GROSS MUSCULAR ANATOMY OF *LIMULUS POLYPHEMUS* (XIPHOSURA, CHELICERATA) AND ITS BEARING ON EVOLUTION IN THE ARACHNIDA

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ABSTRACT. Due to their widespread use as model systems and their reputation as living fossils, horseshoe crabs (Xiphosura) have been studied intensively by physiologists and paleontologists. The close phylogenetic relationship between horseshoe crabs and arachnids might also have been expected to inspire studies of xiphosurans by comparative arachnologists, but surprisingly few have been undertaken. Here, the first exhaustive survey of muscular anatomy of the Atlantic horseshoe crab is conducted as part of an on-going study of the evolutionary morphology and phylogeny of arachnids. Dissections of adult and immature individuals established 113 muscle groups comprising over 750 individual muscles, with several being recognized or correctly described for the first time. New insights into skeletomuscular evolution and phylogeny of arachnids were derived primarily from the axial muscle system. Specifically, it is argued that *Limulus* retains a box-truss axial muscle system like that of plesiomorphic members of other arthropod groups, that this is also a plesiomorphic condition for Chelicerata, and that arachnids are united by the loss of one component of this system, the anterior oblique muscles. Combined with comparative morphological and molecular evidence from previous studies, this study adds greater weight to the widely held view that, among extant chelicerates, Xiphosura and Arachnida are monophyletic sister groups and counters recent speculation that scorpions are more closely related to xiphosurans than to spiders, whipscorpions and other arachnids.

Keywords: Horseshoe crab, morphology, phylogeny, muscles

Due to its large size, availability to investigators and reputation as a "living fossil," the Atlantic horseshoe crab, *Limulus polyphemus* (Linneaus 1758) (Xiphosura, Chelicerata), is one of the most intensively studied invertebrates (e.g., Cohen 1979; Bonaventura et al. 1982; Sekiguchi 1988), and aspects of its external and internal anatomy are routinely depicted in textbooks. Investigations of its skeletomuscular anatomy were undertaken repeatedly in the nineteenth and early twentieth centuries (e.g., Milne-Edwards 1873; Owen 1873), with the works of Lankester (1881, 1885; Lankester et al. 1885) and Patten (1893, 1912; Patten & Redenbaugh 1899–1900; Patten & Hazen 1900) being the most influential. Lankester's work led to the conclusion that *Limulus* is a chelicerate (originally "arachnid") rather than a crustacean, and subsequent workers have tended to adopt his terminology and muscle numbering system (e.g., Snodgrass 1952; Manton 1964; Wyse & Dwyer 1973). Although Patten's studies generally surpassed Lankester's in quality and detail, the reputation of Patten's

descriptive work may have suffered from its association with his failed attempt to demonstrate the origin of vertebrates from chelicerates (Patten 1912). Later workers often based their phylogenetic and functional inferences on these early descriptions (e.g., Versluys & Demoll 1922; Størmer 1944; Fage 1949; Manton 1964; Wyse & Dwyer 1973), and cursory empirical work has tended to corroborate the classic treatments.

Despite the influence of the early anatomical studies, important discoveries were made whenever detailed exploratory surveys were undertaken, especially those focusing on embryonic or larval stages. For example, Iwanoff (1933) showed the chilaria in *Tachypleus gigas* (Müller 1785) (formerly *Limulus moluccans*) to be appendages of postoral somite VII and refuted morphological speculations of Versluys & Demoll (1922), who hypothesized the derivation of xiphosurans from arachnids. Scholl (1977) showed that the dorsal hinge between the cephalothorax and abdomen is a tergal specialization of postoral somite VIII, discovered muscles associated with the pedal

coxae inserting on the walls of the preoral chamber, and showed that postoral somite I (cheliceral somite) migrates rearward during ontogeny and thereby distorts the metameric pattern in the adult. Interestingly, most of these features are also evident in adults and subadults and, as demonstrated here, would have been revealed by more detailed descriptions of these stages. Given that new skeletomuscular features have been discovered by each careful survey of skeletomuscular anatomy, and the absence of a single treatment encompassing all known skeletal muscles, I chose to undertake an exhaustive survey of skeletal muscles in *Limulus*, with the specific goal of integrating the resulting data with those obtained from original dissections of arachnids (Shultz 1993, 1999, 2000).

The present survey documents 113 muscle groups which encompass over 750 individual muscles. Most have been described in earlier studies, but several evolutionarily significant muscles were undescribed, described imprecisely or incorrectly, or described correctly in poorly known publications. These features include 1) two sets of three cheliceral muscles arising on the carapace that are generally depicted as one muscle; 2) four intrinsic cheliceral muscles; 3) a preoral sphincter elaborated from the coxosternal region of the prosoma; 4) muscles that originate on the coxae of legs 1–4 and insert on the preoral chamber; 5) extrinsic chilarial muscles; 6) muscles associated with the chondrites of the opisthosomal appendages (i.e., chilaria and opercula); 7) evidence that the axial muscles of the abdomen are homologous with the box-truss muscle system of other plesiomorphic arthropods; 8) evidence that the so-called "branchio-thoracic" muscles are axial muscles rather than extrinsic muscles of the opercula; 9) evidence that the first six pairs of dorsal endosternal suspensor muscles are members of a single metameric series rather than two different series; 10) thin, sheet-like ligaments connecting the ventral surfaces of the endosternite to the pliable intercoxal cuticle; and 11) the absence of the ventral esophageal dilator muscle described by Lankester et al. (1885). Combined with information currently available for arachnids, these and other new perspectives on the muscular anatomy of *Limulus* provide insights in the phylogeny and evolutionary morphology of arachnids. Notably, this information confirms the widely held view derived from morphological and molecular evidence that Arachnida is monophyletic with respect to Xiphosura and contradicts recent proposals that scorpions are more closely related to xiphosurans than to other arachnids (e.g., van der Hammen 1989; Dunlop 1998).

METHODS

Preserved specimens of *Limulus polyphemus* were obtained from Ward's Natural Science Establishment, Inc. and Carolina Biological Supply Co. and ranged in mid-sagittal carapace length from 2–12 cm. Dissections were performed using a Leica M10 dissecting microscope at magnifications of $1\times$ to $1280\times$. Only standard dissection equipment and techniques were used. Drawings were made with a drawing tube, scanned electronically and transformed into black-and-white bitmaps, which were then enhanced and labeled using a variety of graphics software.

RESULTS

This study does not provide a complete redescription of skeletomuscular anatomy *Limulus* but surveys the skeletal muscles in an attempt to 1) corroborate descriptions of earlier workers (i.e., Lankester et al. 1885; Patten 1912; Snodgrass 1952; Manton 1964; Scholl 1977), 2) clarify ambiguities and correct errors in earlier descriptions, 3) describe "new" features, and 4) document gross muscular anatomy in a manner comparable to descriptions being generated for other chelicerates (Shultz 1993, 1999, 2000). The "Results" section highlights novel observations, but a brief description of all muscles is provided in Table 1 and sources for detailed descriptions are provided in the text. Italicized Arabic numerals refer to the muscles listed in Table 1, and Roman numerals refer to postoral somites.

