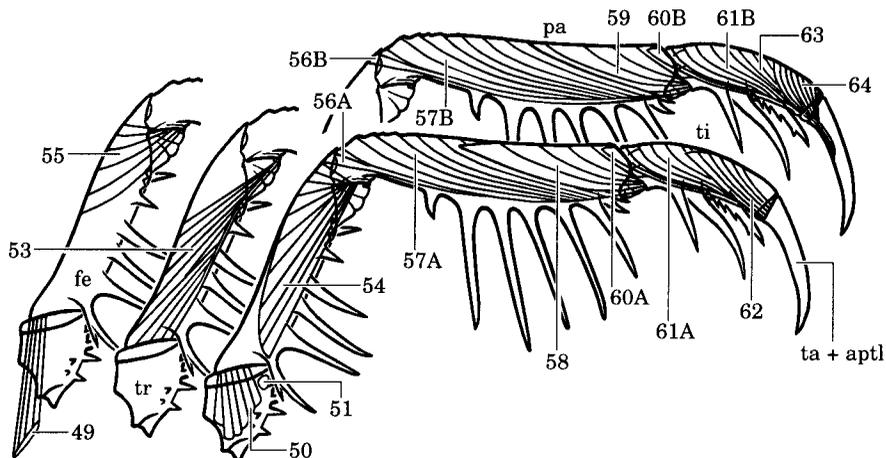


Figure 7. Skeletomuscular anatomy and intrinsic muscles of the palp distal to the coxa. The morphologically anterior surface is depicted. Numbered muscles are described in Table 1. Abbreviations: aptl, apotele; fe, femur; pa, patella; ta, tarsus; ti, tibia; tr, trochanter.

14). The posterior operculum also has a pair of booklungs on its posterolateral margin, but there are no structures reminiscent of the gonopods in *Phrynus*. However, a pair of eversible ventral sacs is present in many other amblypygids (Weygoldt, 1996). The skeletomuscular anatomy of these sacs is treated below for one species, *Charon grayi* (Charontidae), and the results are consistent with the hypothesis that the ventral sacs of the posterior operculum are metameric homologues to the gonopods of the anterior operculum.

As noted above, the first opisthosomal sternite is a functional component of the prosoma, where it is fused with the medial margins of the fourth leg pair (Figs 1, 2C). The second sternite is represented by a pair of weakly sclerotized sclerites embedded within the pliable cuticle forming the ventral connection between the first opisthosomal sternite and the anterior (genital) operculum (Fig. 12B). This sternite is generally obscured from external view, as it occupies the roof of a fold that overlies the anterior margin of the anterior operculum. The third sternite forms the roof of the pregenital chamber and is difficult to see without dissection (Fig. 12B). Its presence is indicated only by muscular attachments and is otherwise undifferentiated from the pliable cuticle that constitutes the surfaces of the pregenital chamber. In contrast to the condition in the *Mastigoproctus*, in which the third sternite is sclerotized (Shultz, 1993), no sclerotized element of this sternite was observed in *Phrynus longipes*, *P. marginemaculatus* or *Charon grayi*. The fourth sternite is composed of a broad plate with two internal processes projecting from its anterior margin (Fig. 12B). Most of the remaining sternites are relatively simple plates (Figs 1, 12).

Muscular anatomy

The principal findings of the survey of skeletal muscles in *Phrynus longipes* have been summarized in Table 1. Each of the 115 muscles or muscle groups was numbered, given an anatomical name, and described. Representatives of virtually all muscle groups are illustrated in Figures 2–13. In the few cases where illustrations are not

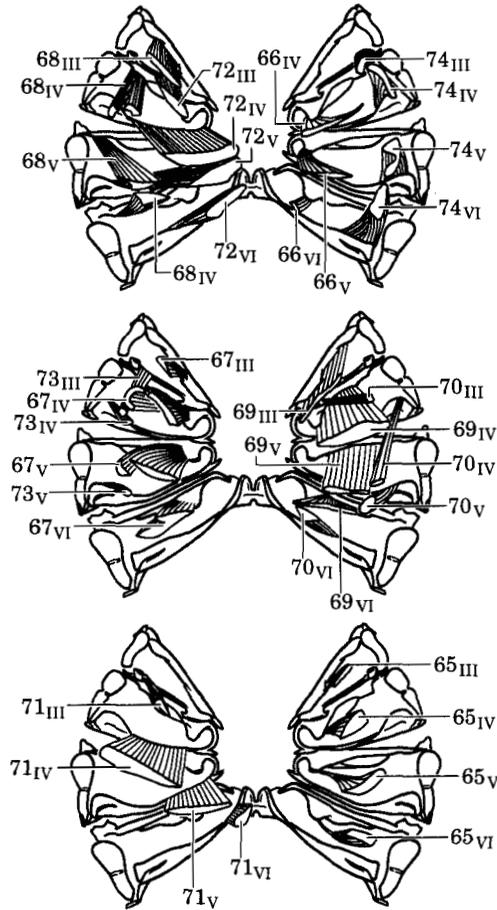


Figure 8. Dorsal view of the pedal coxae and their tergocoxal muscles (62–71). Compare to Fig. 2. Numbered muscles are described in Table 1.

