

# Muscular anatomy of the giant whipscorpion *Mastigoproctus giganteus* (Lucas) (Arachnida: Uropygi) and its evolutionary significance

JEFFREY W. SHULTZ\*

Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221-0006, U.S.A.

Received September 1992, accepted for publication March 1993

Skeletal muscles in the whipscorpion *Mastigoproctus giganteus* are surveyed and compared with those of several other chelicerates to clarify the evolutionary morphology and phylogenetic relationships of arachnids. Representatives from 90 muscle groups are described and illustrated, and their possible functions are proposed. Principal results of this analysis include new proposed homologies for the anterior opisthosomal appendages and sclerites in tetrapulmonate arachnids (that is, Trigonotarbida, Araneae, Amblypygi, Uropygi), the discovery that muscular attachments in arthropods can shift from the mesodermal endosternite to the ectodermal exoskeleton, a reconstruction of the evolutionary transformations associated with the apparent uncoupling of pharyngeal and locomotor complexes in the prosoma of Pedipalpi (that is, Amblypygi and Uropygi), and an expanded list of unique synapomorphies supporting the sister-group status of Amblypygi and Uropygi.

ADDITIONAL KEY WORDS: ---Arachnida – Uropygi – Thelyphonida – morphology – muscles – evolution – phylogeny – homology

## CONTENTS

Introduction . . . . .	335
Material and methods . . . . .	338
Results . . . . .	338
Discussion . . . . .	338
Evolutionary morphology of the pharyngeal apparatus . . . . .	338
Evolutionary morphology of the anterior opisthosoma and reproductive apparatus . . . . .	356
Phylogenetic implications . . . . .	363
Acknowledgements . . . . .	364
References . . . . .	364

## INTRODUCTION

This investigation focuses on the skeletomuscular anatomy of the giant whipscorpion *Mastigoproctus giganteus* (Lucas) (Uropygi: Thelyphonida) (Fig. 1) and explores the evolutionary, functional and phylogenetic implications of muscle structure in arachnids. Comparisons between *Mastigoproctus* and other chelicerates conducted here provide new insights into the evolutionary morphology of the pharyngeal complex, intersegmental tendon system, genital apparatus and opisthosomal exoskeleton in Uropygi and related lineages.

\*Present address: Department of Entomology, University of Maryland, College Park, MD 20742-5575, U.S.A.

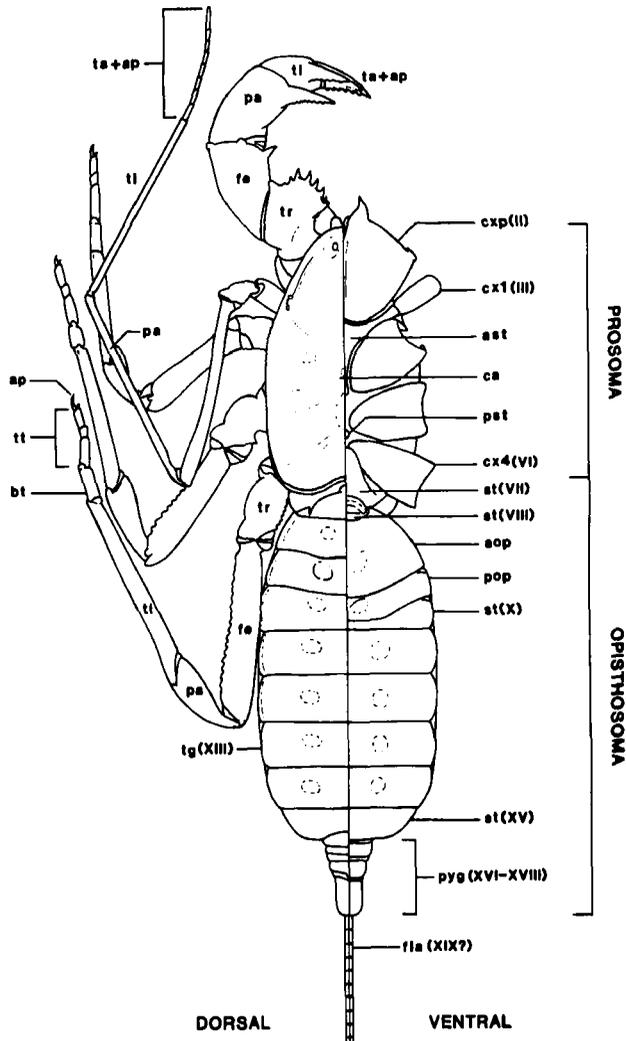


Figure 1. External anatomy of the giant whipscorpion, *Mastigoproctus giganteus*. Abbreviations: aop, anterior (genital) operculum; ap, apotele; ast, anterior sternum; bt, basitarsus; ca, carapace; cx, pedal coxa; exp, palpal coxa; fe, femur; fla, flagellum; pa, patella; pop, posterior operculum; pst, posterior sternum; pyg, pygidium; st, sternite; ta, tarsus; tg, tergite; ti, tibia; tr, trochanter; tt, telotarsus. Roman numerals (II–XIX) indicate post-oral somites; Arabic numerals (1–4) indicate legs.

Skeletomuscular characters revealed in this analysis strongly support the sister-group status of Uropygi and Amblypygi.

Progress toward an understanding of chelicerate evolution suffers from inadequate development of such basic disciplines as comparative skeletomuscular anatomy. Despite an extensive literature devoted to arachnid anatomy, much of the available information is inadequate or inappropriate for resolving ordinal relationships with modern systematic methods. These shortcomings are due largely to the systematic assumptions and methods that guided early arachnologists in their anatomical studies. Until recently, arachnologists tended to use either typological criteria (key diagnostic

characters) to 'define' taxa or subjective evaluations of overall similarity to gauge phylogenetic affinity. As a consequence, the arachnological literature is replete with partial and superficial anatomical descriptions, the vast majority of which focus exclusively on the exoskeleton. The practice of conducting exhaustive anatomical surveys to discover large numbers of characters and to establish the state of each character in all relevant taxa is a relatively new approach that has emerged with the widespread acceptance and computerization of hennigian systematic principles. Many shortcomings of traditional morphology-based phylogenies can thus be attributed to shortcomings in the systematic assumptions that guided early morphologists rather than to inadequacies of morphological characters.

The value of conducting intensive comparative studies in the light of cladistic principles has been illustrated by a recent anatomical survey focusing on the fourth leg of arachnids (Shultz, 1989). Although arachnid appendicular morphology has been examined repeatedly (for example, Gaubert, 1892; Börner, 1921; Barrows, 1925; Wood, 1926; Ewing, 1928; Snodgrass, 1952; van der Hammen, 1989), these studies contributed little toward resolving ordinal relationships, a situation that inspired Weygoldt & Paulus (1979) to caution against the use of appendicular characters in phylogenetic analysis. In contrast, Shultz's survey revealed several new characters, some of which strongly support ordinal relationships different from those generally favoured by arachnologists. For example, the analysis provided the first concrete evidence that scorpions are not the plesiomorphic sister to all other arachnids but are allied with orders generally regarded as highly derived (that is, Opiliones, Pseudoscorpiones, Solifugae). Computer-aided parsimony analysis of the newly discovered appendicular characters, together with 'traditional' characters, corroborated the novel phylogenetic hypotheses suggested by appendicular characters alone (Shultz, 1990). Preliminary studies of other skeletomuscular complexes (for example, pharyngeal, genital and endosternal complexes) in arachnids indicate that many morphological features remain to be discovered and exploited for reconstructing arachnid phylogeny (personal observations). In light of advances in systematic methodology and the success of recent morphological surveys in discovering phylogenetically significant information, now is an appropriate time to accelerate the search for characters that can resolve phylogenetic relationships among chelicerates.

This investigation provides an intensive analysis of skeletomuscular anatomy in the giant whipscorpion, *Mastigoproctus giganteus* (Uropygi), and is the first in a planned series of such surveys that will ultimately include representatives from all major chelicerate lineages. Uropygid whipscorpions hold an important place in studies of the evolutionary morphology of arachnids. Comparison with palpigrades, the apparent plesiomorphic sister of tetrapulmonates (that is, Trigonotarbida, Araneae, Uropygi, Amblypygi) (Shear *et al.*, 1987; Shultz, 1990; Selden, Shear & Bonamo, 1991) suggests that the uropygid opisthosoma retains many features that are primitive for tetrapulmonates. An understanding of opisthosomal anatomy in whipscorpions may clarify the evolutionary morphology of the more derived opisthosoma of spiders (Coddington & Levi, 1991) and may aid in interpreting the morphology of fossil arachnids such as trigonotarbids and *Gelastinotarbus* (Shear *et al.*, 1987; Selden *et al.*, 1991). Similarly, the structure of the uropygid prosoma approximates that of the

hypothetical primitive condition of arachnids (Shultz, 1991), and, consequently, *M. giganteus* has been used as a model of the primitive locomotor apparatus in recent functional studies (Shultz, 1991, 1992a, b). The present investigation was undertaken in the expectation that an intensive analysis of muscular anatomy in the largest living uropygid whipscorpion would provide further insights into the evolutionary and functional morphology of arachnids.

#### MATERIAL AND METHODS

Thirty adult *Mastigoproctus giganteus* preserved in 70% ethanol were obtained from biological supply companies. The skeleton and muscles were examined with a binocular dissecting microscope using standard dissection techniques. Several living specimens were collected near Portal, Arizona, U.S.A. and maintained for several months for behavioural and functional observations. Interpretations of muscle function were generally based on behavioural and anatomical observations (that is, muscle origin, insertion, fibre orientation) and should therefore be regarded as tentative. Anatomical observations of certain endosternal and appendicular muscles were supplemented by electromyographic analyses, and results of these investigations have been published elsewhere (Shultz, 1991, 1992a, b). Potential homologues for most muscles were identified in other chelicerate taxa on the basis of similarity in a skeletal attachment, fibre structure and placement with respect to other muscles. The proposed homologies should be regarded as hypotheses that are open to testing by results of future developmental, neuroanatomical and phylogenetic studies.

#### RESULTS

The principal findings of this analysis have been summarized in Table 1. Each of the 90 muscle groups are numbered, named, described and illustrated (Figs 2–10). The Table also includes comments on the evolution and functional morphology of each muscle and lists possible homologues described in previous studies of xiphosurans, scorpions and spiders (Araneae).

#### DISCUSSION

##### *Evolutionary morphology of the pharyngeal apparatus*

The precerebral digestive tract of most arachnids typically functions as a sucking pharynx, but the pharyngeal apparatus of *Mastigoproctus* and other pedipalpid is especially well developed. In contrast to the more primitive condition of spiders (Araneae), where the primary pharyngeal dilators arise from the carapace and anterior endosternal horns (Whitehead & Rempel, 1959; Palmgren, 1978), the dilators in pedipalpid arise from a rigid framework formed by sclerotized processes associated with the intercheliceral septum and palpal coxae (Figs 2, 3, 5, 10). The dorsal dilator (muscle 7) in *Mastigoproctus* arises from an epipharyngeal (intercheliceral) sclerite rather than the carapace, and the bilaterally paired posterior dilator (muscle 6) arises from large processes of the palpal coxae rather than the endosternal horns. The epipharyngeal sclerite and coxal processes are apparently braced against contractions of the pharyngeal

TABLE 1. Muscles of the adult giant whipscorpion, *Mastigoproctus giganteus*. The Table summarizes information from 90 muscle groups. The name proposed for each muscle group is derived from anatomical characteristics (for example, origin insertion or fibre direction) rather than on interpretations of function. Hypotheses of muscle function are speculative and based on anatomical criteria, but the functions of certain endosternal and appendicular muscles have been investigated using electromyography. Comments on the evolutionary significance of the muscle are generally concerned with taxonomic distribution or phylogenetic significance. An attempt is made to homologize each muscle with those of *Limulus* (Xiphosura), scorpions (Scorpiones) and spiders (Araneae). References used in determining homologies include BR, Bowerman & Root (1978); LBB, Lankester, Benham & Beck (1885); M, Manton (1958); P, Palmgren (1978); RR, Ruhland & Rathmayer (1978); Sh, Shultz (1989); Sn, Snodgrass (1952); WR, Whitehead & Rempel (1959)