General anatomy.—The chelicerate body consists of two tagmata, prosoma and opisthosoma. The prosoma includes a preoral region and six embryologically postoral appendage-bearing somites (I-VI) (Damen et al. 1998; Telford & Thomas 1998). The primitive opisthosoma was probably composed of 11 or 12 somites and a terminal peri- or post-anal structure, the telson (Weygoldt & Paulus 1979; Shultz 1990; Anderson & Selden 1997). *Limulus* and other extant xiphosurans depart secondarily from this organization in several

ways. Specifically, the first opisthosomal somite (VII), along with its appendages (chilaria), and medial tergal elements of the second (VIII) are incorporated into the prosoma to form a "cephalothorax" (Scholl 1977) (Fig. 3B). The remaining opisthosomal somites are consolidated dorsally, laterally and posteriorly into a heavily sclerotized abdomen (Figs. 1, 2) which bears six opercular appendages (i.e., the anterior genital operculum with paired genital openings and lacking book gills and five opercula with book gills) inserted into a pliable ventral cuticle (Fig. 2). The hard dorsal surface of the abdomen is here termed the tergum and the hard posterior ventral surface is termed the postopercular sternum. There are seven well-defined opisthosomal somites (VIII-XIV) within the abdomen which are indicated by the arrangement of dorsal entapophyses (i.e., internal projections formed by invagination of the tergal exoskeleton), marginal spines, and appendages (Figs. 1, 3). There is internal evidence of another somite (XV) in the form of a crescent-shaped site of muscle attachment on the abdominal tergum (Fig. 1A: *36, 37*). The musculature of somite XV is more complicated in larval stages and resembles that of the more anterior abdominal somites but lacks a dorsal entapophysis (Scholl 1977: fig. 5).

Appendicular muscles.—The skeletomuscular anatomy of appendages in *Limulus* has been described by several workers, notably Lankester et al. (1885), Patten (1912), Vachon (1945), Snodgrass (1952), Manton (1964), Wyse & Dwyer (1973) and Shultz (1989). Their observations were largely confirmed in the present study (Table 1, Figs. 1–8), and another detailed description of this skeletomuscular system is not provided here. However, the literature contains persistent errors and omissions regarding muscles of the chelicerae, opercular chondrites, chilaria and preoral coxosternal apparatus. Consequently, these systems are described in greater detail here and in the following section on the preoral apparatus.

Cheliceral muscles: The chelicerae comprise three articles: protomerite, deutomerite and tritomerite (Fig. 5). Each chelicera is bordered medially by the epistome and posteriorly to laterally by the procurved epistomal horns (Fig. 4). Each chelicera is operated by four extrinsic muscles (Fig. 5), three carapace-protomerite muscles (*45–47*) that originate from a small region on the anteromedial surface of the carapace (Fig. 1) and one endosternite-protomerite muscle (Fig. 5) that originates on the medial surface of the anterior endosternal horn. Lankester et al. (1885) were mistaken in regarding muscles *45–47* as a single muscle and in considering muscle *15* a second endosternite-protomerite muscle. The intrinsic muscles are described here for the first time. The protomerite-deutomerite joint is equipped with an extensor (*49*) and a flexor (*50*), and the deutomerite-tritomerite joint is operated by a closer (*51*) and an opener (*52*) (Fig. 5).

Opercular chondrites and associated muscles: Muscles of the abdominal appendages have been treated in detail elsewhere (e.g., Lankester et al. 1885; Patten 1912) and these are described briefly in Table 1 and illustrated in Figs. 1 and 8. Only those associated with the opercular chondrites will be described here. Opercular chondrites are paired, roughly cylindrical structures composed of a pliable cartilaginous material (Patten & Hazen 1900; Fahrenbach 1999). Each chondrite attaches ventrally at an oval region on the anterior surface of each operculum (Fig. 8: bchdt) and projects anterodorsally, but it terminates before reaching the abdominal tergum and adheres medially to the lateral surface of the dorsal entapophysis of the same somite as the appendage from which the chondrite originates (Fig. 2C). Longitudinally adjacent chondrites interconnect dorsally through a thin horizontal sheet (Fig. 7C) composed of the same cartilaginous tissue. The shaft of each chondrite has three muscles whose fibers pass downward and attach to the anterior opercular surface near the base of the chondrite (Fig. 8: *97, 99, 100*). These muscles presumably function in compressing and/or flexing the chondrite, which may act, in turn, as an elastic and/or hydrostatic skeleton for operating the operculum.

Chilarial muscles: Xiphosurans are the only extant chelicerates to retain distinct appendages (chilaria) (Figs. 2, 4) on somite VII as adults. Each chilarium has a cartilaginous bar (chilarial chondrite) that originates near its posterior margin (Fig. 4: cht) and extends dorsally to attach to the posterior margin of the endosternite (Patten & Redenbaugh 1899: "capsuliginous bars"). This structure is composed of the same material as the opercular

Table 1.—Muscles of *Limulus polyphemus*, numbered and described. *Abbreviations:* O, origin; I, insertion; H: homologs in other studies. References to homologs consist of abbreviated author name and the reference number or name that author used in denoting the muscle. Author abbreviations: LBB, Lankester, Benham & Beck (1885); M, Manton (1964); P, Patten (1912); Sch, Scholl (1977); Sh, Shultz (1989); Sn, Snodgrass (1952).

Axial and gut muscles

1 Hundreds of loosely packed strands passing through hepatopancreas and other viscera. O: cephalothoracic carapace, dorsal surface of marginal fold. I: cephalothoracic carapace, ventral surface of marginal fold (not illustrated). H: Sch, lDvm.

2 Many long strands. O: cephalothoracic carapace, dorsal anterior surface of marginal fold. I: cephalothoracic carapace, ventral anterior surface of marginal fold (Fig. 2). Probably enlarged components of 1. H: LBB 66? (Because these muscles pass along the lateral surfaces of the crop, LBB may have mistaken these for pharyngeal muscles.)

3 Transverse, unpaired. O: base of right epistomal horn. I: base of left epistomal horn (Figs 2, 4). May be a component of 5.

4 Hundreds of short, tightly packed strands. O: abdominal tergum, dorsal surface of marginal fold. I: abdominal tergum, ventral surface of marginal fold (not illustrated).

5 Five elements (5_{II}–5_{VI}). Fibers span crests of adjacent and subadjacent intercoxal folds and epistomal horns to form preoral sphincter (Figs 2, 4).

6 O: subendosternal subneural plastron. I: anterior surface of endostoma, interdigitates with 5 (Figs 2, 4).

7 O: medial surface of endosternal horn and lateral ventral surface of endosternite. I: dorsal and dorsolateral surfaces of esophageal portion of foregut (Figs 2, 7C). H: LBB, 67; Sch, MuVd.