provided, references are given to relevant illustrations in other sources. Table 1 also includes comments on the evolutionary, functional and phylogenetic significance of each muscle group and lists possible homologues described in an earlier study of the giant whipscorpion *Mastigoproctus giganteus* (Uropygi) (Shultz, 1993).

Skeletomuscular anatomy of eversible ventral sacs in Charon grayi

The posteromedial margin of the posterior operculum in many amblypygid species is equipped with a pair of eversible ventral sacs, but these are absent in *Phrynus* and its close relatives (Weygoldt, 1996). The sacs are apparently everted by haemocoelic pressure and retracted by muscles (Kaestner, 1968), and there is evidence that they function in osmotic or ionic regulation (Alberti *et al.*, 1992). Because the precise arrangement of the muscles has yet to be recorded, the skeletomuscular anatomy of the eversible ventral sacs of an adult female specimen of *Charon grayi* (Charontidae) was examined.

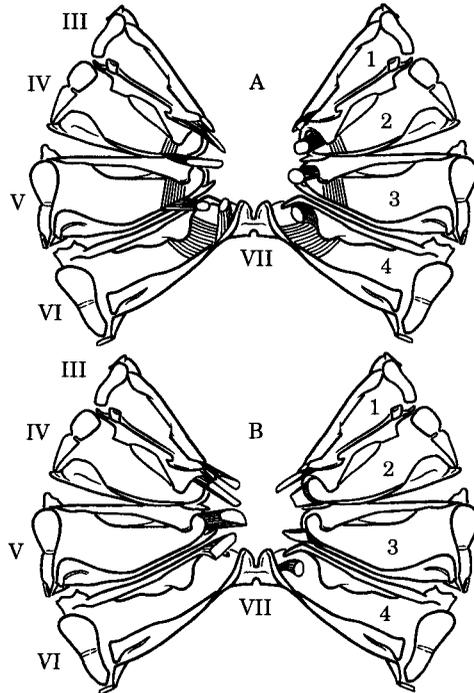


Figure 9. Dorsal view of the pedal coxae and the endosternocoxal and intracoxal muscles. Postoral somites are labeled with Roman numerals and pedal coxae are labeled with Arabic numerals. A, Posterolateral endosternocoxal muscles (78) are depicted on the left, the anterolateral endosternocoxal muscles (76) on the right, and the intracoxal muscles (79) on both sides. B, Anteromedial endosternocoxal muscles (75) on the left and the posteromedial endosternocoxal muscles (77) on the right. Note that the lateral margins of sternite VII are fused with the medial margins of the fourth pedal coxae.

The retracted ventral sacs are indicated externally by a pair of oval sclerites on the posteromedial margin of the posterior operculum. Each sclerite articulates with the operculum via a broad hinge along its anterior margin. When a ventral sac is everted, the sclerite pivots more than 90° at the hinge and thereby forms a sclerotized anterior rim on the otherwise pliable sac. Dissection of the posterior and anterior opercula revealed that each sac is equipped with two extrinsic muscles. Both extrinsic muscles attach broadly on the internal surface of the sac. The fibres of the more ventral muscle pass anterolaterally medial to the posterior extrinsic opercular muscle (muscle 112_{IX} in Table 1) and the booklung of the posterior operculum. The muscle attaches to the posterior operculum near its anterior margin. The fibres of the more dorsal muscle pass anteriorly and insert on the intersegmental tendon associated with the dorsoventral muscle of postoral somite IX (muscle 21 in Table 1) along with the posterior extrinsic opercular muscle of the anterior operculum (muscle 112_{VIII} in Table 1), and the ventral longitudinal muscles (muscle 23 in Table 1).