No. Name	Description	Proposed function and evolution	Proposed homology
<i>Labral, pharyngeal and anterior double muscles</i>			
1 Anterior transverse labral m	Unpaired, weakly developed. Arises on one side of labral lobe; passes transversely; inserts on opposite side (Fig. 3)	Lateral compressor of labral lobe (see 4). A plesiomorphic muscle widespread in Arachnida (Snodgrass, 1948)	Araneae: P crv WR 18
2 Posterior transverse labral m	Unpaired, well developed. Arises on one side of epistome; passes transversely; inserts on opposite side (Fig. 3)	Lateral compressor of epistome (see 4). A plesiomorphic muscle widespread in Arachnida (Snodgrass, 1948)	Araneae: P crd WR 17
3 Anterior dorsoventral labral m	Unpaired. Arises dorsally from anterior margin of epistome; passes anteroventrally between muscles 1 and 2; inserts on ventral surface of labrum (i.e. roof of pre-oral cavity) (Fig. 3)	Levator of labral floor (see 4). Dorsoventral labral muscle is primitive in Arachnida, but division into anterior and posterior components (3, 4) by transverse labral muscle (2) may be derived	Scorpiones: LBB 98? Araneae: P dphm? WR 19?
4 Posterior dorsoventral labral m	Unpaired. Arises broadly from dorsal surface of epistome; passes ventrally; inserts on ventral surface of labrum (Fig. 3)	Levator of epistomal floor. Muscles 1–4 may work together to dilate pre-oral chamber during feeding (see 3)	Scorpiones: LBB 98? Araneae: P dphm WR 19
5 Anterior extrinsic pharyngeal m	Paired. Arises broadly from ventral surface of anterior process of palpal coxa; passes anteroventrally; inserts on ventral surface of pharynx and posterolateral margins of hypostome. Fibre bundles interdigitate with those of muscle 6 (Fig. 10)	Pharyngeal constrictor. Muscle may be primitive in arachnids, but function may vary. Large labro-coxal process in eurypterids (Selden, 1981) suggests presence of this muscle in these chelicerates, thus plesiomorphic for Arachnida	Araneae: P dphl WR 20
6 Posterior extrinsic pharyngeal m	Paired. Arises broadly from ventral surface of anterior process of palpal coxa posterior to 5; passes posteromedially; inserts on lateral walls of pharynx. Fibre bundles interdigitate with those of muscles 5 and 10 (Figs 3, 10)	Pharyngeal dilator. Primitively arose from endosternite as in Araneae but 'migrated' to anterior process of palpal coxa with other endosternal muscles (i.e. 13, 15, 32, 33). See text for details	Scorpiones: LBB 99? Araneae: P does WR 24

TABLE 1.—*continued*

No. Name	Description	Proposed function and evolution	Proposed homology
7 Dorsal extrinsic pharyngeal m	Paired. Arises dorsally from ventral surface of epipharyngeal sclerite; passes anteroventrally; inserts on dorsal surface of pharynx (Fig. 3)	Pharyngeal dilator. Primitively inserted on minute interchelicerar sclerite as in Palpigradi. Sclerite and associated muscles greatly enlarged in Pedipalpi, interchelicerar insertion lost in Araneae. See text for details	Xiphosura: LBB 66? Scorpiones: LBB 62? Araneae: P da + dp WR 21 + 22
8 Anterior epipharyngeal m	Paired. Arises dorsally from anteromedial surface of carapace; passes posteroventrally; inserts along anterior margin of epipharyngeal sclerite (Figs 2, 3)	May generate torque on epipharyngeal sclerite, balancing that caused by muscle 7. Epipharyngeal apparatus may be synapomorphic for Uropygi and Amblypygi. See text for details	Xiphosura: LBB 66? Scorpiones: LBB 62? Araneae: P da WR 21
9 Posterior epipharyngeal m	Asymmetrically paired. Right component arises on midline of carapace; passes posteroventrally; inserts on tip of epipharyngeal sclerite. Left component arises on midline of carapace; passes anteroventrally; inserts on tip of epipharyngeal sclerite (Figs 2, 3)	Function uncertain. Unusual geometry suggests involvement in sensing displacement of epipharyngeal sclerite caused by muscle 7, thus allowing compensatory contraction by muscle 8. See text for details	Xiphosura: LBB 66? Scorpiones: LBB 62? Araneae: P dp? W 22?
10 Intrinsic pharyngeal m	Paired. Arises from lateral margins of dorsal pharyngeal sclerite; inserts on posterior half of ventral pharyngeal sclerite. Fibre bundles interdigitate with those of muscle 6 (Fig. 3)	Pharyngeal constrictor	Xiphosura: LBB 5 Scorpiones: LBB 130 Araneae: absent?
11 Anterior doublure m	Paired, each component with two heads. Arises dorsally from anterior surface of carapace; inserts on upper medial surface of anterior doublure (Figs 2–4)	Function uncertain. It is not clear from adult morphology whether this muscle is derived from a pre-oral or post-oral somite	Scorpiones: LBB 61 Araneae: absent?
<i>Intersegmental tendon system and endosternite</i>			
12 Suboral endosternal m	Paired, thin. Arises from medial surface of anterior endosternal horn at base of dorsal (13) and ventral (15) suspensors of somite III; passes anteromedially; inserts on small suboral sclerite via long tendon (Figs 2, 3)	Function uncertain. Presence of similar muscles in xiphosurans, scorpions and palpigrades (Millot, 1943) indicates that the muscle is plesiomorphic	Xiphosura: LBB 67? Scorpiones: LBB 84? Araneae: absent?
13 Dorsal endosternal suspensor m	Paired, somites II–VII. Arises from dorsal surface of endosternite III–VII or coxal process (II); inserts on carapace (II–VI) or tergite (VII). Insertions typically represented externally by fossae (Figs 2, 3, 5, 7, 10)	Dorsoventral compressor of prosoma. Generates hydraulic pressure used in extension of femur-patella joints (Shultz, 1991). Plesiomorphic. See text for details on evolution of suspensors of somite II	Xiphosura: LBB 49–54? Scorpiones: LBB 93–95 (III–V)? 63 (VI), 65 (VII) Araneae: P sc? WR 4? (V)

14	Dorsolateral endosternal suspensor m	Paired, somites IV–VII. Arises from dorsal surface of endosternite, often via tendinous processes shared with corresponding muscle 13; inserts on carapace (IV–VI) or tergite (VII). Carapacial insertions represented externally by fossae (Figs 2, 5, 7)	Dorsoventral compressor of prosoma. Generates hydraulic pressure used in extension of femur–patella joints (Shultz, 1991). Plesiomorphic	Xiphosura: LBB 57–59? Scorpiones: LBB 83 (VI)? Araneae: P sl–4 WR 1–3,5 (III–VI)
15	Ventral endosternal suspensor m	Paired, somites II–VII. Components III–VII arises from ventral surface of endosternite, often via tendinous processes; component II arises from palpal coxa. They insert on prosomal sternum (IV), medial coxal process of appendages of anteriorly adjacent somite (III, V–VII) or medial margin of palpal coxa (II) (Figs 2, 3, 5, 10)	Dorsoventral compressor of prosoma. Sternal insertion is primitive; retained in certain spiders and palpigrares (Firstman, 1973, 1990; Firstman & Benton, 1988). Suspensors of somites III, V–VII have shifted to coxae of anteriorly adjacent somite in Pedipalpi	Xiphosura: absent Scorpiones: absent
16	Endosternotergal m	Paired. Arises from dorsal surface of endosternite between tendinous process V and VI; inserts on lateral margin of first opisthosomal tergite (VII) (Figs 2, 5, 7)	Levator/rotator of prosoma–opisthosoma juncture. Plesiomorphic	Scorpiones: LBB nf? Araneae: P le WR 74
17	Dorsoventral m	Paired, somites VIII–XIV. Arises from opisthosomal tergite; inserts on sternite of same somite (Figs 7, 8)	Dorsoventral compressor of opisthosoma. Metameric homologue of dorsal and ventral endosternal suspensors (13). Misidentification of anterior sternites reflected as incorrect numbering system in Araneae (e.g. Millot, 1949b; Whitehead & Rempel, 1959). Plesiomorphic	Xiphosura: LBB 12 Scorpiones: LBB 66–71 (VIII–XIII) Araneae: WR 77, 86
18	Ventral longitudinal m	Paired, spanning somites VII–X. Anterior pair (18a) arises from posterolateral margins of endosternite; inserts on anterolateral margin of sternite VIII. Middle pair (18b) arises from posterolateral margin of sternite VIII; inserts on anterolateral processes of sternite IX. Posterior pair (18c) arises from anterolateral processes of sternite IX; inserts on anterolateral processes of sternite X (Figs 7, 9)	Longitudinal compressor of anterior opisthosoma. Primitively, paired ventral longitudinal muscles spanned the entire length of the opisthosoma but are preserved in Uropygi and Amblypygi in only the first three opisthosomal somites. Much longer ventral longitudinal muscles are retained in Xiphosura, Scorpiones and Araneae	Xiphosura: LBB 5 Scorpiones: LBB 25–30, 51? Araneae: WR 7, 8, 83–85, 90
<i>Extrinsic leg muscles</i>				
19	Anteromedial tergocoxal m	Legs 1–4. Arises from lateral surface of carapace; passes medially; inserts on or near anterior coxal process (Figs 2, 4)	Coxal rotator. Precise function probably varies from leg to leg	Xiphosura: LBB, M, Sn 27 Araneae: P cl WR 15

TABLE 1.—*continued*

No.	Name	Description	Proposed function and evolution	Proposed homology
20	Anterolateral tergoxal m	Legs 1–4. Arises from medial surface of carapace; passes laterally; inserts on anterolateral coxal margin (Figs 2, 4)	Coxal levator/rotator. Precise function probably varies from leg to leg (cf. 28)	Xiphosura: LBB, M, Sn 26 Scorpiones: LBB 112?, 115?, 116?, 118? Araneae: P c2 WR 13
21	Posteromedial tergoxal m	Legs 1–4. Arises from carapace; inserts on posterior coxal margin (Figs 2, 4)	Coxal rotator. Precise function probably varies from leg to leg	Xiphosura: LBB, M, Sn 29 Scorpiones: LBB 126? 127? Araneae: P c4 WR 16
22	Posterolateral tergoxal m	Legs 1–4. Arises from medial surface of carapace; passes laterally; inserts on posterolateral coxal margin (Figs 2, 4)	Coxal levator/rotator. Precise function probably varies from leg to leg (cf. 29)	Xiphosura: LBB, M, Sn 28 Scorpiones: LBB 114?, 128?, 117?, 119? Araneae: P c3 WR 14
23	Pleurotergal m	Legs 1–4. Arises from lateral surface of carapace; ventrolaterally; inserts on sclerites within pleural membrane dorsally adjacent to coxae (Fig. 2)	Coxal levator? (Shultz, 1991). Apparently derived from lateral tergoxal muscle when insertion shifted to pleural membrane. Analogous to <i>musculi laterales</i> of spiders	Xiphosura: LBB, M, Sn 25 Scorpiones: LBB, 126?, 127? Araneae: P M1 WR 31
24	Anteromedial endosternocoxal m	Legs 1–4. Arises from endosternite; inserts on anteromedial coxal margin (Fig. 5)	Function probably varies from leg to leg (cf. 32)	Xiphosura: LBB 38, 40, 43, 45 + 46 Araneae: Pc7 WR 11
25	Anterolateral endosternocoxal m	Legs 1–4. Arises from endosternite; inserts on anterolateral coxal margin (Fig. 5)	Function probably varies from leg to leg (cf. 30)	Xiphosura: LBB 35o, 38q, 41s, 44y Araneae: P c5 WR 9
26	Posteromedial endosternocoxal m	Legs 1–4. Arises from endosternite; inserts on posteromedial coxal margin (Fig. 5)	Function probably varies from leg to leg (cf. 33)	Xiphosura: LBB 37, 39, 42, 47 + 60 Scorpiones: LBB 74? 78? Araneae: P c8 WR 12
27	Posterolateral endosternocoxal m	Legs 1–4. Arises from endosternite; inserts on posterolateral coxal margin (Fig. 5)	Function probably varies from leg to leg (cf. 31)	Xiphosura: LBB 35p, 38r, 41t, 44z Scorpiones: LBB, 79?, 81?, 86a? Araneae: P c6 WR 10
<i>Extrinsic palpal muscles</i>				
28	Dorsal palpal tergoxal m	Arises broadly from anterolateral surface of carapace; inserts narrowly on anterodorsal coxal margin (Figs 2, 4)	Function uncertain. Probably a metameric homologue of leg tergoxal muscle 20	Xiphosura: LBB 26 Scorpiones: LBB 112? Araneae: P pe WR 13p