8 Encircles foregut, well developed around crop and gizzard (Figs 2, 7C). H: LBB, S.

9 O: postopercular sternum, anterior margin. I: rectum, ventral wall (Figs 2, 7C).

10 Sheetlike. O: tergum, posteromedial dorsal surface. I: rectum, dorsolateral surface (Figs 1, 2, 7C). Separates 36 and 37 (Fig 7B,C).

11 Nine serial groups. O: carapace and tergum, dorsal medial surfaces. I: dorsal pericardium (Fig. 1).

12 "Veno-pericardiac muscles." Nine serial members. O: ventral pericardium. I: lateral surface of endosternite (2) or ventral venous sinus (7) (Fig. 2). They span the abdominal space between muscle groups 22 and 26, and interdigitate with the members of 22. H: LBB, 68; Sch, Vpkm.

13 Six serial members, 13_I–13_{VI}. O: endosternite, dorsal surface. I: central carapace. (Figs 1, 7A). Probably serial homologs of 17. H: LBB, 49–52, 57–59; Sch, SuE 1–6.

14 O: endosternite at base of tendinous process shared with 13_{VI}. I: first dorsal entapophysis (Fig. 7A, C). May be anteriormost member of series 22 (i.e. 22_{VI}). H: LBB, 53; Sch, SuE; M: Fig. 16.

15 O: endosternal horn. I: anterior half of epistomal horn and anteriorly adjacent series of sclerites (Figs 2, 4, 9B). May be anteriormost member of series 16. H: LBB, 30 (Error: not a cheliceral muscle).

16 Three or four serial members, 16_{III}?, 16_{IV}–16_{VI}. Sheetlike. O: lateral surface of endosternite and associated marginal membrane. I: pliable cuticle between coxae of legs 1–5 (Fig. 4). See 15.

17 Seven serial members, 17_{VIII}–17_{XIV} but the "trilobite larva" has 17_{XV} (Scholl 1977: fig. 5). O: subneural plastrons (17_{VIII}–17_{XIII}) or postopercular sternum (17_{XIV}). I: tergum medial to dorsal entapophyses (Figs 1, 7C). See 13. H: LBB, 12 (errors); Sch, Dvm.

18 Thin sheet of connective tissue. O: postopercular sternum, anterior medial surface. I: tergum, medial surface posterior to 7th dorsal entapophysis (somite XIV) (Figs 1, 2).

19 Seven serial members, 19_{VII}–19_{XIII}. O: endosternite (19_{VII}) or subneural plastron (19_{VIII}–19_{XIII}). I: posteriorly adjacent subneural plastron (19_{VII}–19_{XII}) or postopercular sternum (19_{XIII}) (Figs 7C, 9B). H: LBB 5.

20 Variably expressed. O: endosternite or subneural plastron. I: subneural plastron or postopercular sternum, two or more somites posterior to origin (Figs 7C, 9B).

21 Variably expressed. O: subneural plastrons. I: dorsal entapophysis of more posterior somite. Arrangement of one individual depicted in Fig. 7C. H: LBB 13–17.

22 Seven serial members, 22_{VIII}–22_{XIV}, but the "trilobite larva" has 22_{XV} (Scholl 1977: fig. 5). O: endosternite, posterior dorsal surface. I: 1st to 7th dorsal entapophyses. Anterior-to-posterior sequence of insertions reflected in medial-to-lateral sequence of origins (Figs 7A, 9B). H: LBB, 1, 2, 54–55, 83–87, 103–107; Sch, Ent.

Table 1.—Continued.

23 Seven serial members, 23_{VIII}–23_{XIV}. O: dorsal surface of endosternite; anterior origins smaller, more medial. I: subneural plastrons of somites (23_{VIII}–23_{XIII}) and anterior margin of postopercular sternum (23_{XIV}) (Fig. 7C). H: LBB, 3 (in part).

24 Five serial members, 24_{IX}–24_{XIII}. O: medial margin of 2nd to 6th ventral entapophyses (somites IX-XIII). I: postopercular sternum, anterior margin (Fig. 7A). H: LBB, 3, 16 (in part).

25 Variable, up to four serial members. O: medial margin of 1st to 4th ventral entapophyses (somites VIII-XI); if fewer, absent posteriorly. I: 7th dorsal entapophysis (somite XIV) (Fig. 7A).

26 Seven serial members, 26_{VIII}–26_{XIV}. O: lateral margins of cardiac lobe of carapace and second dorsal entapophysis (26_{XIV} in part). I: ventral entapophyses (somites VIII-XIV) (Figs 1, 7A, B, 9B). Origin of posterior six members in quasi-concentric pattern with anteriormost element (26_{IX}) located ''centrally'' (Fig. 1). H: LBB, 18, 19; Sch, Btm.

27 O: carapace, cardiac lobe. I: hollow apodeme formed by invagination of hinge between carapace and tergum (Figs 1, 7B, 9B). H: LBB, 78; Sch, Dlm 7.

28 O: carapace, cardiac lobe. I: anterior margin of hinge between carapace and tergum (Figs 1, 7B, 9B). H: LBB, 78; M, ''retractor dorsalis''; Sch, Dlm 7.

29 O: 1st dorsal entapophysis (somite VIII). I: hinge between carapace and tergum (Fig. 7B).

30 Four serial members, 30_{IX}–30_{XII}. O: 1st dorsal entapophysis (somite VIII). I: 2nd through 5th dorsal entapophyses (somites IX–XII) (Figs 7B, 9B). H: LBB, 4a.

Telson muscles

31 O: abdominal tergum, medial to 6th dorsal entapophysis (somite XIII). I: telson, dorsal process (Figs 1, 7B). H: LBB, 6, 120?

32 O: abdominal tergum, medial to 7th dorsal entapophysis (somite XIV). I: telson, dorsal process (Figs 1, 7B). H: LBB: 6, 101?

33 O: abdomen, 5th dorsal entapophysis (somite XII). I: telson, dorsal process (Fig. 7B). H: LBB, 93.

34 O: abdomen, 6th dorsal entapophysis (somite XIII). I: telson, dorsal process (Fig. 7B). H: LBB, 92.

35 O: abdomen, 7th dorsal entapophysis (somite XIV). I: telson, dorsal process (Fig. 7B). H: LBB, 91.

36 O: abdomen, tergum posterior to 7th dorsal entapophysis (somite XIV) medial to 37. I: telson, dorsal process (Figs 1, 7B). H: LBB, 7.

37 O: abdomen, tergum posterior to 7th dorsal entapophysis (somite XIV) lateral to 36. I: telson, dorsal process (Figs 1, 7B). H: LBB, 8.

38 O: abdomen, postopercular sternum. I: telson, dorsal process (Fig. 7B). H: LBB, 94–97.

39 O: abdomen, tergum lateral to 7th dorsal entapophysis (somite XIV). I: telson, ventrolateral process (Figs 1, 7A). Sometimes with second part originating between 36 and 37 (somite XV?).