The ventral sacs and their extrinsic muscles appear to correspond to the gonopods and associated extrinsic muscles in the male *Phrynus longipes* (Fig. 12). Both ventral sacs and gonopods are appendage-like structures that occupy a posterior median location in their respective opercula and are positioned medial to the posterior extrinsic opercular muscles and booklungs. Both also have two extrinsic muscles, one attaching laterally on the associated operculum (i.e. muscle 114 in Table 1) and

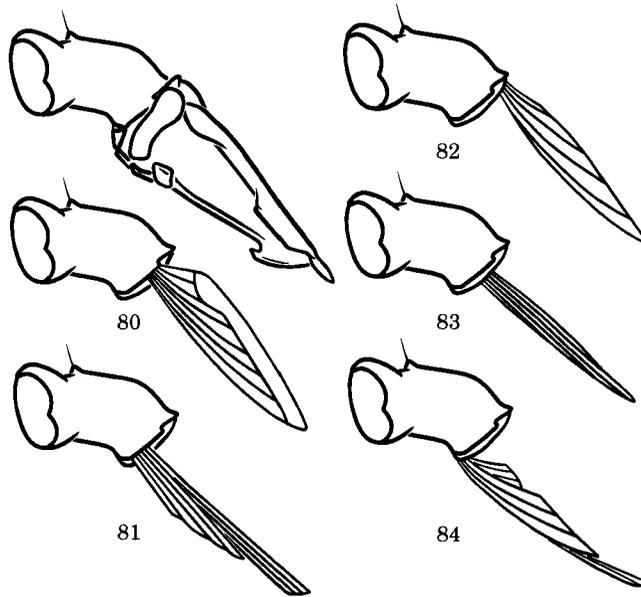


Figure 10. Dorsal view of the coxa-trochanter muscles of the first leg. Numbered muscles are described in Table 1.

one passing anteriorly to attach near the dorsoventral muscle of the anteriorly adjacent somite (i.e. muscle 113 in Table 1). Consequently, it is reasonable to hypothesize that the eversible ventral sacs of the posterior operculum in *Charon grayi* are serial homologues of the gonopods of the anterior operculum.

DISCUSSION

Evolutionary and functional morphology of the precerebral pharyngeal complex

The Pedipalpi (Orders Amblypygi, Schizomida, Thelyphonida) are united by presence of a highly derived precerebral pharyngeal complex. The ingestive apparatus in Araneae and Palpigradi appears to have retained a more primitive organization and thus provides information for understanding the evolution of the pharynx in Pedipalpi. The preoral chamber in Araneae and Palpigradi is formed dorsally by a large labrum and ventrally by a sternal projection (labium or tritosternum) (Milot, 1942, 1943; Snodgrass, 1948). The labral complex attaches to the medial margins of the palpal coxa via the epistome, which gives rise to a pair of pharyngeal dilator muscles. Additional dorsal pharyngeal dilator muscles arise from an interchelicer epipharyngeal sclerite and the carapacial midline; a pair of lateral dilator muscles arise from the endosternite; and a ventral dilator arises from the anterior sternal region (Milot, 1942, 1943; Meyer, 1981; Marples, 1983). This organization is probably symplesiomorphic rather than synapomorphic for these two orders given the apparent monophyly of Araneae, Amblypygi, Schizomida and Thelyphonida as well as the presence of many similar features in other arachnid orders (Snodgrass, 1948). Consequently, this arrangement was probably present in an ancestor of Pedipalpi.