29	Lateral palpal tergocoxal m	Arises broadly from anterolateral surface of carapace; inserts on dorsolateral coxal margin (Figs 2, 4)	Function uncertain. Probably a metameric homologue of leg tergocoxal muscle 22	Xiphosura: LBB 28 Scorpiones: LBB 113? Araneae: P pm WR 14p
30	Medial palpal endosternocoxal m	Arises from anterior end of endosternal horn; passes anteriorly; inserts at posterior end of anterior coxal process (Figs 5, 10)	Muscular tissue connection between anterior process of palpal coxa and anterior endosternal horn may represent metameric homologue of endosternocoxal muscle 25 or a muscularized portion of endosternal connective tissue	Xiphosura: LBB 32m Araneae: P as WR 9p
31	Lateral palpal endosternocoxal m	Arises broadly from anterolateral surface of anterior endosternal horn; inserts broadly on lateral coxal margin (Figs 5, 10)	Function uncertain. Probably a metameric homologue of leg endosternocoxal muscle 27	Xiphosura: LBB 32n Scorpiones: LBB 76? Araneae: P ai WR 10p
32	Medial palpal coxal m	Arises from ventral surface of anterior coxal process near its posterior end; passes ventrally; inserts on posteromedial coxal margin near medial process (Figs 5, 10)	Function uncertain. Probably a metameric homologue of leg endosternocoxal muscle 24. See text for details	Xiphosura: LBB 34 Scorpiones: LBB 75? Araneae: P pi WR 11p
33	Lateral palpal coxal m	Arises from ventral surface of anterior coxal process; passes laterally; inserts on lateral coxal margin (Figs 5, 10)	Function uncertain. Probably a metameric homologue of leg endosternocoxal muscle 26. See text for details	Xiphosura: LBB 33 Scorpiones: LBB 72? Araneae: P ps WR 12p
<i>Intrinsic leg and palpal muscles</i>				
34	Intracoxal m	Legs 2–4. Arises from tip of anterior coxal process; passes dorsolaterally; inserts on internal dorsolateral margin of coxa. Extremely thin in leg 2; well developed in leg 4 (Fig. 4)	Function uncertain. May represent a modified portion of anteromedial tergocoxal muscle (19)	* * *
35	Dorsal coxa-trochanter m	Arises from medial coxal surface on or near medial coxal process; inserts dorsally on proximal margin of trochanter. Second head in palps and legs 3–4 arises near anterior coxal process. Third head in leg 4 arises from distoposterior coxal surface. Not illustrated	Levator of coxa-trochanter joint	Xiphosura: Sn 1 Scorpiones: BR 1 Araneae: RR 4, 6, 9 WR 48–50
36	Anteroventral coxa-trochanter m	Arises broadly with many heads from ventral coxal surface; inserts ventrally on trochanteral plagula and proximal margin of trochanter. Not illustrated	Promotor/depressor of coxa-trochanter joint	Xiphosura: Sn 2 Scorpiones: BR 2–4 Araneae: RR 1–3, 5, 7 WR 44–47
37	Posteroventral coxa-trochanter m	Arises from posterior coxal surface in legs and ventrolateral coxal surface in palps; inserts on posterior margin of trochanter near its posterior articulation with coxa. Second head in legs 2–4 arises from anteroventral coxal surface. Not illustrated	Remotor/depressor of coxa-trochanter joint	Xiphosura: Sn 3 Scorpiones: BR 5 Araneae: RR 8 WR 51

TABLE 1.—*continued*

No. Name	Description	Proposed function and evolution	Proposed homology
38 Coxotrochanter–femur m	Arises broadly from dorsal surface of trochanter and distoanterior surface of coxa dorsal to <i>coxa costalis</i> ; inserts dorsally on proximal margin of femur (Fig. 6)	Levator of trochanter–femur joint (Shultz, 1992a). Coxal head may function as sensory organ in scorpions (Bowerman & Root, 1978)	Chelicerata: Sh 13 Scorpiones: BR 6+8 M 13+14 Araneae: RR 10–12 WR 52–54
39 Ventral trochanter–femur m	Arises broadly from ventral surface of trochanter; inserts anteroventrally on proximal margin of femur (Fig. 6)	Depressor of trochanter–femur joint (Shultz, 1992a)	Chelicerata: Sh 11 Xiphosura: Sn 4 Scorpiones: BR 7 M 15
40 Diagonal trochanter–femur m	Legs only. Arises from anterior surface of trochanter just proximal to anterior condyle of trochanter–femur joint; inserts on posterior surface of femur just distal to posterior condyle of trochanter–femur joint (Fig. 6). Relative size greater in anterior legs	Function uncertain. May be rudimentary muscle associated with undeveloped basifemur–telofemur joint (Shultz, 1989)	Chelicerata: Sh 10 Xiphosura: Sn 5 or 6 Scorpiones: M <i>dep. fem. a.</i> Araneae: RR 13
41 Trochanterofemur–patella m	Anterior component (41a) arises from distoanterior surface of trochanter and anterior dorsal surface of femur. Posterior component (41b) arises from posterior surface of femur. Both insert on patellar plagula via a common tendon. Femoral components absent in leg 1 (Fig. 6)	Femoral head may function as a flexor of the femur–patella joint. Trochanteral head may act as an internal linkage maintaining coordination between trochanter–femur and femur–patella joints (Shultz, 1992a). Plesiomorphic	Chelicerata: Sh 8c, 8d Xiphosura: Sn 10 Scorpiones: BR 9 M 18 Araneae: RR 16–18 WR 58, 59
42 Femur–patella m	Palp, anterior and posterior components (42a, 42b) symmetrically arranged about femur–patella joint. Arise from distal surface of femur; insert broadly on proximal margin of patella. Legs, asymmetrical. 42a arises on anterior surface of femur; inserts on patellar plagula. 42b arises on distoposterior surface of femur; inserts broadly on ventral rim of patella (Fig. 6)	Flexor of femur–patella joint (Shultz, 1992a). Asymmetrical patellar insertion in legs is synapomorphic for Uropygi and Amblypygi	Chelicerata: Sh 8a, 8b Xiphosura: Sn 8 Scorpiones: BR 10 M 16, 17 Araneae: RR 14, 15, 19 WR 58, 59
43 Femoropatella–tibia m	Anterior and posterior components (43a, 43b) symmetrically arranged at patella–tibia joint. Palp: arises from patella and distal surfaces of femur; inserts on tibial plagula via tendons. Leg 1: femoral components absent; inserts on margin of tibia. Legs 2–4: 43a with femoral and patellar components; 43b absent (Fig. 6)	Flexor of patella–tibia joint. Shultz (1989) erroneously described 44b in legs 3–4. Absence of 44b is synapomorphic for Uropygi and Amblypygi	Chelicerata: Sh 6, 7 Xiphosura: Sn 16, 17 Scorpiones: BR 11, 12 M 20–23 Araneae: RR 23, 24 WR 62?

44	Patella–tibia m	Anterior and posterior components (44a, 44b) symmetrically arranged at patella–tibia joint. Arises broadly from distal surface of patella; inserts broadly on proximal margin of tibia (Fig. 6)	Flexor/rotator of patella–tibia joint Plesiomorphic	Chelicerata: Sh 4, 5 Xiphosura: Sn 14, 15 Scorpiones: BR 13 M 21a Araneae: RR 21, 22 WR 60, 61
45	Patellotibia–tarsus m	Palp only. Anterior and posterior components (45a, 45b) symmetrically arranged about tibia–tarsus joint. Arises from tibial and distodorsal patellar surfaces; inserts on tarsal plagula via a common tendon. Not illustrated	Flexor of tibia–tarsus and patella–tibia joints. Absence of patellar head in legs may be synapomorphic for Uropygi, Amblypygi and Araneae; total absence synapomorphic for Uropygi and Amblypygi	Chelicerata: Sh 3 Araneae: RR 27, 28 WR 63, 64
46	Tibia–tarsus m	Anterior and posterior components (46a, 46b) symmetrically arranged about tibia–tarsus joint. Arises from tibia; inserts ventrally on proximal margin of tarsus (Fig. 6)	Flexor of tibia–tarsus joint. Plesiomorphic	Chelicerata: Sh 3 Xiphosura: Sn 18?, 19? Scorpiones: BR 15 M 24 Araneae: RR 25, 26 WR 65, 66
47	Patellotibia–apotele m	Legs only. Legs 2–4: arises on posterior surface of patella and proximal surface of tibia; inserts on ventral rim of apotele via long tendon (Fig. 6). Leg 1: patellar component absent; tendon inserts at terminus of tarsus. Apotele is apparently absent	Depressor of tarsus–apotele joint. Barrows (1924) described this muscle in the palp of <i>Mastigoproctus</i> , but it was absent in all specimens examined here. Absence from palp may be autapomorphic in Thelyphonida	Chelicerata: Sh 2 Xiphosura: Sn 21 Scorpiones: BR 14 M 26 Araneae: RR 29 WR 68
48	Tarsus–apotele m	Legs only. Legs 2–4: arises from basitarsus; inserts on apotele via long tendon (Fig. 6). Leg 1: arises from proximal tarsomere; inserts at terminus of tarsus. Apotele is apparently absent	Levator of tarsus–apotele joint. Barrows (1925) described this muscle in the palp of <i>Mastigoproctus</i> , but it was absent in all specimens examined here. Absence from palp may be autapomorphic in Thelyphonida	Chelicerata: Sh 1 Xiphosura: Sn 20 Scorpiones: BR 16 M 25 Araneae: RR 30 WR 67
<i>Cheliceral muscles</i>				
49	Anterolateral lateral tergocheliceral m	Arises broadly from anterolateral surface of carapace; inserts on protuberance of cheliceral process (Figs 2, 4)	Protractor of chelicera. May represent one of three subdivisions of a single muscle retained in Araneae	Xiphosura: LBB 24? Araneae: P al WR 14c
50	Anteromedial lateral tergocheliceral m	Arises from anteromedial surface of carapace; passes posterolaterally deep to 51; inserts near protuberance of chelicera process (Figs 2, 4)	Protractor/abductor of chelicera. May represent one of three subdivisions of a single muscle retained in Araneae	Xiphosura: LBB 24? Araneae: P al WR 14c
51	Medial lateral tergocheliceral m	Arises near anterior midline of carapace; passes posterolaterally; inserts on protuberance of cheliceral process (Figs 2, 4)	Protractor/abductor/rotator of chelicera. May represent one of three subdivisions of a single muscle retained in Araneae	Xiphosura: LBB 24? Araneae: P al WR 14c
52	Posteromedial lateral tergocheliceral m	Arises from anterolateral margin of posterior median fossa of carapace; inserts on protuberance of cheliceral process (Figs 2, 4)	Retractor of chelicera	Xiphosura: LBB 24? Araneae: P la? WR 10c?

TABLE 1.—*continued*

No.	Name	Description	Proposed function and evolution	Proposed homology
53	Dorsal lateral tergocheliceral m	Arises from carpace directly above posterior end of fully retracted chelicera; inserts on lateral surface of cheliceral process near protuberance (Figs 2, 4)	Retractor/depressor of chelicera	Xiphosura: LBB 24? Araneae: P av? WR 13c?
54	Posterior lateral tergocheliceral m	Small. Arises from carpace medial to insertion of dorsal endosternal suspensor (13) of somite III; inserts near posterior tip of cheliceral process (Figs 2, 4)	Retractor/rotator of chelicera	Xiphosura: LBB 24? Araneae: P lp? WR 16c?
55	Posterior dorsal tergocheliceral m	Arises near anterior median fossa of carpace; inserts on anteromedial margin of proximal cheliceral segment via tendon (Figs 2, 4)	Retractor of chelicera	Xiphosura: LBB 24? Araneae: P pd? WR 9c?
56	Medial ventral tergocheliceral m	Arises near midline of carpace; inserts broadly on medial margin of proximal cheliceral segment (Figs 2, 4)	Retractor/rotator of chelicera	Xiphosura: LBB 24? Araneae: P rd? WR 15c?
57	Posterior ventral tergocheliceral m	Arises on carpace; inserts on ventral margin of proximal cheliceral segment via tendon shared with 58 (Figs 2, 4)	Retractor of chelicera	Xiphosura: LBB 24? Araneae: P mc WR 12c
58	Endosterno-cheliceral m	Arises from medial surface of anterior endosternal horn near tendinous processes associated with dorsal suspensor (13) of somite III; inserts with 57 at ventral margin of proximal cheliceral segment (Fig. 5)	Retractor of chelicera	Xiphosura: LBB 30, 31 Scorpiones: LBB 96 or 97 Araneae: P me WR 11c
59	Ventral cheliceral apotele m	Arises broadly from walls of proximal cheliceral segment; inserts on ventral plagula of cheliceral apotele. Not illustrated	Closer of cheliceral chela	Araneae: WR 70–72
60	Dorsal cheliceral apotele m	Arises from dorsal surface of proximal cheliceral segment; inserts on dorsal margin of cheliceral apotele. Not illustrated	Opener of cheliceral chela	Araneae: WR 69
<i>Opisthosomal muscles</i>				
61	Dorsal pleural m	Paired, sheetlike, somites VII–XV. Arises from lateral surface of tergite; passes ventrally; inserts on adjacent region of dorsal pleural fold (Fig. 7)	Regulates expansion of opisthosomal pleural membrane (cf. 63)	Scorpiones: LBB 15–19? Araneae: WR 92