40 O: abdomen, 5th dorsal entapophysis (somite XII). I: telson, ventrolateral process (Fig. 7A). H: LBB, 88.

41 O: abdomen, 6th dorsal entapophysis (somite XIII). I: telson, ventrolateral process (Fig. 7A). H: LBB, 89.

42 O: abdomen, 7th dorsal entapophysis (somite XIV). I: telson, ventrolateral process (Fig. 7A). H: LBB, 90.

43 O: abdomen, postopercular sternum medial to 44. I: telson, ventrolateral process (Fig. 7A). H: LBB, 10.

44 O: abdomen, postopercular sternum lateral to 43. I: telson, ventrolateral process (Fig. 7A). H: LBB, 11.

Cheliceral muscles

45 Long, thin. O: carapace, anteromedial; sometimes with additional fibers originating on endosternal horn. I: protomerite, anterior margin (Figs 1, 5). H: LBB, 24; Sch, MuCh.

46 Long, thin. O: carapace, anteromedial. I: protomerite, medial margin (Figs 1, 5). H: LBB, 24; Sch, MuCh.

47 Long, thin. O: carapace, anteromedial. I: protomerite, lateral margin (Figs 1, 5). H: LBB, 24; Sch, MuCh.

48 O: endosternal horn, medial surface. I: protomerite, posterior process (Fig. 5). H: LBB, 31.

49 O: protomerite, dorsolateral and ventroproximal surfaces. I: deutomerite, dorsal margin (Fig. 5).

50 O: protomerite, dorsomedial and ventroproximal surfaces. I: deutomerite, ventral margin (Fig. 5).

51 O: deutomerite. I: tritomerite, medial margin (Fig. 5).

52 O: deutomerite, lateral surface. I: tritomerite, lateral margin (Fig. 5).

Table 1.—Continued.

Leg muscles (legs 1–5 are appendages of somites II–VI)

53 All legs. O: carapace, near extrinsic muscles of anteriorly adjacent appendage. I: coxa, anteromedial margin (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 27.

54 All legs. O: carapace, near extrinsic muscles of anteriorly adjacent leg. I: coxa, anterolateral margin (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 26.

55 All legs. O: carapace, near extrinsic muscles of posteriorly adjacent leg. I: coxa, posteromedial margin (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 29.

56 All legs. O: carapace. I: coxa, posterolateral margin (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 28.

57 All legs. O: carapace. I: coxa, posterolateral process (Figs 1, 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 25.

58 Leg 5. Small, thin. O: carapace, posterior. I: coxa, posterolateral (Fig. 1; see also fig. 15 in M). H: M, "dorsal coxal muscle".

59 All legs. O: endosternite, ventral surface. I: coxa, anteromedial margin (Fig. 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 34, 37, 40, 43, 46.

60 All legs. O: endosternite, ventral surface. I: coxa, anterolateral margin (Fig. 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 32m, 35o, 38q, 41s, 44y.

61 All legs. O: endosternite, ventral surface. I: coxa, posteromedial margin (Fig. 3A; see also figs 14, 15 and 17 in M). H: LBB, M, Sn, 33, 36, 39, 42, 45.

62 All legs. O: endosternite, ventral surface. I: coxa, posterolateral margin (Fig. 3A; see also figs 14, 15 and 17 in M). H: LBB, Sn, 32n, 35p, 38r, 41t, 44z.

63 Leg 5. O: endosternite, ventral surface. I: coxa, anterior margin (not illustrated but see figs 15 and 17 in M). H: LBB, M, 47.

64 Leg 5. O: endosternite, ventral surface. I: coxa, posterior margin (not illustrated but see figs 15 and 17 in M). H: LBB, M, 60.

65 Legs 1–4. O: inner wall of preoral chamber. I: coxa, posteromedial margin with 66 in legs 2–4 and corresponding region in leg 1 (Fig. 4; see also fig. 14 in M). H: M, "sternite muscle".

66 Legs 2–4. O: coxa, posteromedial margin. I: moveable endite, anterior surface (Fig. 4; see also fig. 14 in M). H: M, "coxal endite muscle".

67 All legs. O: coxa, proximal anterior and posterior margins. I: trochanter, dorsal margin and arthrodial membrane (Fig. 6). H: Sn, 1 Leg 5. O: tarsus, ventral surface. I: apotele, ventral margin (Fig. 6). H: Sh, 2; Sn, 21.

68 All legs. O: coxa, ventral anterior surface. I: trochanter, anteroventral margin (Fig. 6). H: Sn, 2.

69 All legs: O: coxa, dorsal posterior and dorsal anterior surfaces. I: trochanter, ventral margin via heavily sclerotized tendons (Fig. 6). H: Sn, 2+3.

70 All legs. O: coxa, ventral posterior surface. I: trochanter, posteroventral margin (Fig. 6). H: Sn, 3.

71 All legs. O: dorsal arthrodial membrane of trochanter-femur joint. I: femur, proximal half with anterior, dorsal and posterior parts (71a–71c) (Fig. 6). H: Sh, 12; Sn, 7.

72 All legs. O: trochanter, posterior and ventroposterior surfaces. I: femur, posterior ventral margin (Fig. 6). H: Sh, 11; Sn, 4.

73 All legs. O: trochanter, distal anterior surface. I: femur, proximal posterior surface (Fig. 6). H: Sh, 10; Sn, 6.

74 All legs. O: trochanter, anterior and ventral surfaces. I: patellar sclerite, proximal end (Fig. 6). H: Sh, 8d; Sn, 10.

75 All legs. O: femur, middle dorsoanterior surface. I: patellar sclerite, distal shaft (Fig. 6).

76 All legs. O: femur, middle ventroposterior surface. I: patellar sclerite, distal shaft (Fig. 6). H: Sh, 8c.

77 All legs. O: femur, distal anterior surface. I: patellar sclerite, anterior arm (Fig. 6). H: Sh, 8a; Sn, 8.

78 All legs. O: femur, distal posterior surface. I: patellar sclerite, posterior arm (Fig. 6). Sh: 8b, Sn: 8.

79 All legs. O: femur, distal dorsal surface, and patella, anterior and anteroventral surfaces. I: tibia, ventral margin (Fig. 6). H: Sh, 6; Sn, 16.

80 All legs. O: femur, distal dorsal surface, and patella, posterior and posteroventral surfaces. I: tibia, ventral margin (Fig. 6). H: Sh, 7; Sn, 17.

81 All legs. O: patella, anterodorsal surface. I: tibia, anterodorsal process (Fig. 6). H: Sh, 4a; Sn, 12.

82 All legs. O: patella, posterodorsal surface. I: tibia, posterodorsal process (Fig. 6). H: Sh, 5a; Sn, 13.

83 All legs. O: patella, anterior surface. I: tibia, anterior margin (Fig. 6). H: Sh, 4b; Sn, 14.

84 All legs. O: patella, posterior surface. I: tibia, posterior proximal margin (Fig. 6). H: Sh, 5b; Sn, 15.

Table 1.—Continued.