The feeding apparatus of extant Pedipalpi, as represented by *Phrynus* (present

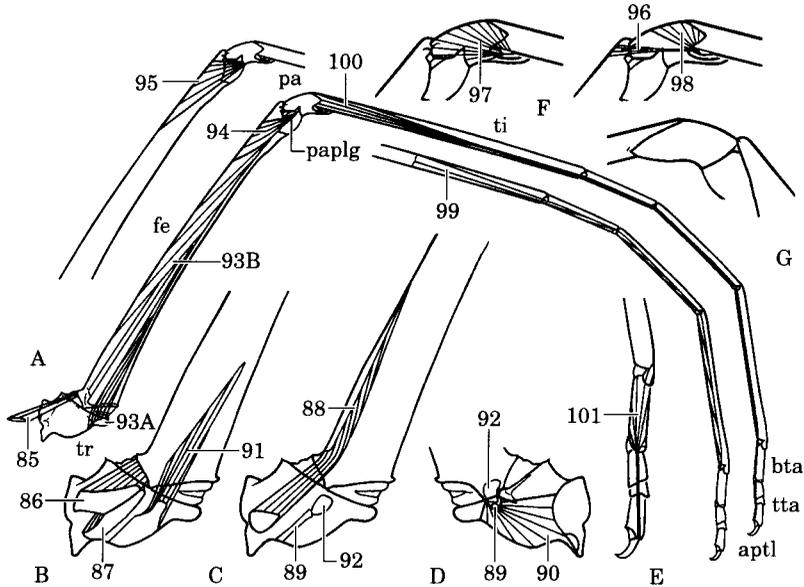


Figure 11. Skeletomuscular anatomy and intrinsic muscles of the fourth walking leg. A, view of morphologically anterior surface of leg distal to coxa. B, C, enlarged view of morphologically anterior surface of trochanter and proximal portion of femur. D, enlarged view of morphologically posterior surface of trochanter and proximal portion of femur. E, enlarged view of morphologically anterior surface of apotele, tarsus and distal region of tibia. F, enlarged views of morphologically anterior surface of patella and adjacent podomeres. G, enlarged view of morphologically posterior surface of patella and adjacent podomeres to show arrangement of skeletal elements only. Only anterior and posterior attachment sites are depicted for muscles 89 and 92. Numbered muscles are described in Table 1. Abbreviations: aptl, apotele; bta, basitarsus; fe, femur; pa, patella; paplg, patellar plagula; ti, tibia; tr, trochanter; tta, telotarsus.

study) and *Mastigoproctus* (Shultz, 1993), has undergone several important evolutionary modifications. First, the palpal coxae replaced the labium in forming the posterior wall of the preoral chamber. Second, the epistome fused proximally with the epipharyngeal sclerite, which is greatly enlarged and now projects posteriorly into the prosoma to provide an expanded surface for the attachment of a set of pharyngeal dilator muscles (muscle 3 in Table 1). Third, the lateral dilator muscles that arose primitively from the endosternite shifted to the medial surfaces of the palpal coxae along with several other endosternal muscles. Finally, the precerebral pharyngeal dilators arising from the carapace and sternum were lost. The principal effect of these modifications was to generate a new skeletal framework from the epipharyngeal sclerite and palpal coxae that apparently functions solely for the attachment of dilator muscles of the precerebral pharynx (Shultz, 1993).

Despite the many derived similarities between the 'new' precerebral pharyngeal complex in *Phrynus* and *Mastigoproctus*, the functional morphology of this apparatus appears to differ in these two taxa. In *Mastigoproctus*, the epistome-epipharyngeal complex and palpal coxae are largely immobile with respect to the precerebral pharynx, and thus forms a rigid framework that allows powerful contraction of the pharyngeal dilator muscles that would not affect other skeletomuscular elements, such as the endosternite or carapace (Shultz, 1993). In contrast, the epistome-epipharyngeal complex and palpal coxae in *Phrynus* can move with respect to the

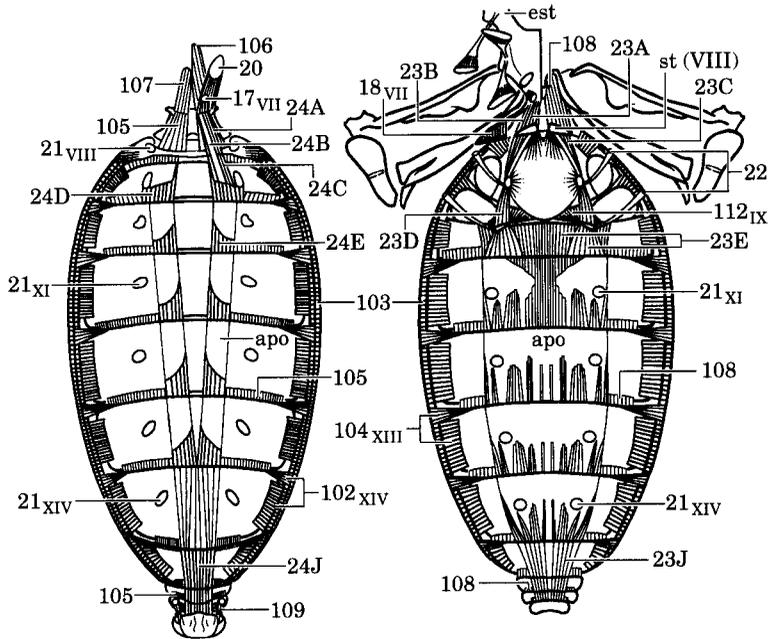


Figure 12. Muscles of the opisthosoma based on frontal section. Only attachment sites of dorsoventral muscles (21) are shown. A, ventral view of inner surface of dorsal skeleton. B, dorsal view of inner surface of ventral skeleton. Numbered muscles are described in Table 1. Abbreviations: apo, aponeurosis of dorsal and ventral longitudinal muscles (23, 24); est, endosternite; st, sternite. Number of postoral somite is indicated in Roman-numeral subscripts.