62	Middle pleural m	Paired, sheetlike, somites VII–XV. Arises from dorsal pleural fold; inserts on ventral pleural fold. Not illustrated	Regulates expansion of opisthosomal pleural membrane (cf. 63)	Araneae: WR 92
63	Ventral pleural m	Paired, sheetlike, somites VIII–XV. Arises from lateral surface of operculum (VIII, IX) or sternite (X–XV); passes dorsally; inserts on adjacent region of dorsal pleural fold (Fig. 7)	Regulates expansion of opisthosomal pleural membrane. Muscles 61–63 probably evolved from a continuous muscular sheet. Division into three components is probably synapomorphic for Uropygi and Amblypygi	Araneae: WR 92
64	Intertergal m	Unpaired (except where divided by pericardium), somites VII–XVII. Arises anteriorly from tergite; passes posteriorly; inserts on intertergal membrane or anterior margin of posteriorly adjacent tergite (Figs 7, 8)	Longitudinal compressor of opisthosoma	Scorpiones: LBB 9–14 Araneae: WR 79
65	Medial carapacotergal m	Paired. Arises from medial surface of carapace at posterior border of posterior median fossa; passes posteriorly; inserts on anteromedial margin of tergite VII via tendon (Figs 2, 7)	Levator of opisthosoma. When contracted, this muscle may provide a pivot point about which the opisthosoma can be rotated	Scorpiones: LBB 1 or 2 Araneae: P lt, WR 73
66	Lateral carapacotergal m	Paired. Arises broadly from posterior and posteromedial surface of carapace; passes posteriorly; inserts on anterolateral margin of tergite VII and associated pleural membrane (Figs 2, 7)	Lateral flexor/rotator of opisthosoma	Scorpiones: LBB 1 or 2 Araneae: P pt, WR 75
67	Dorsal longitudinal m	Paired. Arises on posterolateral surface of tergite VII posterior to dorsoventral muscle (17). Short head (67a) inserts on anterolateral margin of tergite IX; middle head (67b) inserts on tergite IX just anterior to dorsoventral muscle (17); long head (67c) inserts on anterolateral margin of tergite X (Fig. 7)	Longitudinal compressor of opisthosoma. These muscles may represent remnants of dorsal components of the primitive intersegmental tendon system of arthropods, as in mesothele spiders (Millot, 1949b). Note that in <i>Mastigoproctus</i> they are retained in the first three opisthosomal somites, as are the ventral longitudinal muscles (18)	Scorpiones: LBB 3–8? Araneae: WR 80
68	Intersternal m	Unpaired, somites VII–XVII. Arises anteriorly from sternite; passes posteriorly; inserts on intersternal membrane or anterior margin of posteriorly adjacent sternite (Figs 7–9)	Longitudinal compressor of opisthosoma	Scorpiones: LBB 21–24, 50a, 25–30 Araneae: WR 91?

TABLE 1.—*continued*

No. Name	Description	Proposed function and evolution	Proposed homology
69 Venopericardiac m	Paired, somites VI–XV. Arises from ventrolateral surface of pericardium; passes ventrolaterally anterior to dorsoventral muscle of corresponding somite; inserts on pulmonary sinus (VIII, IX) or sternite. Not illustrated	Dilator of pericardial and pulmonary sinuses. Plesiomorphic	Xiphosura: LBB 68 Scorpiones: LBB 65? 131–137 Araneae: WR hol
<i>Pygidial muscles</i>			
70 Short dorsal extrinsic pygidial m	Paired, straplike. Arises from medial surface of tergite XIV; inserts dorsally on anterior margin of first pygidial somite (XVI) (Figs 7, 8)	Retractor/dorsal flexor of pygidium. May work in concert with other pygidial muscles to produce more complex movements	***
71 Middle dorsal extrinsic pygidial m	Paired, straplike. Arises from medial surface of tergite XIV; passes posteriorly deep to 70; inserts dorsally on anterior margin of second pygidial somite (XVII) (Figs 7, 8)	Retractor/dorsal flexor of pygidium. May work in concert with other pygidial muscles to produce more complex movements	***
72 Long dorsal extrinsic pygidial m	Paired, straplike. Arises from medial surface of tergite XIV; passes posteriorly deep to 71; inserts dorsally on anterior margin of third pygidial somite (XVIII) (Figs 7, 8)	Retractor/dorsal flexor of pygidium. May work in concert with other pygidial muscles to produce more complex movements	***
73 Short ventral extrinsic pygidial m	Paired, straplike. Arises from medial surface of sternites XIV and XV; inserts ventrally on anterior margin of first pygidial somite (XVI) (Figs 7, 8)	Retractor/ventral flexor of pygidium. May work in concert with other pygidial muscles to produce more complex movements	***
74 Middle ventral extrinsic pygidial m	Paired, straplike. Arises from medial surface of sternites XIV and XV; passes posteriorly deep to 73; inserts ventrally on anterior margin of second pygidial somite (XVII) (Figs 7, 8)	Retractor/ventral flexor of pygidium. May work in concert with other pygidial muscles to produce more complex movements	***
75 Long ventral extrinsic pygidial m	Paired, straplike. Arises from medial surfaces of sternites XIV and XV; passes posteriorly deep to 74; inserts ventrally on anterior margin of third pygidial somite (XVIII) (Figs 7, 8)	Retractor/ventral flexor of pygidium. May work in concert with other pygidial muscles to produce more complex movements	***

76	Intrinsic pygidial m	Paired. Arises from lateral surface of first pygidial somite (XVI) and ventrolateral surface of second pygidial somite (XVII); inserts dorsolaterally on anterior margin of third pygidial somite (XVIII) (Fig. 8)	Dorsal/lateral flexor of pygidium. May work in concert with other pygidial muscles to produce more complex movements	***
77	Dorsal pygidioflagellum m	Paired. Arises from anterolateral surface of third pygidial somite (XVIII); inserts on dorsolateral process at base of opisthosomal flagellum (Fig. 8)	Flagellum levator. Works with ipsilateral 78 to move flagellum laterally	Xiphosura: LBB 6–8, 91–95 Scorpiones: LBB 44?
78	Ventral pygidioflagellum m	Paired. Arises from anterolateral and dorsomedial surfaces of third pygidial somite (XVIII); passes posteriorly medial to 77 inserts ventrally on base of opisthosomal flagellum (Fig. 8)	Flagellum depressor. Works with ipsilateral 77 to move flagellum laterally	Xiphosura: LBB 9–11, 88–90 Scorpiones: LBB 60?
79	Anterior rectal m	Paired, straplike. Arises from medial surface of tergite IX; passes posteriorly deep to 72; inserts on dorsal surface of rectum near its terminus (Fig. 8)	Rectal retractor/anal closer	***
80	Ventral rectal m	Paired. Arises from ventral surface of third pygidial somite (XVIII); inserts on ventral surface of rectum near its terminus (Fig. 8)	Rectral retractor/anal closer	***
81	Lateral rectal m	Paired. Arises from posterolateral surface of third pygidial somite (XVIII); inserts near lateral border of anus (Fig. 8)	Anal closer. May also function in ‘aiming’ turrets of pygidial defensive glands that open lateral to anus	***
<i>Opercular and genital muscles</i>				
82	Anterior extrinsic opercular m	Paired, anterior operculum only. Arises from posterolateral margin of sternite VIII; passes ventromedially; inserts on anteromedial surface of anterior operculum (Fig. 9)	Function unclear. May function in elevating the anterior operculum, thus closing the opening to the pre-genital chamber. Probably a metameric homologue of an endosternocoxal muscle	Araneae: WR 116, 118
83	Posterior extrinsic opercular m	Paired. Arises from ventromedial surface of operculum (VIII) or intersternal membrane (IX); inserts on anterior processes of sternites IX and X, respectively (Fig. 9)	Function unclear. The muscle associated with the anterior operculum may function in elevating the operculum, thus closing the opening to pre-genital chamber. Probably a metameric homologue of an endosternocoxal muscle	Xiphosura: LBB 48? Araneae: WR 117, 119

TABLE 1.—*continued*

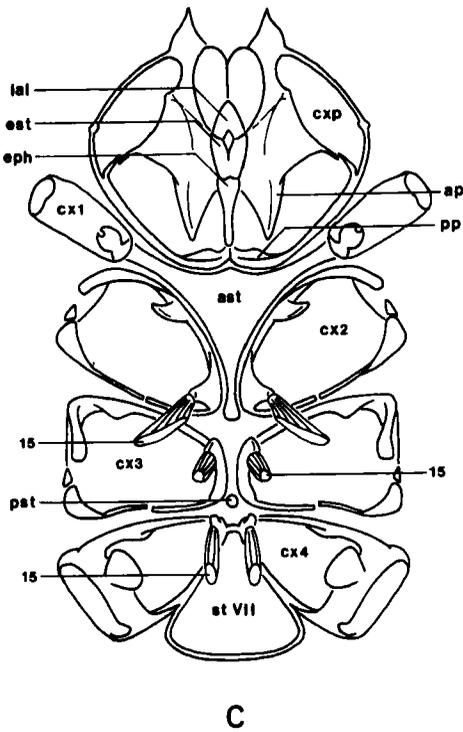
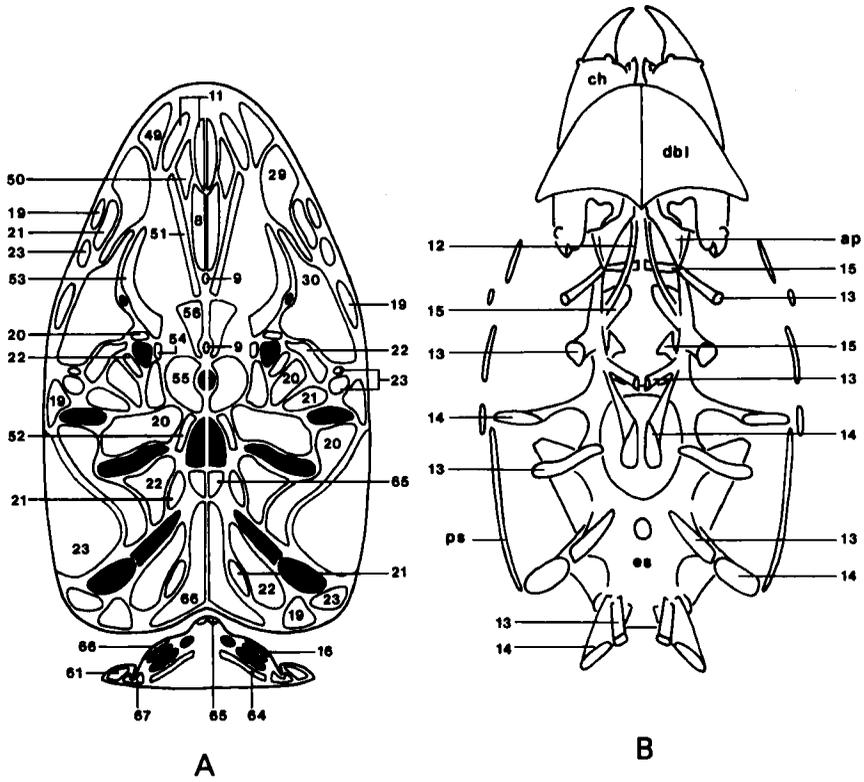
No. Name	Description	Proposed function and evolution	Proposed homology
84 Anterior pulmonary m	Paired. Arises from lateral surface of operculum (VIII) or intersternal membrane (IX); inserts on anterior surface of pulmonary sinus (Fig. 9)	Dilator of pulmonary sinus	***
85 Lateral pulmonary m	Paired. Arises from dorsal surface of lateral pulmonary process; inserts on adjacent regions of ventral pleural fold (Figs 7, 9)	Function uncertain. Lateral pulmonary process may act as a valve to close venous route from pulmonary sinus to heart. Muscle 85 may open valve	***
86 Anterior gonopodial m	Paired, both sexes. Arises from posterolateral margin of sternite VIII; passes posteriorly deep to 18a and 68; inserts on tip of gonopodial process (Fig. 9)	Gonopodial abductor. The gonopod is probably homologous to the telopodite in the opisthosomal opercula in Xiphosura	Araneae: WR 96?
87 Lateral gonopodial m	Paired, both sexes. Arises from posteromedial surface of anterior operculum; passes anterodorsally; inserts on ventral surface of gonopodial process (Fig. 9)	Gonopodial adductor	Xiphosura: LBB 114?
88 Posterior gonopodial m	Paired, both sexes. Arises from posteromedial surface of anterior operculum; passes anterodorsally; inserts on ventral surface of gonopodial process (Fig. 9)	Gonopodial levator	Xiphosura: LBB 114?
89 Anterior gonoporal m	Paired, male only. Arises from ventromedial surface of anterior operculum; passes posteriorly; inserts on lateral margin of gonoporal sclerite. Not illustrated	Function unclear. May act to stabilize the gonoporal sclerite during construction of spermatophore	***
90 Posterior gonoporal m	Paired, male only. Arises from ventral surface of gonopodial sclerite near its tip; passes posteriorly; inserts on lateral margin of gonoporal sclerite. Not illustrated	Function unclear. May act to stabilize the gonoporal sclerite during construction of spermatophore	***

dilators by muscles derived from the primitive dorsal dilator (muscles 8, 9) and extrinsic muscles of the palpal coxae (muscle 33).