85 Leg 5. O: tibia, anterior surface. I: tarsus, anterior margin (Fig. 6). H: Sh, 3b; Sn 18.
86 Leg 5. O: tibia, anterior and posterior surfaces. I: tarsus, posterior margin (Fig. 6). H: Sh, 3a; Sn 19.
87 All legs. Legs 1–4: O: tibiotarsus, dorsal surface (not illustrated). I: apotele, dorsal margin. Leg 5: O: tarsus, dorsal surface. I: apotele, dorsal margin (Fig. 6). H: Sh, 1; Sn, 20.
88 All legs. Legs 1–4: O: tibiotarsus. I: apotele, ventral margin (not illustrated). Leg 5: O: tarsus, ventral surface. I: apotele, ventral margin (Fig. 6). H: Sh, 2; Sn, 21.

Chilarial muscles
89 Long, thin. O: carapace, medial posterior region. I: chilarium, lateral flange (Figs 1, 4).
90 O: endosternite, posterior margin. I: chilarium, lateral flange (Fig. 4).
91 O: endosternite, posterior ventral surface near attachment of chilarial chondrite. I: chilarium, anteromedial margin (Figs 2, 4).
92 O: subendosternal subneural plastron, posterior margin. I: chilarium, medial surface (Figs 2, 4).
93 O: subendosternal subneural plastron, posterior margin. I: chilarium, lateral surface (Fig. 4).
94 Transverse. O: right chilarium at base of chondrite. I: left chilarium at base of chondrite (Figs 2, 4).

Opercular muscles
95 Genital operculum only. 0: carapace, posteromedial surface (Fig. 1). I: chondrite, dorsal surface near attachment to 1st dorsal entapophysis (not illustrated).
96 Postgenital opercula, 96_{VIII}–96_{XIII}. O: posteromedial surface of carapace (96_{VIII}) (Fig. 1) or posterior margin of dorsal entapophysis (96_{IX}–96_{XIII}). I: anterior margin of operculum of posteriorly adjacent somite near 100 (Fig. 8). H: LBB, 21, 22+23?; Sn, pmcl.
97 Opercula, 97_{VIII}–97_{XIII}. O: chondrite, anterior surface. I: operculum, anterior surface with 96 (Fig. 8).
98 Opercula, 98_{VIII}–98_{XIII}. O: tergum, near dorsal entapophysis (Figs 1, 8). I: operculum, anterior surface proximal to transverse ridge (Fig. 8). H: LBB, 20; Sn, rmcl.
99 Opercula, 99_{VIII}–99_{XIII}. O: chondrite, posteromedial surface. I. operculum, anterior surface medial to longitudinal ridge (Fig. 8).
100 Opercula, 100_{VIII}–100_{XIII}. O: dorsomedial surface of chondrite and adjacent regions of tergum; tergal part smaller posteriorly (Figs 1, 8). I: operculum, anterior surface distal and lateral to intersection of longitudinal and transverse ridges (Fig. 8). H: LBB, 20, 113.
101 Opercula, 101_{VIII}–101_{XIII}. O: carapace (101_{VIII}) (Fig. 1) or dorsal entapophysis (IX-XIII). I: anterior surface of operculum of posteriorly adjacent somite (Fig. 8). H: LBB, 21–23?
102 Opercula, 102_{VIII}–102_{XIII}. O: subneural plastron, ventral. I: chondrite, lateral face (Fig. 8). H: LBB, 48?
103 Opercula, 103_{VIII}–103_{XIII}. O: subneural plastron, ventral surface. I: basal posterior face of chondrite and/or adjacent region of operculum (Fig. 8). H: LBB, 115.
104 Opercula, 104_{VIII}–104_{XIII}. O: chondrite, posterior surface. I: exopod, medial margin of posterior plate (not illustrated).
105 Opercula, 105_{VIII}–105_{XIII}. Many separate fibers. O: anterior surface. I: posterior surface. More developed near lamellae (not illustrated).
106 Opercula, 106_{VIII}–106_{XIII}. O: operculum, medial anterior margin. I: telopod (Fig. 8). H: LBB, 114.
107 Opercula, 107_{VIII}–107_{XIII}. O: operculum, anterior surface. I: telopod base (Fig. 8). H: LBB, 112.
108 Postgenital opercula, 108_{IX}–108_{XIII}. O: telopod protopodite. I: telopod deutomerite (Fig. 8). H: LBB, 114.
109 Postgenital opercula, 109_{IX}–109_{XIII}. Telopod. O: protomerite, distal margin. I: deutomerite, proximal margin (Fig. 8).
110 Postgenital opercula, 110_{IX}–110_{XIII}. Telopod. O: deutomerite. I: tritomerite (Fig. 8).
111 Postgenital opercula, 111_{IX}–111_{XIII}. Telopod. O: deutomerite. I: tritomerite (Fig. 8).
112 Opercula, 112_{IX}–112_{XIII}. O: telopod, base. I: exopod lobe, proximal margin (Fig. 8).
113 Opercula, 113_{IX}–113_{XIII}. O: operculum, anterior surface. I: exopodial lobe, proximal margin (Fig. 8).
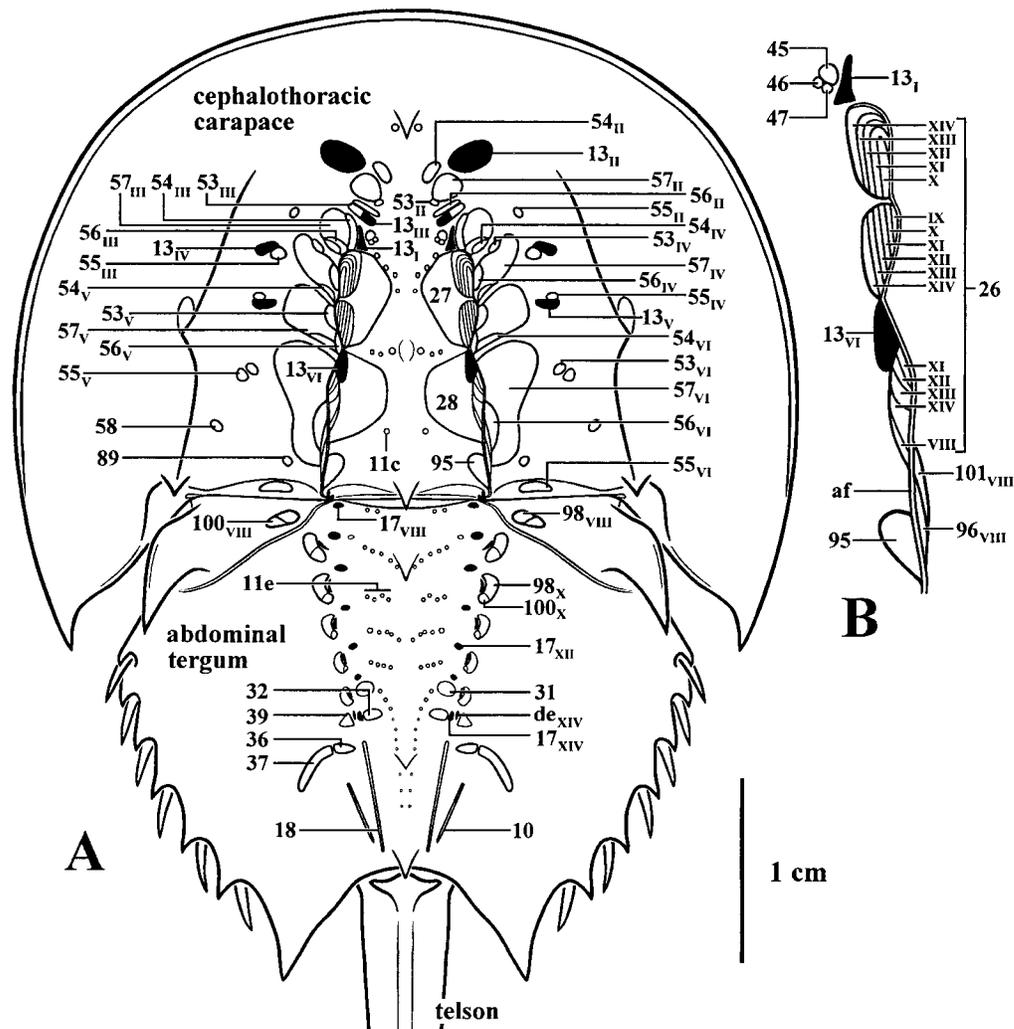
Figure 1.—Dorsal muscle attachments of an immature *Limulus polyphemus*. A, Cephalothoracic carapace, abdominal tergum and base of the telson. Muscles with attachments depicted in black arise from the endosternite or subneural plastrons (compare Fig. 7). B, Details of muscle attachments on the right side of the cardiac lobe of the carapace showing quasi-concentric arrangement of attachments of muscle series 26. Arabic numerals correspond to muscles listed in Table 1. Roman numerals correspond to the postoral somite with which the indicated muscle or structure is associated. *Abbreviations:* af, axial furrow; de, invagination associated with dorsal entapophysis.