precerebral pharynx, and, in fact, their organization indicate that they serve as lever arms which allow another set of muscles to assist the dorsal and lateral pharyngeal dilators in expanding the pharyngeal lumen (Fig. 14). Unlike the situation in thelyphonids, the epistome in *Phrynus* articulates with the palpal coxae, and the palpal coxae are capable of independent movement, because the only sclerotized linkage between them is the sublateral sclerite that forms the floor of the preoral chamber (Fig. 14). Contraction of the tergo-epipharyngeal muscles (muscles 7–9 in Table 1) would likely cause an anterodorsal rotation about the epistome-coxa articulation, thus assisting the dorsal pharyngeal dilator muscle in expanding the pharynx. Similarly, contraction of the palpal anterolateral tergo-coxal muscles would likely abduct the medial margins of the palpal coxae thus assisting the lateral pharyngeal dilator muscles (muscle 4 in Table 1). This model of ingestion in Amblypygi offers a functional explanation for the peculiar organization of the anterior coxal process of the palp. However, more comparative analyses, especially of Schizomida, Araneae, and Palpigradi, will be required to determine whether the dynamic ‘amblypygid’ pharyngeal complex or the static ‘uropygid’ complex is closer to the primitive condition for Pedipalpi.

Evolutionary and functional morphology of the pedal coxae

A preliminary survey of chelicerate skeletomuscular anatomy (Shultz, 1990, 1991) has revealed a common and probably primitive arrangement of extrinsic coxal

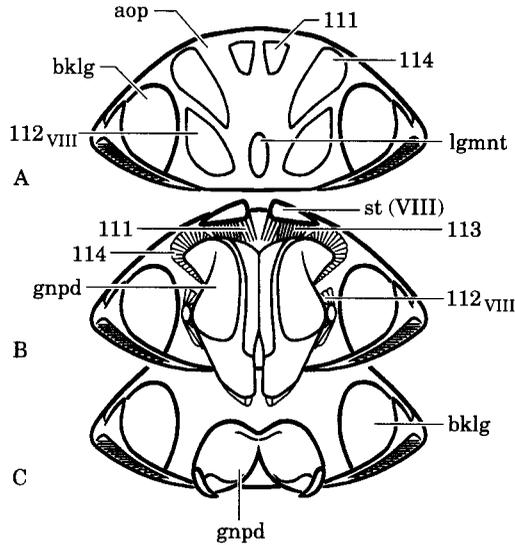


Figure 13. Skeletomuscular anatomy of the anterior (genital) operculum. A, dorsal view of the interior ventral surface of the male genital operculum showing attachment sites of principal muscles. B, dorsal view of the male genital region showing arrangement of male gonopods and muscles. The dorsal surface of the pregenital chamber (sternite IX and its associated soft cuticle) have been removed (c.f. Fig. 12). C, dorsal view of the posterior margin of the female genital operculum showing the gonopods. Numbered muscles are described in Table 1. Abbreviations: aop, anterior (genital) operculum; bklg, booklung; gnpd, gonopod; lgmnt, ligament attaching gonopod to operculum; st, sternite.

muscles in Arachnida. Specifically, each coxa attaches broadly to the prosoma via flexible cuticle; there appears to have been no sclerotized articular structure uniting the coxae with the carapace or sternum. Each coxa was apparently equipped with nine extrinsic muscles consisting of four endosternocoxal muscles that originated on the endosternite and five tergocoxal muscles that originated on the carapace. These muscles inserted along the coxal margins via cuticular tendons in a roughly symmetrical pattern about the long axis of the leg. This basic arrangement of muscle origins and insertions is present in *Mastigoproctus* (Uropygi) (Shultz, 1993) and was probably present in the common ancestors of Pedipalpi (i.e. Amblypygi, Schizomida, Thelyphonida). However, the sternocoxal arrangement in Pedipalpi differed from the hypothetical primitive condition in some or all postcheliceran appendages in having a distinct articulation between the coxa and sternum.