I suggest that evolutionary changes associated with the formation of the pharyngeal complex in Pedipalpi (Fig. 10) uncoupled the mechanics of feeding from the mechanics of locomotion, an evolutionary transformation that may have allowed these processes to be performed efficiently at the same time. Because the primitive ingestive and locomotor mechanisms involve many of the same skeletal elements (specifically, the carapace and endosternite), it is possible that the patterns of force generated during the two activities were incompatible or interfered with one another to an extent that they could not be performed effectively at the same time. In the plesiomorphic process of hydraulic leg extension, fluid pressure is increased by dorsoventral compression of the prosoma by the endosternal suspensor muscles (muscles 13–15) (Shultz, 1991). In addition, the endosternite serves as the internal skeletal attachment for extrinsic leg muscles (Fig. 5). Similarly, contraction of the dorsal dilator in the primitive pharyngeal apparatus would have tended to compress the prosoma dorsoventrally, and contraction of the posterior pharyngeal dilators would place tension on the endosternite. The evolution of a new extrinsic pharyngeal skeleton (that is, the epipharyngeal sclerite and enlarged processes of the palpal coxae) may have allowed the pharyngeal dilators to contract strongly without affecting the locomotor apparatus and vice versa. Feeding and locomotion could thus be performed effectively at the same time. One prediction of this hypothesis is that pharyngeal dilators can function effectively during locomotion in whipscorpions but not in arachnids that retain a more primitive pharyngeal complex, such as spiders. The events in the apparent evolution of the primary components of the pedipalpid pharyngeal complex are discussed below.

#### *Epipharyngeal sclerite and dorsal pharyngeal dilators*

Superficially, the epipharyngeal sclerite in *Mastigioproctus* appears to be a posterior projection of the labral epistome (Figs 2, 3) but is, in fact, a separate structure representing a sclerotized invagination of the intercheliceral septum (Pocock, 1902; Snodgrass, 1948). The dorsal pharyngeal dilator (muscle 7) inserts on the ventral margin of the sclerite, and the epipharyngeal muscles (muscles 8, 9) arising from the carapace insert along its dorsal margin (Figs 2, 3). A weakly developed epipharyngeal complex may be synapomorphic for the megoperculate arachnids (that is, Palpigradi, Araneae, Uropygi, Amblypygi), although it is especially well developed in Pedipalpi and absent in Araneae. In palpigrades (specifically *Eukoenenia mirabilis*), which may be the plesiomorphic sister to the other orders (Shultz, 1990), the dorsal pharyngeal dilator has two components, a small anterior component that intersects the membranous intercheliceral septum as it passes anterodorsally to the carapace and a large posterior component that passes directly to the carapace (Roewer, 1934; Millot, 1943). Spiders appear to lack the anterior component, or at least the intersection with the intercheliceral septum (Whitehead & Rempel, 1959; Palmgren, 1978; personal observations), while uropygids and amblypygids apparently lack the posterior component. The epipharyngeal apparatus in Uropygi and Amblypygi probably evolved through the enlargement of the primitive anterior element of the dorsal pharyngeal dilator and its intercheliceral attachment.



I suggest that the dorsal elements of the primitive anterior dilator in *Mastigoproctus* [that is, the anterior and posterior epipharyngeal muscles (muscles 8, 9)] function in preventing displacement of the epipharyngeal sclerite caused by contraction of the dorsal pharyngeal dilator. The posterior end of the epipharyngeal sclerite rests against the dorsal surface of the supra-oesophageal ganglion (personal observation), and contraction of the dorsal pharyngeal dilator may cause the sclerite to rotate downward, placing pressure on the ganglion. Contraction of the large, symmetrically paired anterior epipharyngeal muscle (muscle 8) could function in balancing the rotational forces caused by contraction of the dorsal dilator (Fig. 3). I further suggest that the unusual bilateral asymmetry of the small posterior epipharyngeal muscle (muscle 9) allows displacement of the epipharyngeal sclerite to be detected. Downward rotation of the sclerite would generate different tensile forces on each component of the posterior muscle; these forces would be identical if the muscle was symmetrically paired. Detection of tensile asymmetry in the posterior muscle could provide proprioceptive information to allow compensatory contraction by the anterior epipharyngeal muscle. Intramuscular tension receptors such as those required by the hypothesis developed here have been identified in scorpions and other arthropods (Bowerman, 1972a, b; Root, 1990).

#### *Palpal processes and posterior pharyngeal dilators*

The posterior pharyngeal dilators in *Mastigoproctus* and other pedipalps arise from large anterior processes on the palpal coxae (Figs 2, 3, 5, 10), but in spiders they arise from the anterior endosternal horns (Fig. 10), an organization that is regarded here as primitive. In fact, an entire complement of muscles once associated with the endosternal horns has apparently 'migrated' to the anterior process of the palpal coxae. These muscles include the dorsal and ventral endosternal suspensors of somite II (muscles 13, 15) (identified here for the first time) and at least three extrinsic muscles of the palpal coxae (muscles 30, 32, 33) (Fig. 10). The 'migratory muscle' hypothesis conflicts with generally accepted notions of morphological evolution in arachnids as it calls for muscle

---

Figure 2. Muscular anatomy of the prosoma and first opisthosomal somite in *Mastigoproctus giganteus*. A, Dorsal view of the carapace and first opisthosomal tergite showing approximate sites of muscular attachment. Extrinsic appendicular muscles of odd-numbered post-oral (I, III, V) somites are indicated on the left side and even-numbered somites (II, IV, VI) are indicated on the right side (see also Fig. 4). Attachments of endosternal suspensor muscles are depicted in black. B, Dorsal view of prosoma and first opisthosomal somite with carapace and tergite removed to show chelicerae (ch), anterior carapacial doublure (dbl), pleural sclerites (ps), endosternite (es) and anterior processes of palp coxae (ap). Dorsal, dorsolateral and ventral endosternal suspensors (muscles 13–15) of odd-numbered post-oral somites are indicated on the left side and even-numbered somites on the right side. Note that the anterior doublure is continuous with the carapace (see Fig. 3). C, Dorsal view of the ventral exoskeleton of the prosoma and first opisthosomal somite. Three sternal elements are depicted, namely the anterior sternum (ast), posterior sternum (pst) and first opisthosomal sternite (st VII) or metasternum. The palpal coxae (cxp) are fused with one another and with the labrum. The labrum is composed of a flexible lobe (lal) and sclerotized epistome (est). The epipharyngeal sclerite (eph) attaches firmly to the epistome but represents a sclerotized invagination of the intercheliceral septum. The coxae of all post-cheliceral appendages are equipped with two processes, an anterior process and posterior process. The ventral endosternal suspensors (muscle 15) of somites V–VII arise from the ventral surface of the endosternite and insert on the posterior processes of coxae 2–4.

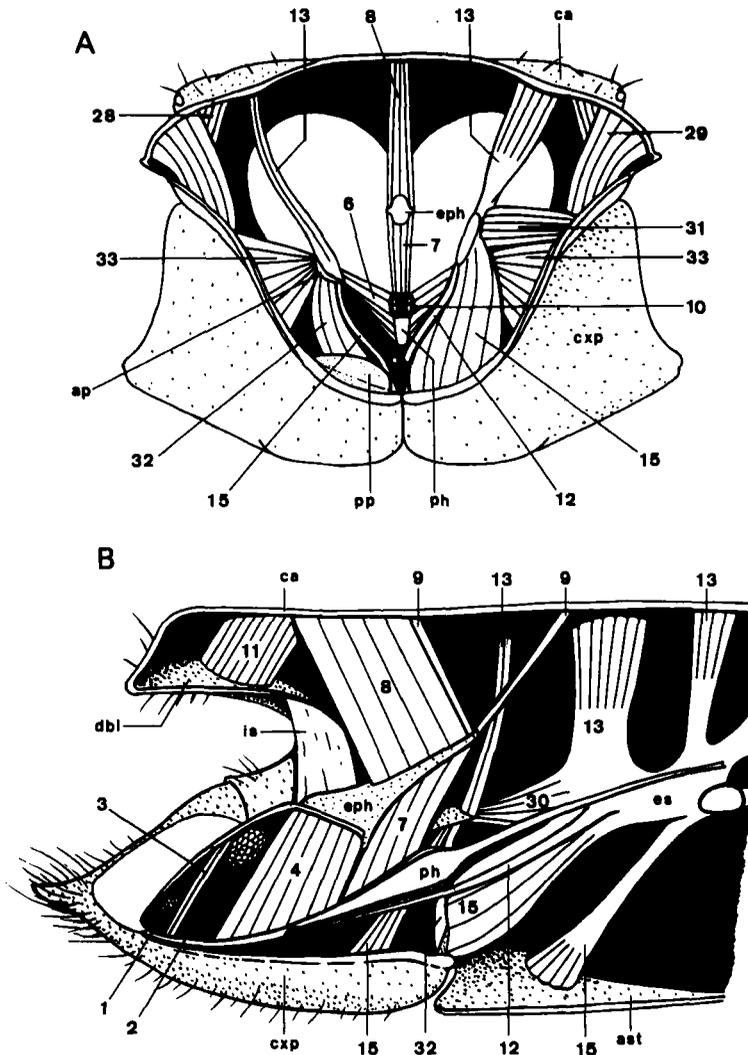


Figure 3. Skeletomuscular anatomy of the anterior region of the prosoma and pharyngeal apparatus with chelicerae and cheliceral muscles removed. A, A posterior cross-sectional view of the prosoma. The left half depicts palpal muscles with the anterior endosternal horn and associated muscles removed. B, A sagittal section of the anterior region of the prosoma showing muscles associated with the pharyngeal apparatus. Note that the extrinsic pharyngeal muscles arise from a skeletal framework formed by the epipharyngeal sclerite and anterior processes of the palpal coxae. Abbreviations: ap, anterior process of palpal coxa; ast, anterior sternum; ca, carapace; cxp, palpal coxa; dbi, anterior carapacial doublure; eph, epipharyngeal sclerite; es, endosternite; is, intercheliceral septum; ph, pharynx; pp, posterior process of palpal coxa.

attachments to shift from a mesodermal structure, the endosternite, to an ectodermal structure, the anterior process of the palpa coxa (Firstman, 1973). However, this hypothesis provides the simplest explanation for a suite of unusual features in the pharyngeal complex. Specifically, the hypothesis identifies two atypical muscles (muscles 32, 33) that arise and insert within the palpal coxa as modified 'extrinsic' endosternocoxal muscles whose endosternal attachments have migrated with the posterior pharyngeal dilator (muscle 6) to the coxal

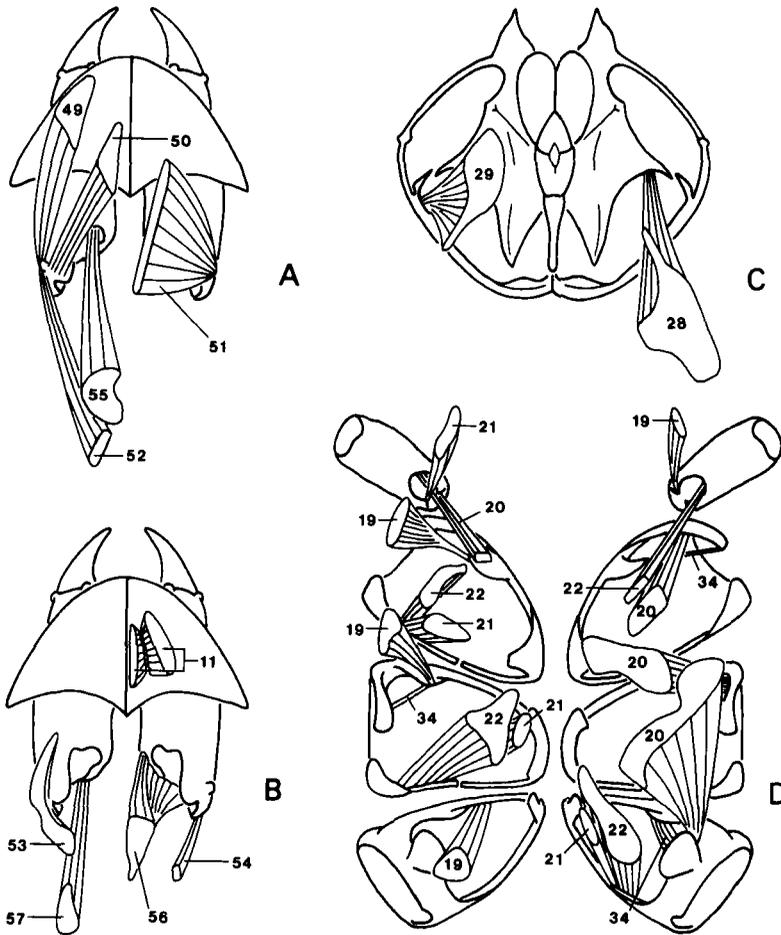


Figure 4. Dorsal view of extrinsic appendicular muscles arising from the prosomal carapace. A, B, Tergochelicer muscles (49–57) and anterior doublure muscle (11). C, Palpal tergocoxal muscles (28, 29). D, Pedal tergocoxal muscles (19–22) and intracoxal muscle (34). See Table 1 for details; compare with Fig. 2.

process. It also accounts for the firm connective tissue attachment between the anterior coxal processes and anterior endosternal horns (see Table 1: 30). Finally, the hypothesis explains the presence of apparent dorsal and ventral 'endosternal' suspensors (muscles 13, 15) that appear to arise from the terminus of the coxal process. Alternative explanations for the origin of the pharyngeal complex in Pedipalpi would require the independent origin of several new muscles that attach to the coxal process and the independent loss of an equal number that attached to the endosternite.