chondrites (Patten & Redenbaugh 1899) and is probably serially homologous with them. A transverse muscle (*94*) passes from the base of one chilarial chondrite to the base of the other (Figs. 2, 4). Each chilarium also has two muscles that originate on the subendosternal subneural plastron (*92, 93*) and two that originate on the endosternite (*90, 91*) (Figs. 2, 4). A long, thin muscle (*89*) originates on the carapace among extrinsic muscles of the append-

age of somite VI (i.e., leg 5) (Fig. 1), passes ventrally lateral to the axial muscles (*26*), and inserts on the lateral flange of the chilarium (Fig. 4).

Axial muscles.—*Endosternite:* The endosternite of *Limulus* has been described and illustrated especially well by Patten & Redenbaugh (1899) (see also Lankester et al. 1885; Pocock 1902; Snodgrass 1952; Manton 1964; Firstman 1973; Yamasaki et al. 1988) and will
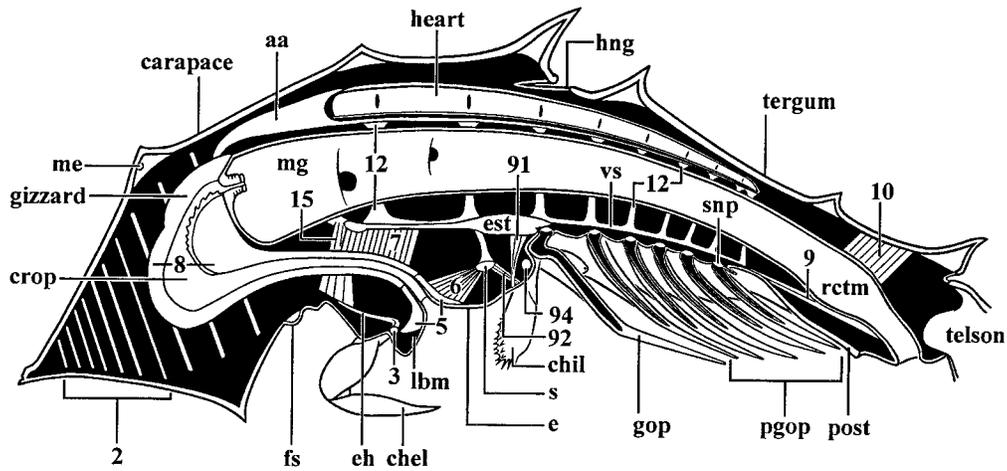
Figure 2.—Medial view of mid-sagittal section of an immature *Limulus polyphemus*. All extrinsic appendicular and axial skeletal muscles, including the endosternal suspensors, have been removed. Arabic numerals correspond to muscles listed in Table 1. *Abbreviations:* aa, anterior aorta; chel, chelicera; chil, chilarium; e, endostoma; eh, epistomal horn; est, endosternite; fs, frontal sclerite; gop, genital operculum; hng, hinge between carapace and tergum; lbm, labrum; me, medial eye; mg, midgut with openings to digestive caeca; pgop, postgenital opercula; rctm, rectum; post, postopercular sternum; s, subendosternal subneural plastron; snp, subneural plastron; vs, venous sinus (collapsed).

therefore be treated here in a general manner. The endosternite (Figs. 2, 3, 7, 9) is a mesodermally derived endoskeleton composed of a tough, fibrous connective tissue (Fahrenbach 1999). It is a roughly rectangular, horizontal sheet with a pair of anterior projections, the anterior horns (Figs. 2, 7); a pair of sheetlike posterolateral projections; and a posteromedial projection. It serves primarily as an attachment for extrinsic leg muscles (*67–72*) (Fig. 3A; see also Lankester et al. 1885; Manton 1964); axial muscles that attach to various sites in the abdomen (*14, 19, 22, 23*) (Figs. 7, 9B); pharyngeal dilator muscles (*7*) (Figs. 2, 7), which originate from the concave ventral surface of the endosternite; and the first two "veno-pericardiac" muscles (*12*) (Fig. 2). It is suspended from the carapace by six paired muscles that attach to dorsal projections which are continuous with the body of the endosternite (*13*) (Figs. 1, 7, 9B).

The endosternite is also connected to the body wall by a less well-understood system of ventrolateral muscles (*15*) and ligaments (*16*). The dorsal lateral margin of the endosternite is modified into a flexible marginal membrane which extends from the attachment of the first "venopericardiac" muscle (12) posteriorly to