The sternocoxal articulation in Pedipalpi may have evolved by the fusion of the lateral part of the sternum with the medial portion of the coxa, because the posteriorly adjacent ventral endosternal suspensor muscle (muscle 19 in Table 1), which has a primitive sternal insertion, inserts on the medial margin of the palpal and pedal coxae in *Phrynus* (Fig. 2C) and *Mastigoproctus* (Shultz, 1993), except in the smaller and laterally displaced coxa of leg 1. The evolutionarily intermediate ‘sternal bridge’ predicted by this hypothesis may be expressed in the fourth walking leg, where the medial margins of the coxae and the lateral margins of the first opisthosomal sternite are fused such that there is no apparent demarcation between them. The ventral endosternal suspensor of postoral somite VII inserts on this shared surface (Fig. 2C). If this ‘sternal bridge’ hypothesis is correct, then the articulation formed by this

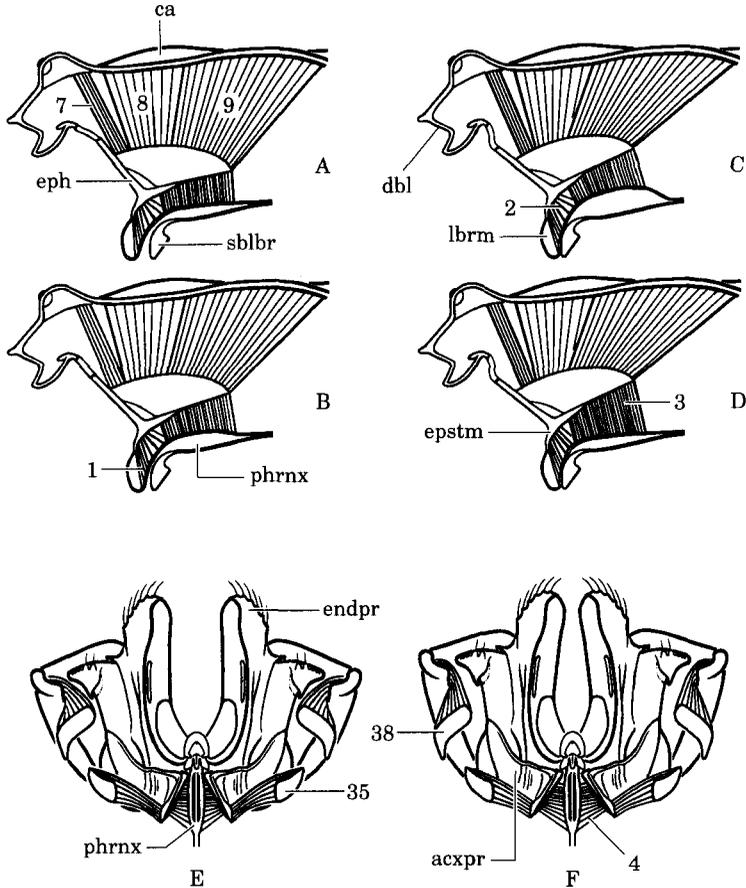


Figure 14. Functional model for operation of the precerebral pharyngeal apparatus. A–D, proposed function of the epipharyngeal mechanism in assisting dilation of the precerebral pharynx. A, the pharynx is constricted and the preoral cavity is open in preparation for ingestion of liquefied food generated by maceration by chelicerae and external digestion. B, tergo-epipharyngeal muscles 8 and 9 contract rotating the epipharyngeal sclerite counterclockwise at the epistome-coxa articulation. This action narrows the preoral cavity and assists the dorsal pharyngeal dilator (muscle 3) in dilating the pharynx. Food is sucked into the precerebral pharynx during this phase. C, the precerebral pharynx is fully dilated and the preoral cavity is closed. D, relaxation of the dorsal pharyngeal dilator along with contraction of precerebral pharyngeal constrictor muscles (Fig. 3) and, probably, the dilators of the postcerebral pharynx (Fig. 3) allows liquefied food to move out of the precerebral pharynx, through the transcerebral pharynx (oesophagus) and into the postcerebral pharynx (cf. Fig. 5). Once this phase has been completed, the epipharyngeal sclerite rotates clockwise and returns to the condition depicted in A. This rotation may occur through contraction of tergo-epipharyngeal muscle 7. E & F, proposed function of the coxal mechanism in assisting dilation of the precerebral pharynx. E, this phase corresponds to A above. The pharyngeal lumen is constricted in preparation for ingestion. Contraction of the anteromedial tergo-coxal muscles (35) rotates the palpal coxae at their connection at the sublabral sclerite such that the coxal processes are abducted and enditic processes are adducted. This action would assist the lateral pharyngeal dilator (4) in dilating the pharynx. F, the pharynx is fully dilated. Contraction of the lateral tergo-coxal muscle (38) returns the coxae to the condition shown in E and probably occurs in association with contraction of the pharyngeal constrictor muscles (see Fig. 3). Abbreviations: acxpr, anterior coxal process; ca, carapace; dbi, anterior doublure of carapace; endpr, enditic process of palpal coxa; eph, epipharyngeal sclerite; epstm, epistome; lbrm, labrum; phrnx, precerebral pharynx; sblbr, sublabral sclerite linking palpal coxae.