The proposal that muscular attachments can migrate from the mesodermally derived endosternite to the ectodermally derived exoskeleton may also have phylogenetic significance, as surveys of endosternal structure have yielded possible synapomorphies at the ordinal level (Firstman, 1973; Shultz, 1990). For example, the presence of two pairs of prosomal endosternal suspensors has been hypothesized as synapomorphic for the clade comprising Opiliones, Scorpiones,

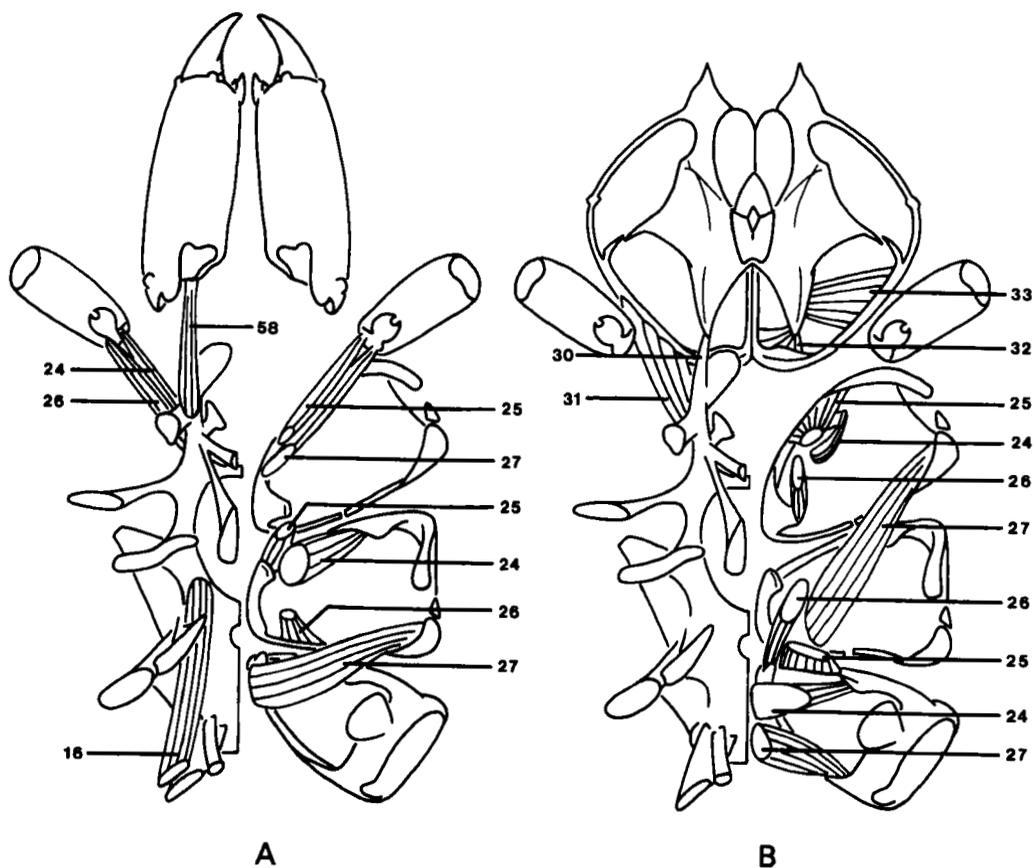


Figure 5. Dorsal view of the endosternotergal muscle (16) and extrinsic appendicular muscles arising from the prosomal endosternite (cf. Fig. 2). Note that muscles 32 and 33 arise and insert within the palpal coxa. It is hypothesized here that muscular components associated with the anterior endosternal horn, including these extrinsic palpal muscles, shifted their attachment to the anterior process of the palpal coxae. See Fig. 10 and text for details.

Pseudoscorpiones and Solifugae (that is, Dromopoda in Shultz, 1990). However, examinations of scorpions (Lankester, Benham & Beck, 1885; Vyas, 1974; personal observation) have revealed evidence of an evolutionary transformation analogous to that discovered in Pedipalpi. Specifically, the anterior endosternal horns of scorpions attach to the posterior ends of large, bilateral epistomal processes, and there has been an apparent migration of pharyngeal dilators, extrinsic cheliceral muscles and up to three pairs of dorsal suspensor muscles from the endosternite to the epistomal processes. Further research is needed to establish the ontogenetic process underlying this novel class of evolutionary migrations as well as its evolutionary frequency and functional significance.

#### *Evolutionary morphology of the anterior opisthosoma and reproductive apparatus*

Comparative arachnologists have traditionally relied on external landmarks when homologizing elements of the exoskeleton, an approach that has resulted in several conflicting interpretations of the ventral sclerites of uropygids and their

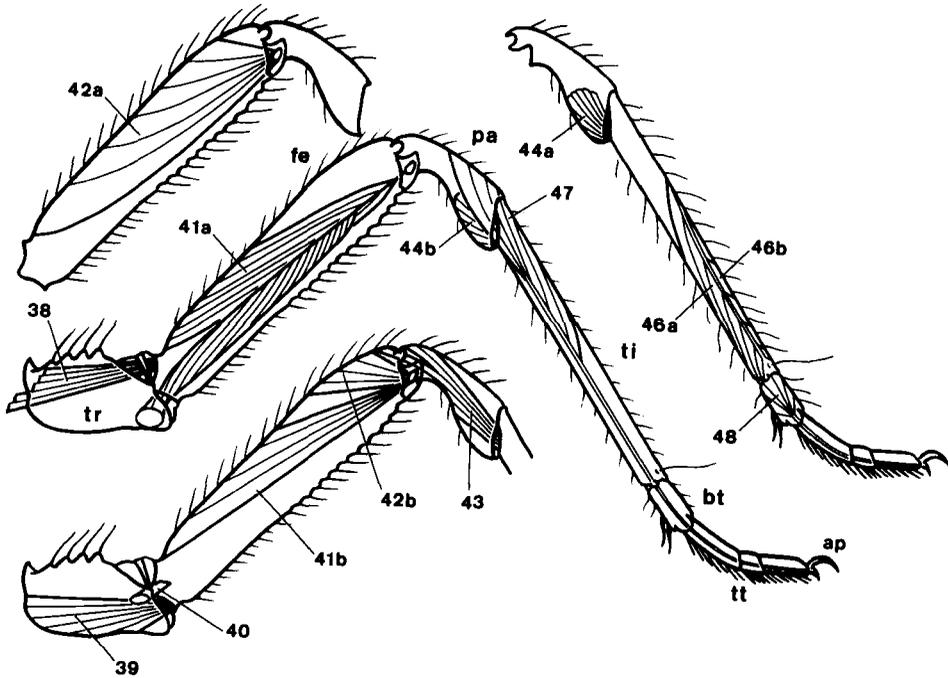


Figure 6. Anterior view of telopodial segments of left leg 4. Abbreviations: ap, apotele; bt, basitarsus, fe, femur; pa, patella, ti, tibia; tr, trochanter; tt, telotarsus.

relatives. In the present analysis, muscle morphology was used to establish explicit criteria for distinguishing sternites from other ventral opisthosomal sclerites. Dissections of *Mastigoproctus* and other arachnids, notably scorpions, indicate that sternites provide attachments for three muscle groups: dorsoventral muscles (muscle 17), intersternal muscles (muscle 68) and ventral longitudinal muscles (muscle 18). In addition to providing means for distinguishing sternites from other sclerites, the metameric organization of these muscle groups provides criteria for establishing the somite to which a particular sternite belongs. Specifically, the paired dorsoventral muscles (muscle 17) pass from a tergite to the sternite of the same somite. Intersternal muscles (muscle 68) arise anteriorly from one sternite and pass posteriorly to insert on the posteriorly adjacent sternite along its anterior margin. The paired ventral longitudinal muscles (muscle 18) may pass from one sternite to another as well, inserting at the attachment of the dorsoventral muscles. However, their course may be interrupted by endosternal elements, such as the pectinal endosternite in scorpions, and therefore may attach to the sternite only indirectly through ventral endosternal suspensors. Interpretations of the opisthosomal sclerites in *Mastigoproctus* derived from these muscular criteria are unambiguous and mutually supportive but conflict with previous interpretations based on external morphology.

The sternite of the first opisthosomal somite (VII) is a large, subtriangular sclerite located between the coxae of the fourth leg pair (Figs 1, 2, 7). This interpretation is consistent with the muscular criteria used here for homologizing sternites. (1) The ventral endosternal suspensor (muscle 15) that corresponds to

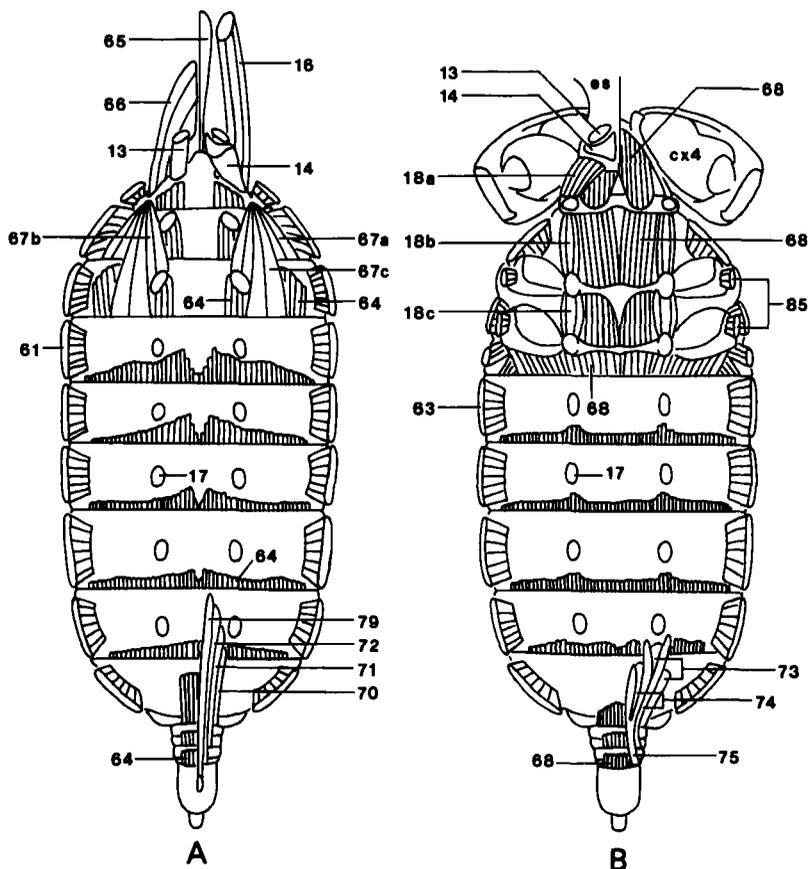


Figure 7. Skeletomuscular anatomy of the opisthosoma. A, A ventral view of the dorsal exoskeleton; B, a dorsal view of the ventral exoskeleton. See Fig. 8 for detailed illustration of the pygidium and Fig. 9 for detailed illustration of anterior sternites and opercula. Abbreviations: cx, coxa; es, endosternite.

the unambiguous dorsal endosternal suspensor of somite VII inserts on the anterolateral portion of the sclerite, where it attaches to the medial margin of coxa 4 (Fig. 2). This arrangement indicates that the metasternum represents sternite VII as the dorsal and ventral endosternal suspensors (muscles 13, 15) are metamERICALLY homologous with the dorsoventral muscles (muscle 17) of the more posterior opisthosomal somites. (2) A large intersternal muscle (muscle 68) arises from the ventral surface of this sclerite and inserts on the anterior margin of the second opisthosomal sternite (VIII) and its associated membranes (Fig. 7). (3) The ventral longitudinal muscles associated with somite VII insert at the posterior border of the endosternite and so would not be expected to have a direct sternal attachment but to attach indirectly via the ventral endosternal suspensor.