the attachment of the second "venopericardiac" muscle (Fig. 2). Posteriorly, the membrane becomes bilayered, merges with a large lateral venous sinus and continues rearward to form the ventral sinus of the abdomen. The floor of the sinus is firmly connected to the abdominal floor and is attached dorsally to the pericardium via the seven remaining venopericardiac muscles (Fig. 2: *12*). The endosternal attachment points of the first two venopericardiac muscles have membranous ligaments (*16*) that pass ventrolaterally from the marginal membrane to the pliable cuticle between the leg coxae. Specifically, there are two ligaments associated with the anterior "venopericardiac" muscle, one attaching between the appendages of somites III and IV (legs 1 and 2) and the other between appendages of somites IV and V (legs 2 and 3) (Fig. 4). The ligament associated with the posterior "venopericardiac" muscle is especially well developed and attaches between legs 3 and 4 (Fig. 4). An apparent ligament was observed extending from the lateral surface of the endosternal horn and inserting on the intercoxal cuticle between legs 1 and 2, but this was not confirmed in all individuals. Muscle *15* arises from the ventral surface of the anterior en-
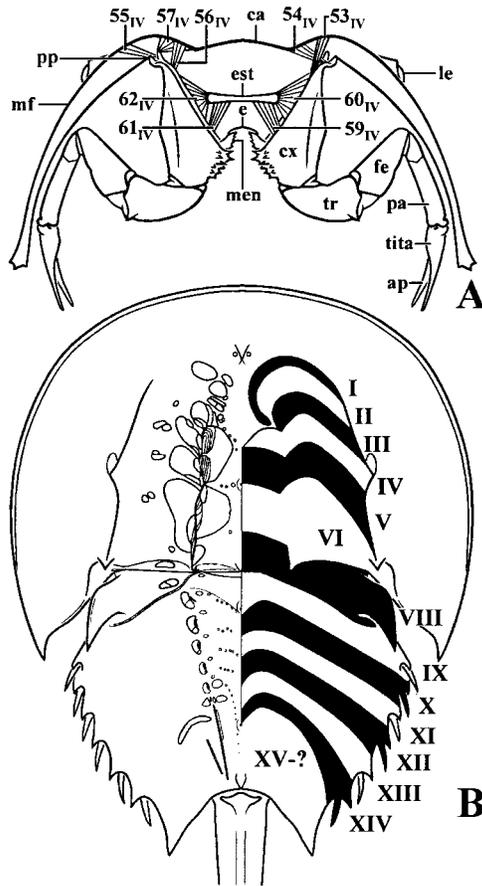
Figure 3.—A, Anterior view of cross section through cephalothorax showing arrangement of extrinsic muscles of the third leg (after Wyse & Dwyer 1973). B, Dorsal view showing approximate locations of "muscular somites" composing the carapace and tergum. Note the posterior displacement of somite I (cheliceral somite) and that the lateral portions of the hinge between the carapace and tergum are specializations of somite VIII. Arabic numerals correspond to muscles listed in Table 1. Roman numerals correspond to the postoral segment with which the indicated muscle is associated. *Abbreviations:* ap, apotele or moveable finger of chela; ca, carapace; cx, coxa; e, endostoma; est, endosternite; fe, femur; men, moveable endite; mf, marginal fold; le, lateral eye; pa, patella; pp, pivot point between ventral surface of marginal fold and coxa; tita, tibiotarsus; tr, trochanter.

dosternal horn and inserts on the epistomal horn that is embedded in the flexible cuticle between the chelicera and leg 1. Muscle *15* was mistaken for an extrinsic cheliceral muscle by Lankester et al. (1885).

Subneural plastrons: The subneural plastrons are metamerically arranged endoskeletal elements composed of material similar to that of the endosternite (Patten & Redenbaugh 1899). Despite apparent similarities in composition, it is unlikely that the plastrons and endosternite are serial homologs, because the endosternal element and subneural plastron of somite VII are both present (Figs. 2, 9B), and the central nervous system passes ventral to the endosternite and dorsal to the plastrons. The anteriormost subneural plastron is suspended from the ventral surface of the endosternite by processes of connective tissue (Figs. 2, 4: s) and is an attachment site for muscles of the preoral chamber and chilaria (Figs. 2, 4: *6, 92, 93*). It appears to be associated with somite VII, the chilarial somite. The remaining six subneural plastrons are located on the floor of the abdomen (Figs. 2, 7, 8: snp) and appear to belong to somites VIII to XIII (Figs. 2, 7, 9B). Each abdominal plastron spans the crests of two folds in the pliable cuticle of the ventral body wall (Fig. 2) and thereby forms a series of transverse "tunnels." Muscles (*102, 103*) arising from the opercula pass medially through these tunnels to insert on the ventral surface of the plastron (Fig. 8). A bilateral pair of connective-tissue processes project dorsally from each plastron and serves as attachment sites for a variety of axial muscles that are described in detail below.

Axial muscles of the abdomen: A notable incongruity in *Limulus* is a complex axial muscle system in the abdomen (Figs. 7, 9B), a tagma that lacks dorsal mobility between its constituent somites. The system is apparently used in flexing the dorsal hinge between the carapace and tergum during defensive "enrollment" and in moving the opercula. Lankester et al. (1885) provided a description of the axial muscle system, but it is confusing, imprecise and sometimes incorrect. The axial muscles are here categorized into four groups, 1) the dorsal longitudinal complex, 2) ventral longitudinal complex, 3) the posterior oblique complex, and 4) the anterior oblique complex.

Muscles in the dorsal longitudinal complex pass from one dorsal cuticular attachment to another. Seven muscles span the dorsal hinge between the carapace and tergum. Three paired muscles insert on the pliable fold of the dorsal hinge, two originating from the cardiac lobe of the carapace (Figs. 1, 7B: *27, 28*) and
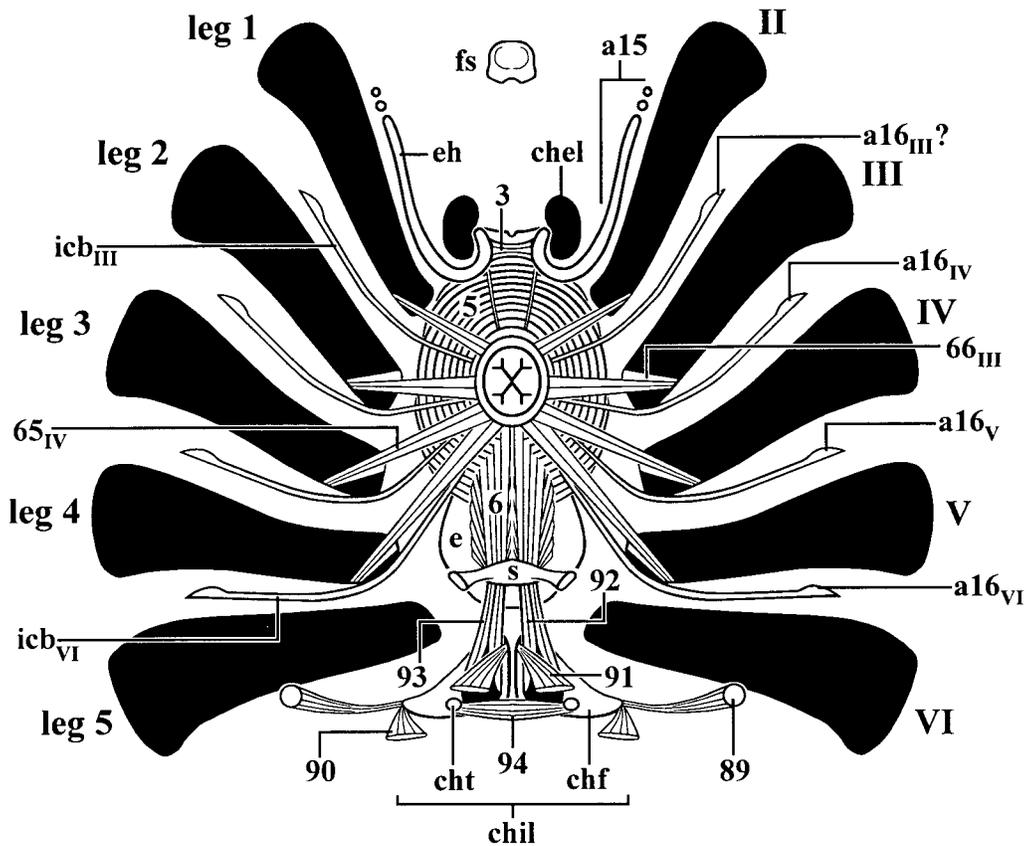
Figure 4.—Semi-diagrammatic dorsal view of the ventral surface of the cephalothorax showing the preoral apparatus. The esophagus has been cut and reflected posteriorly to better show the arrangement of the skeletomuscular elements (compare Fig. 2). Note also that the inter-coxal bands (icb) would not normally be visible dorsally in the region of the preoral sphincter (5), because they are covered by muscle fibers that pass from each band to bands that are not directly adjacent. Note that dilator muscles (65) pass from the leg coxae and attach to the walls of the preoral chamber; their site of attachment may represent the position of the true mouth. Arabic numerals correspond to muscles listed in Table 1. Roman numerals correspond to the postoral somite with which the indicated muscle or structure is associated. *Abbreviations:* a15, attachment of muscle 15; $a16_{III}$–$a16_{VI}$, attachments of 16_{III}–16_{VI}; chel, attachment site of chelicera; chf, lateral flange of chilarium; chil, chilaria; cht, base of chilarial chondrite; e, endostoma; eh, epistomal horn; fs, frontal sclerite; icb, inter-coxal band; s, subendosternal subneural plastron with tendinous attachments to the endosternite cut (compare Fig. 2).