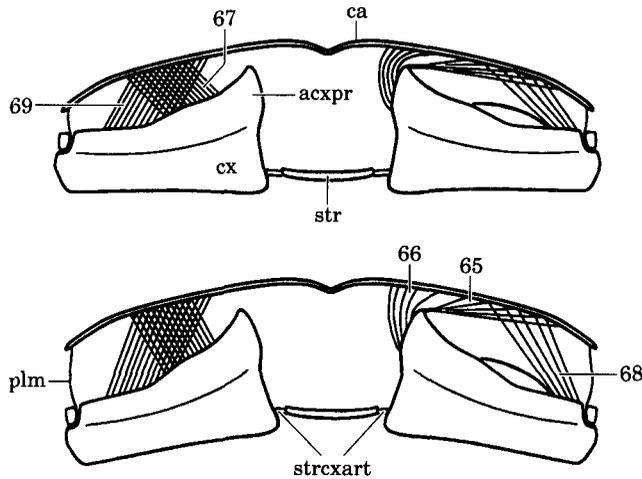


Figure 15. Functional model for operation of the sternocoxal mechanism of the legs. A semi-diagrammatic anterior view of the coxae of leg 2 is depicted. The upper figure depicts the coxae in the fully levated position and the lower figure depicts the depressed position. Tergocoxal muscles with 'dark' fibres (67, 69) and lower mechanical advantage at the sternocoxal articulation (strcxart) are depicted on the left. These muscles are interpreted as 'low-gear' muscles used in slow walking. They appear to function only as coxal levator muscles. Coxal depression may occur by inflation of the pleural membrane by high haemolymph pressure, a mechanism that has been proposed as primitive for arachnids (Shultz, 1991). Tergocoxal muscles with 'light' fibres (65, 66, 68) and higher mechanical advantage at the sternocoxal articulation are depicted on the right. These muscles are interpreted as 'high-gear' muscles used in brief, rapid movements, as during escape or prey capture. Muscles arising from the distal part of the anterior coxal process (65, 66) appear to function as coxal depressors. A suite of other 'high-gear' muscles (e.g. 68) act as levators. Numbered muscles are described in Table 1. Abbreviations: acxpr, anterior coxal process; ca, carapace; cx, coxa; plm, pleural membrane; str, sternum; strcxart, sternocoxal articulation.

structure is actually a modification of the sternum only, even though it functions as a sternocoxal articulation.

The sternocoxal apparatus of amblypygids, as represented by *Phrynus longipes*, has undergone a substantial modification from the primitive condition. Specifically, a distinct sternocoxal articulation is present and well developed in all walking legs in *Phrynus*, and the insertion site of the anteromedial tergocoxal muscle has enlarged to form an anterior coxal process (Figs 9, 15). In addition, most of the five 'primitive' tergocoxal muscles have divided to form two or more separate muscles that appear to have segregated into two functionally distinct systems, one specialized for rapid, powerful coxal movements and the other for slower, less powerful movements (Fig. 15). This functional differentiation is expressed in both anatomical placement and possible histochemistry. Muscles with highest mechanical advantage at the sternocoxal articulation (e.g., muscles 65, 66, 68, 71 and 73 in Table 1) are composed of 'light' fibres, which are suggestive of a glycolytic metabolism (Meyer, 1981; Maier, Root & Seyfarth, 1987). Muscles with lower mechanical advantage are composed of 'dark' fibres, which is suggestive of an oxidative metabolism. This functional dichotomy is reflected in the behaviour of the living organism, which tends to either walk slowly and deliberately, as when it is exploring its environment undisturbed, or with great speed, as when escaping a predator or an arachnologist (pers. observ.).

Amblypygids appear to differ from most other arachnids in having a mechanism

TABLE 2. Unique synapomorphies of Pedipalpi (= Amblypygi, Schizomida, Thelyphonida). Character polarity was established by outgroup comparisons with Araneae and Palpigradi