Arachnologists have traditionally regarded sternite VII as a prosomal structure equivalent to the sternite of somite VI (Börner, 1902; Hansen & Sørensen, 1905; Millot, 1949c; Petrunkevitch, 1955; Savory, 1964; Kaestner, 1968), but this sclerite had been identified correctly as the first opisthosomal

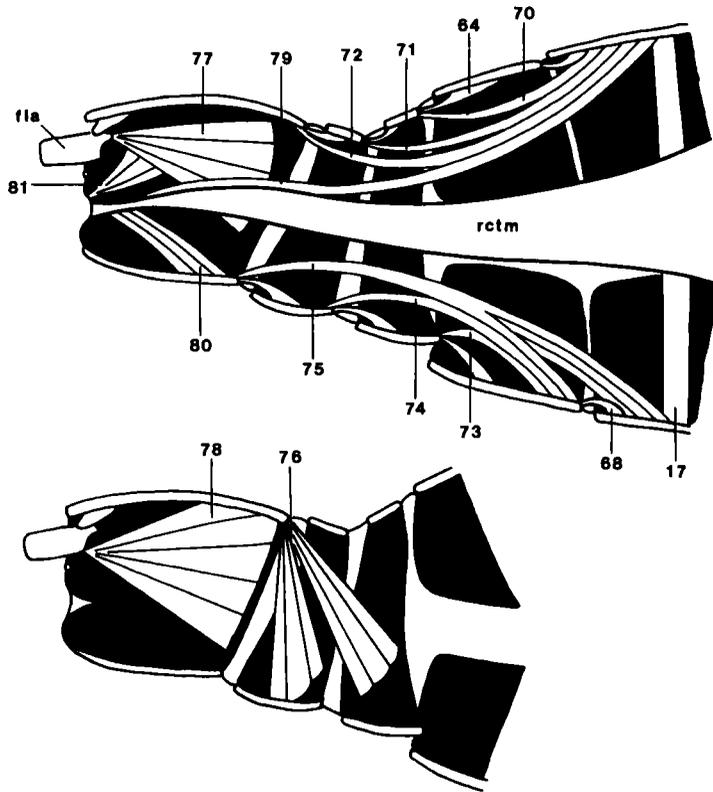


Figure 8. Sagittal view of pygidial and extrinsic rectal muscles. Abbreviations: fla, flagellum; rectm, rectum.

sternite in several recent studies (van der Hammen, 1989; Stockwell, 1989). The incorporation of the first opisthosomal sternite as a functional component of the prosoma is consistent with current understanding of chelicerate evolution, as the appendages of somite VII are integrated into the prosomal feeding apparatus as chilaria in xiphosurans (Manton, 1964) and, perhaps, as the metastoma in eurypterids (Størmer, 1944; Weygoldt & Paulus, 1979; cf. Selden, 1981). The conclusion presented here also refutes the traditional notion that the pedicel or 'waist' of tetrapulmonate arachnids represents a modification of the prosoma–opisthosoma juncture. The ventral components of the pedicel are actually located between the first and second opisthosomal somites (VII–VIII) (Shultz, 1990).

The sternite of the second opisthosomal somite (VIII) is a small sclerite located within the deep ventral fold between sternite VII and the anterior operculum (Figs 1, 7, 9). Three lines of evidence support this interpretation. (1) The sclerite serves as the ventral attachment of the dorsoventral muscles (muscle 17) arising from the second opisthosomal tergite (VIII) (Figs 7, 9). (2) The anterior margin of the sclerite receives fibres from the intersternal muscle (muscle 68) arising from sternite VII, and an additional intersternal muscle arises from the posterior margin of the sclerite and inserts on the anterior margin of sternite IX (Figs 7, 9). (3) The anterior and posterior pairs of ventral

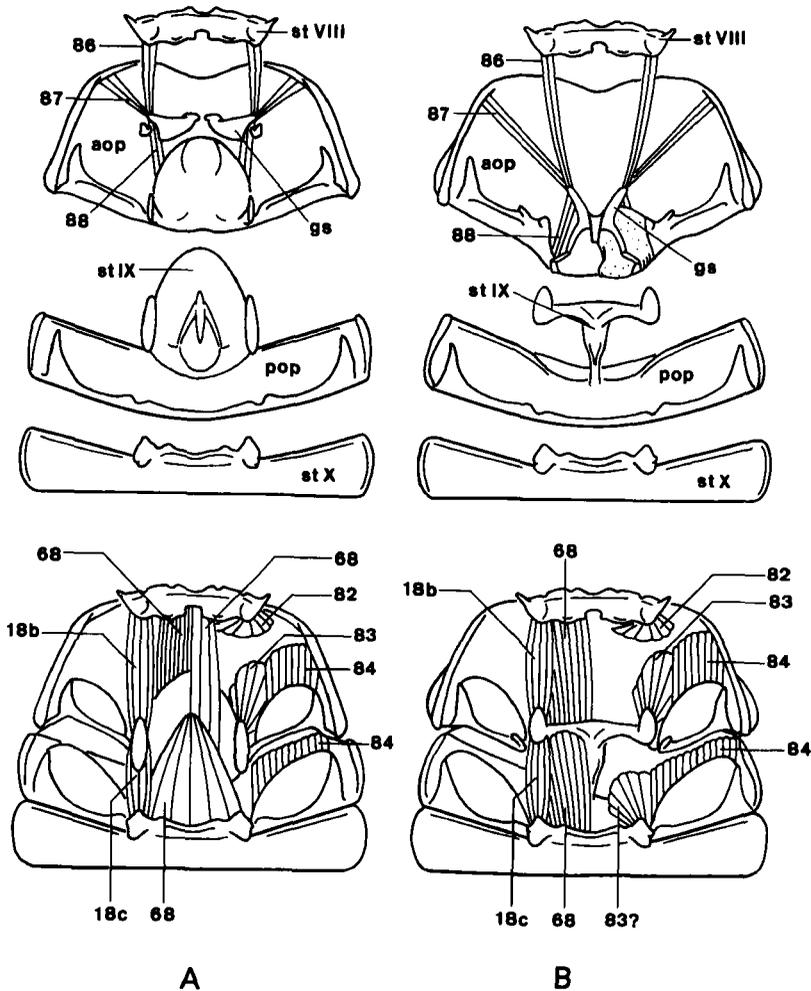


Figure 9. Dorsal view of ventral sclerites of the anterior opisthosomal region and genital apparatus in adult female (A) and adult male (B). The upper drawings depict the disarticulated sternites and opercula and the gonopodial muscles. The membranous regions of the right gonopod in the male are removed to show muscle 88. Abbreviations: aop, anterior (genital) operculum; gs, gonopodial sclerite; pop, posterior operculum; st, sternite.

longitudinal muscles (muscle 18) intersect the sclerite at the insertion of the dorsoventral muscles, the anterior pair arising from the endosternite and the posterior pair from sternite IX (Figs 7, 9).

The external opening to the reproductive tract in Chelicerata is located on the second opisthosomal somite, and the gonopore has therefore been regarded as a prime external landmark for identifying sternite VIII. However, because of the substantial distance between sternite VIII and the apparent genital opening (Fig. 1), it is unlikely that workers relying on external features alone would recognize the actual homology of this structure. In fact, sternite VIII is misidentified as 'sternite VII' in the traditional interpretation (Börner, 1902, etc.). However, certain workers who have correctly identified the metasternum

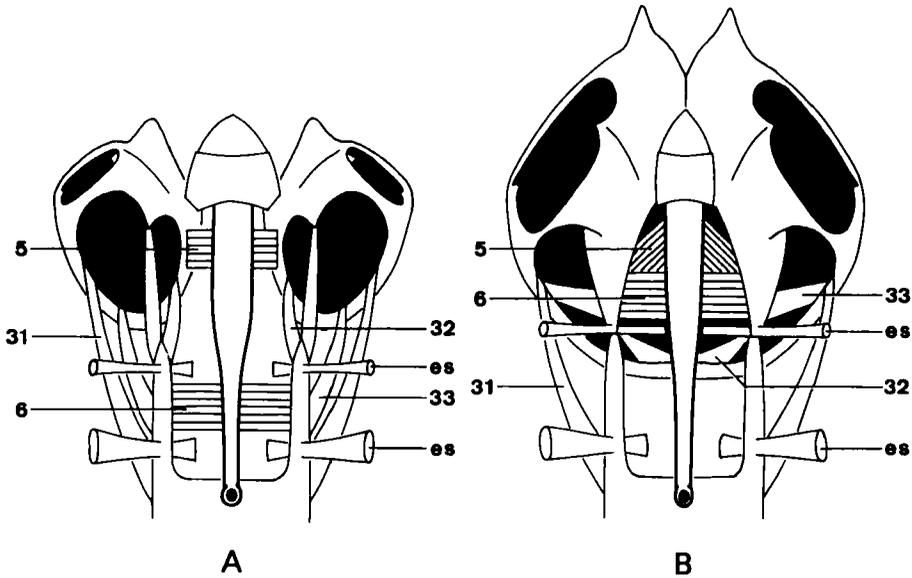


Figure 10. Dorsal views of pharyngeal region showing extrinsic palpal muscles, pharyngeal dilators and endosternite in a hypothetical spiderlike arachnid (A) and a *Mastigoproctus*-like pedipalpid (B) (cf. Figs 2, 3, 5). It is suggested that the palpo-pharyngeal complex of pedipalps evolved by migration of muscular insertions from the anterior endosternal horn to the enlarged anterior process of the palpal coxa. See text for details. Abbreviations: es, endosternal suspensor (dorsal and ventral).

as sternite VII mistakenly regard the anterior operculum as sternite VIII and ignore the true sternite altogether.

The sternite of the third opisthosomal somite (IX) is located within the deep fold (pre-genital chamber) between the anterior and posterior opercula. The sternite is not visible externally and has therefore been overlooked by virtually all comparative arachnologists. It is sexually dimorphic and highly modified in each sex. Despite its modifications, however, sternite IX can be recognized in both sexes using the muscular criteria proposed here.

In the male, sternite IX is a T-shaped sclerite with the thin stem of the T firmly attached to the anteromedian margin of the posterior operculum (Fig. 9). Each lateral arm ends in a large, anteriorly projecting process that serves as a site of attachment for dorsoventral muscles (muscle 17) arising from tergite IX and ventral longitudinal muscles (muscles 18b, 18c) arising from sternite VIII anteriorly and sternite X posteriorly. The ventral surface of each arm is firmly connected to the posterior margin of the anterior operculum medial to the book lungs and lateral to the genital opening. The transverse region of sternite IX receives fibres from two sheetlike intersternal muscles (muscle 68), an anterior muscle arising from sternite VIII and a posterior muscle arising from sternite X.

In the female, sternite IX is a poorly sclerotized (leathery), oval 'sclerite' that forms the roof of the large pre-genital chamber (Fig. 9). The posterolateral margins of this structure bear processes similar to those of the male that serve as attachment sites for the same dorsoventral and ventral longitudinal muscles (muscles 17, 18). A V-shaped sclerite is embedded within the leathery sternite with the apex pointing anteriorly. Intersternal muscles (muscle 68) arising from

sternite VIII insert on the anterior margin of the sternite and the anterior margin of the V-shaped intrasternal sclerite. The posterior intersternal muscles pass from the posterior margin of the V-shaped sclerite and pass the anterior margin of sternite X.

The two large sclerites referred to here as the anterior and posterior opercula (Fig. 1) are traditionally regarded as sternites VIII and IX, respectively. However, the muscular criteria established here clearly show sternites VIII and IX to be small sclerites that have been either misidentified or overlooked by comparative arachnologists. In contrast, at least three lines of evidence suggest that the anterior and posterior opercula represent modified appendages of somites VIII and IX, respectively. (1) Based on the similarity of their cuticular structures and patterns of muscle attachment, the anterior and posterior opercula appear to represent homonomous (metamerically homologous) structures. (2) Both opercula bear respiratory lamellae (book lungs). Comparisons with primitively aquatic chelicerates (for example, xiphosurans and fossil scorpions) show that respiratory lamellae represent a specialized portion of an opisthosomal appendage. (3) Appendage-like structures equipped with extrinsic muscles are present on the anterior operculum and are used as

TABLE 2. Unique synapomorphies of the orders Amblypygi and Uropygi. Character polarity was established by outgroup comparisons with Araneae and Palpigradi

No. Characters	Plesiomorphic state	Apomorphic state
1 Palp	Leglike	Raptorial
2 Leg I	Ambulatory	Tactile, antenniform
3 Sternum	Undivided	Divided into two or more sclerites
4 Gonoporal brood sac	Absent	Present
5 Stalked spermatophore	Absent	Present
6 Telotarsus, legs 2-4	Undivided	Divided into three tarsomeres
7 Femur-patella flexor of legs (42)	Symmetrical insertion on patella	Asymmetrical insertion on patella
8 Coxa 4 and sternite VII	Separate	Fused
9 Posterior femoropatella-tibia muscle (43), legs 2-4	Present	Absent
10 Ventral pharyngeal dilator m	Present	Absent
11 Ventral endosternal suspensors (15)	All inserting on sternite	Some inserting on coxae of anteriorly adjacent somite
12 Patellotibia-tarsus m (45), legs	Present	Absent
13 Opisthosomal pleural membrane; pleural muscles (61-63)	Membrane without longitudinal folds; muscle undivided	Membrane with two longitudinal folds dividing muscle into three components
14 Ventral longitudinal muscles (18)	Spanning length of opisthosoma	Spanning first three opisthosomal somites
15 Palpo-pharyngeal complex	Absent	Present
A Dorsal and ventral endosternal suspensor m (II) (13, 15)	Originating from anterior endosternal horn	Originating from anterior process of palpal coxa
B Posterior extrinsic pharyngeal dilator m (6)	Originating from anterior endosternal horn	Originating from anterior process of palpal coxa
C Anteromedial endosternocoxal muscle of palp (32)	Originating from anterior horn of endosternite	Originating from anterior process of palpal coxa
D Posteromedial endosternocoxal muscle of palp (33)	Originating from anterior horn of endosternite	Originating from anterior process of palpal coxa
16 Epipharyngeal sclerite	Absent or poorly developed	Well developed
17 Anterior coxal process	Absent or poorly developed	Well developed
18 Posterior dorsal extrinsic pharyngeal m	Present; spanning uninterrupted from pharynx to carapace	Absent or highly modified

gonopods in both sexes. These structures may correspond to telopodites of opisthosomal appendages such as occur in Xiphosura. The posterior operculum in *Mastigoproctus* lacks these appendage-like structures, but they are apparently retained in Amblypygi. Kaestner (1968) notes that some amblypygids have '... a pair of median, thin-walled, chitinous sacs in the intersegmental membrane ...' between the posterior operculum and sternite X '... that can be everted by blood pressure and pulled back by muscles.' I concluded that the anterior and posterior opercula represent highly modified appendages of somites VIII and IX.

Among living chelicerates, only xiphosurans retain a primitively marine lifestyle and well-developed opisthosomal appendages. Therefore, an understanding of the evolution of opisthosomal appendages in arachnids must depend largely upon interpretations derived from comparisons with xiphosurans. Using the post-genital appendages of *Limulus* as a general model of the primitive arachnid opisthosomal appendages, I suggest that the opercula in *Mastigoproctus* and its relatives represent the basal portion of fused appendages that have lost their intrinsic segmentation and have greatly expanded their haemocoelic connection with the opisthosoma. The telopodites associated with somite VIII appear to have fused basally (at least in males) but have retained their extrinsic musculature and now function as gonopods. The evolutionary fusion and expansion of the opisthosomal appendages resulted in the reduction and anterior displacement of the sternites such that the sternites came to lie within the apparent intersegmental folds between the opercula. The result of this evolutionary process was an apparent anterior displacement and 'internalization' of sternites VIII and IX in the megoperculate arachnids. This proposal is consistent with the hypothesis that the gonopods of uropygids and amblypygids are homologous with those of eurypterids, which are thought to represent the fused telopodites associated with the genital somite (Weygoldt, Weisemann & Weisemann, 1972; Weygoldt & Paulus, 1979).

#### *Phylogenetic implications*

Few exhaustive studies of arachnid musculature are available for comparison with the present work, and phylogenetic inferences derived from the available evidence must be regarded as tentative. However, a comparison of the skeletomuscular morphology of *Mastigoproctus* with the scattered descriptions of amblypygids (Pocock, 1902; Millot, 1949a), spiders (Whitehead & Rempel, 1959; Palmgren, 1978) and palpigrades (Roewer, 1934; Millot, 1942, 1943) provide a substantial list of apparently unique synapomorphies for Uropygi and Amblypygi (Table 2). In recent decades, Amblypygi and Araneae have been regarded as sister taxa because of three apparent synapomorphies: a narrow prosoma-opisthosoma juncture (pedicel), a well-developed postcerebral pharynx, and absence of opisthosomal ganglia (Kaestner, 1968; Platnick & Gertsch, 1976; Weygoldt & Paulus, 1979; van der Hammen, 1989). Uropygi was regarded as the sister to the Araneae-Amblypygi clade. However, Shear *et al.* (1987) proposed that Amblypygi and Uropygi are sister taxa (Table 2: characters 1-4) and that Araneae is the sister to the Amblypygi-Uropygi clade (Pedipalpi). This hypothesis was corroborated by additional characters (Table 2: characters 5-7) (Shultz, 1989, 1990). The addition of 11 more

characters by the present investigation makes Pedipalpi the most well-supported supraordinal clade in Arachnida.

#### ACKNOWLEDGEMENTS

This study was initiated in the Department of Zoology at Ohio State University and was supported by grants from the Exline-Frizzell Fund for Arachnological Research (California Academy of Sciences) and Sigma Xi.

#### REFERENCES

- Barrows WM. 1925.** Modification and development of the arachnid palpal claw, with especial reference to spiders. *Annals of the Entomological Society of America* **18**: 483–516.
- Börner C. 1902.** Arachnologische Studien, II and III. *Zoologischer Anzeiger* **25**: 433–466.
- Börner C. 1921.** Die Gliedmassen der Arthropoden. In: Lang A, ed. *Handbuch der Morphologie der Wirbellosen Tiere* **4**: 649–694. Jena: Gustav Fischer.
- Bowerman RF. 1972a.** A muscle receptor organ in the scorpion postabdomen I. The sensory system. *Journal of Comparative Physiology* **81A**: 133–146.
- Bowerman RF. 1972b.** A muscle receptor organ in the scorpion postabdomen. II. Reflexes evoked by MRO stretch and release. *Journal of Comparative Physiology* **81A**: 147–157.
- Bowerman RF, Root TM. 1978.** External anatomy and muscle morphology of the walking legs in the scorpion *Hadrurus arizonensis*. *Comparative Biochemistry and Physiology A* **59**: 57–63.
- Coddington JA, Levi HW. 1991.** Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* **22**: 565–592.
- Ewing HE. 1928.** The legs and leg-bearing segments of some primitive arthropod groups, with some notes on leg-segmentation in the Arachnida. *Smithsonian Miscellaneous Collections* **80**: 1–41.
- Firstman B. 1973.** The relationship of the chelicerate arterial system to the evolution of the endosternite. *Journal of Arachnology* **1**: 1–54.
- Firstman B. 1990.** Phylogenetic implications of endosternite development in *Liphistius murphyorum* (Arachnida, Araneae, Mesothelae). *American Arachnology* **42**: 9.
- Firstman B, Benton CLB Jr, 1968.** A comparison of endosternite morphology of a “primitive” true spider, *Filistata hibernalis*, and an atypic mygalomorph spider, *Sphodros* sp., with general comments on inferred endosternite functions in spiders. *American Arachnology* **38**: 5.
- Gaubert P. 1892.** Recherches sur les organes des sens et sur les systèmes tégumentaire, glandulaire et musculaire des appendices des Arachnides. *Annales des Sciences Naturelles (Zoologie), Series 7* **13**: 31–184.
- Hansen HJ, Sörensen W. 1905.** The Tartarides, a tribe of the order Pedipalpi. *Arkiv für Zoologi* **2**: 1–78.
- Kaestner A. 1968.** *Invertebrate Zoology, Vol. 2*. New York: John Wiley & Sons.
- Lankester ER, Benham WBS, Beck EJ. 1885.** On the muscular and endoskeletal systems of *Limulus* and *Scorpio*; with some notes on the anatomy and generic characters of scorpions. *Transactions of the Zoological Society of London* **11**: 311–384.
- Manton SM. 1958.** Hydrostatic pressure and leg extension in arthropods, with special reference to arachnids. *Annals and Magazine of Natural History, Series 13* **1**: 161–183.
- Manton SM. 1964.** Mandibular mechanisms and the evolution of arthropods. *Philosophical Transactions of the Royal Society* **247**: 1–183.
- Millot J. 1942.** Sur l'anatomie et l'histophysiologie de *Koenenia mirabilis* Grassi (Arachnida Palpigradi). *Revue de française Entomologie* **9**: 127–135.
- Millot J. 1943.** Notes complémentaires sur l'anatomie, l'histologie et la répartition géographique en France de *Koenenia mirabilis* Grassi. *Revue de française Entomologie* **9**: 127–135.
- Millot J. 1949a.** Ordre des Amblypyges. In: Grassé P-P, ed. *Traité de Zoologie* **6**: 563–588.
- Millot J. 1949b.** Ordre des Aranéides. In: Grassé P-P, ed. *Traité de Zoologie* **6**: 589–743. Paris: Masson.
- Millot J. 1949c.** Ordre des Uropyges. In: Grassé P-P, ed. *Traité de Zoologie* **6**: 533–562. Paris: Masson.
- Palmgren P. 1978.** On the muscular anatomy of spiders. *Acta Zoologica Fennica* **155**: 1–41.
- Petrunckevitch A. 1955.** Arachnida. In: Moore RC, ed. *Treatise on invertebrate paleontology, Part P, Arthropoda* **2**: 42–162. Lawrence, Kansas: Geological Society of America and University of Kansas Press.
- Platnick NI, Gertsch WJ. 1976.** The suborders of spiders: a cladistic analysis (Arachnida, Araneae). *American Museum Novitates* **2607**: 1–17.
- Pocock RI. 1902.** On some points in the anatomy of the alimentary and nervous systems of the arachnid suborder Pedipalpi. *Proceedings of the Zoological Society of London* **2**: 169–188.
- Roewer C-F. 1934.** Solifugae, Palpigradi. *Bronns Klassen und Ordnungen des Tierreichs* **5**: 1–713.
- Root TM. 1990.** Neurobiology. In: Polis GE, ed. *The biology of scorpions*. Stanford, California: Stanford University Press, 341–413.

- Ruhland M, Rathmayer W. 1978.** Die Beinmuskulatur und ihre Innervation bei der Vogelspinne *Dugesella hentzi* (Ch.) (Araneae, Aviculariidae). *Zoomorphologie* **89**: 33–46.
- Savory T. 1964.** *Arachnida*. London: Academic Press.
- Selden PA. 1981.** Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata; Eurypterida). *Transactions of the Royal Society of Edinburgh: Earth Sciences* **72**: 9–48.
- Selden PA, Shear WA, Bonamo PM. 1991.** A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. *Palaeontology* **34**: 241–281.
- Shear WA, Selden PA, Rohlfs WDI, Bonamo PM, Grierson JD. 1987.** New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). *American Museum Novitates* **2901**: 1–74.
- Shultz JW. 1989.** Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. *Zoological Journal of the Linnean Society* **97**: 1–56.
- Shultz JW. 1990.** Evolutionary morphology and phylogeny of Arachnida. *Cladistics* **6**: 1–38.
- Shultz JW. 1991.** Evolution of locomotion in Arachnida: the hydraulic pressure pump of the giant whipscorpion, *Mastigoproctus giganteus* (Lucas) (Uropygi). *Journal of Morphology* **210**: 13–31.
- Shultz JW. 1992a.** Muscle firing patterns in two arachnids using different methods of propulsive leg extension. *Journal of Experimental Biology* **162**: 313–329.
- Shultz JW. 1992b.** Step-coupled pressure fluctuations may constrain stepping rates in whipscorpions (Uropygi). *Journal of Arachnology* **20**: 148–150.
- Snodgrass RE. 1948.** The feeding organs of Arachnida, including mites and ticks. *Smithsonian Miscellaneous Collections* **110**: 1–93.
- Snodgrass RE. 1952.** *A textbook of arthropod anatomy*. Ithaca, New York: Comstock.
- Stockwell SA. 1989.** *Revision of the phylogeny and higher classification of scorpions (Chelicerata)*. Ph.D. thesis, University of California, Berkeley.
- Størmer L. 1944.** On the relationships and phylogeny of fossil and Recent Arachnomorpha. *Skrifter Utgitt av det Norske Videnskaps-Akademi i Oslo* **5**: 1–158.
- Van der Hammen L. 1989.** *An introduction to comparative arachnology*. The Hague: SPB Academic Publishing Co.
- Vyas AB. 1974.** The cheliceral muscles of the scorpion *Heterometrus fulvipes*. *Bulletin of the Southern California Academy of Sciences* **73**: 9–14.
- Weygoldt P, Paulus HF. 1979.** Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. *Zeitschrift für zoologische Systematik und Evolutionsforschung* **17**: 85–116, 177–200.
- Weygoldt P, Weisemann A, Weisemann K. 1972.** Morphologisch-histologische Untersuchungen an den Geschlechtsorganen der Amblypygi unter besonderer Berücksichtigung von *Tarantula marginemaculata* C. L. Koch (Arachnida). *Zeitschrift für Morphologie der Tiere* **73**: 209–247.
- Whitehead WF, Rempel JG. 1959.** A study of the musculature of the black widow spider, *Latrodectus mactans* (Fabr.). *Canadian Journal of Zoology* **37**: 831–870.
- Wood FD. 1926.** Autotomy in Arachnida. *Journal of Morphology* **42**: 143–185.