	Character	Plesiomorphic state	Apomorphic state
1.	Paired muscle arising from posterior margin of anterior carapacial doublure and inserting on carapace	Absent	Present
2.	Epipharyngeal sclerite	Embedded in intercheliceral membrane	Firm attachment to epistome
3.	Epipharyngeal sclerite	Small, without significant posterior projection	Large, projecting posteriorly to anterior surface of brain
4.	Anterior endosternal horn	Terminating in muscular attachment to labrum	Terminating in muscular attachment to palpal coxa.
5.	Ventroposterior wall of pre-oral chamber	Formed by 'sternite' (tritosternum or labium)	Formed by palpal coxae
6.	Lateral extrinsic precerebral pharyngeal muscle	Arising from anterior endosternal horns	Arising from medial surface of palpal coxa
7.	Ventral extrinsic precerebral pharyngeal muscle	Present	Absent
8.	Tergopharyngeal muscle of precerebral pharynx	Present	Absent
9.	Dorsal endosternal suspensor muscle of postoral somite V	Present	Absent
10.	Lateral tergocheliceral muscle	One head	Three heads
11.	Palp	Pediform	Raptorial
12.	Palpal posteromedial tergocoxal muscle	Present	Absent
13.	Palpal posteromedial endosternocoxal muscle	Originating on endosternite, inserting on coxa	Originating and inserting on coxa
14.	Palpal apotele	Differentiated from tarsus	Not differentiated from tarsus
15.	Palpal apotele levator muscle	Present	Absent
16.	Leg 1	Ambulatory	Antenniform
17.	Apotelic claw of leg 1	Differentiated from tarsus	Not differentiated from tarsus
18.	Telotarsus of legs 2-4 with three tarsomeres	Absent	Present
19.	Pedal anterior femur-patella muscle	Inserting primarily on patellar margin	Inserting primarily on patellar plagula
20.	Pedal posterior femoropatella-tibia muscle	Present	Absent
21.	Pedal patellotibia-tarsus muscle	Present	Absent
22.	Patella-tibia joint with auxilliary posterior articulation	Absent	Present
23.	Intracoxal muscle	Absent	Present
24.	Insertion process of anteromedial tergocoxal muscle	Weakly developed	Large, well developed
25.	Sternocoxal articulation, leg 1	Absent	Present
26.	Coxa 4 and sternite VII	Separate	Fused
27.	Ventral endosternal suspensor muscles	Attaching primarily to sternum	Attaching primarily to coxa of appendage of anteriorly adjacent somite
28.	Opisthosomal pleural muscle	Forming continuous dorsoventral sheet	Divided into three components
29.	Opisthosomal pleural membrane	Without distinct longitudinal folds	With two or more distinct longitudinal folds
30.	Dorsal and ventral longitudinal muscles	Spanning full length of opisthosoma	Spanning the first and, perhaps, last four opisthosomal somites
30.	Prosomal sternum	Without discrete sclerites	With discrete sclerites
31.	Gonoporal brood sac	Absent	Present

of coxal depression operated by direct muscular contraction. Noting that the primitive arachnid appendage apparently lacked any sclerotized connection to the prosoma, Shultz (1991) proposed that depression of the coxa in arachnids was accomplished primitively by inflation of the dorsally adjacent pleural cuticle by increased haemocoelic pressure and that extrinsic coxal muscles acted as coxal levators. Consequently, it is possible that amblypygids replaced the primitive hydraulic mechanism of coxal depression with a muscle-based mechanism formed by the anterior coxal process and its associated muscles. However, only the apparent 'high-speed' muscle system (i.e. those muscles with light fibres and higher mechanical advantage) have apparent depressor muscles. The apparent 'low-speed' system lacks obvious coxal depressor muscles, and it is possible that this system is antagonistic to pressure-induced coxal depression as in the hypothetical primitive system.

Phylogenetic implications

This analysis represents the second in a planned series of exhaustive myological surveys of representative chelicerates aimed at uncovering new characters for reconstructing the relationships among the living arachnid orders. The first study (Shultz, 1993) was devoted to the giant whipscorpion *Mastigoproctus giganteus*. Clearly, it is impossible to acquire meaningful phylogenetic insights from comparison of only two taxa, but similar myological surveys have been conducted by previous workers focusing on other arachnid taxa, especially spiders (Araneae) (Whitehead & Rempel, 1959; Palmgren, 1978) and, to a lesser extent, Palpigradi (Roewer, 1934; Millot, 1942, 1943). Skeletomuscular characters within these arachnid taxa have been used here to polarize muscular characters in *Phrynus* and *Mastigoproctus*, and a tentative list of 31 apparently unique synapomorphies has been constructed (Table 2). This result corroborates the hypothesis that Pedipalpi (i.e. Amblypygi, Schizomida, Uropygi) form a monophyletic group (Shear *et al.*, 1987; Shultz, 1990, 1993) and refutes the proposal that Araneae and Amblypygi form a monophyletic group exclusive of Schizomida and Uropygi (Petrunkevitch, 1955; Kaestner, 1968; Platnick & Gertsch, 1976; Weygoldt & Paulus, 1979; Wheeler & Hayashi, 1998; van der Hammen, 1989).

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