one from the first dorsal entapophysis (Fig. 7B: *31*). The remaining four pairs originate on the posterior margin of the first dorsal entapophysis and insert sequentially on the next four pairs of dorsal entapophyses (Fig. 7B: 30_{IX}–30_{XII}).

Muscles of the ventral longitudinal complex pass from one ventral attachment to another, either a cuticular structure (ventral entapophysis, postopercular sternum) or an endoskeletal structure (endosternite or subneural plastron) (Fig. 7). The complex can be divided into three bilateral longitudinal series: a medial series, a middle series, and a lateral series. Members of the medial series are thin, straplike muscles that originate anteriorly on one endoskeletal element and pass posteriorly to insert on another (Fig. 7C: *19, 20*). In contrast, the middle series (*23*) is best described as a collection of parallel muscle fibers with different posterior attachments. The fibers originate on the dorsal posterior surface of the endosternite and pass posteromedially to insert on the subneural plastrons and anterior margin

of the postopercular sternum, with those fibers inserting more anteriorly originating more medially on the endosternite (Fig. 7C: *23*). The lateral series (*24*) is also composed of "fiber tracts" rather than distinct muscles. In fact, the fibers of the middle series intermingle with those of the lateral series, but the two groups can be distinguished by tracing fibers to their respective attachments. Fibers in the lateral series originate on the postopercular sternum and insert on the cuticular folds of the ventral body wall just medial to the ventral entapophyses of somites IX to XIII (Fig. 7A: *24*).

Muscles of the posterior oblique complex attach dorsally to some element of the dorsal body wall (carapace, tergum, dorsal entapophysis) and ventrally to the ventral body wall or to an endoskeletal structure. This complex can also be divided into medial, middle and lateral series, and these appear to be linked morphologically to the three series of the ventral longitudinal complex. The medial series (*14?, 17, 21*) consists of strap-like muscles that originate on the endosternite or a subneural plastron and insert on the tergum (Figs. 1, 7C: *17*) or a dorsal entapophysis (Fig. 7C: *14, 21*). Members of the middle series (*22*) arise from the dorsal surface of the endosternite and pass dorsoposteriorly to insert on each of the dorsal entapophyses (Fig. 7A). Like the corresponding series in the ventral longitudinal complex, those muscles inserting more anteriorly originate more medially on the endosternite. The lateral series is composed of small muscles (*25*) that originate from the folds of the ventral body wall near the ventral entapophyses along with the fibers of the lateral series of the ventral longitudinal complex (Fig. 7A).

Muscles of the anterior oblique complex (26_{VIII}–26_{XIV}) originate on the carapace at the extreme lateral portion of the cardiac lobe (Fig. 1), and, in one case (26_{XIV}), on the second dorsal entapophysis (Fig. 7C). The first member of this complex (26_{VIII} is a small, thin muscle that inserts on a small infolding, or ventral entapophysis, on the ventral body wall at the attachment of the posterior margin of the endosternite with pliable ventral cuticle anterior to the genital operculum (Fig. 7A: ve_{VIII}). The remaining muscles originate in a quasi-concentric pattern, with those having a more anterior insertion originating nearer to the center of the origin and muscles with more

posterior insertions originating more peripherally (Fig. 1). These muscles insert at the ends of long, hollow tendons which are extensions of infoldings (ventral entapophyses) of the pliable cuticle between adjacent opercula (Fig. 7).

Feeding apparatus.—The basic anatomy of the gnathobasic feeding apparatus and digestive tract of *Limulus* and other xiphosurans is well known and has been described in considerable detail by previous workers (Lankester et al. 1885; Manton 1964; Wyse & Dwyer 1973; Clarke 1979; Yamasaki et al. 1988; Fahrenbach 1999; etc.). Consequently, muscles associated with the feeding and digestive systems have been listed and briefly described in Table 1 but are not described in detail here. However, several features of the anterior digestive tract have been overlooked or inadequately described by previous workers, and these are treated in more detail.

Preoral apparatus: The preoral chamber is shaped like an inverted funnel (Figs. 2, 4) surrounded by the leg coxae (Figs. 3, 4). Its walls are formed by lobes of pliable cuticle, with the moveable and fixed endites of the leg coxae projecting between them (see Manton 1964: figs. 14, 16). The furrows between the lobes are continuous laterally with those formed by the flexible inter-coxal cuticle. The anterior wall of the chamber is an unpaired lobe that is continuous with the labrum and epistome (Fig. 2), and the posterior wall consists of an oblong plate, the endostoma, composed of stiffer but still flexible cuticle (Figs. 2–4). The chamber narrows as it passes deeper into the body and bends anteriorly to pass through the brain and to become the 'esophageal' region of the foregut (Fig. 2). There is no gross cuticular feature demarcating the "true mouth," that is, the junction of the preoral chamber and foregut.

The musculature of the preoral chamber is described in detail here for the first time. The inner surface of the walls of the preoral chamber are surrounded by a roughly circular meshwork of muscle fibers (*5*) that forms a large sphincter (Figs. 2, 4). The sphincter has a radially arranged 'skeleton' formed by strips of connective tissue that begin laterally on the pliable inter-coxal cuticle medially adjacent to the attachments of the endosternite-intercoxal muscles (*21*) and pass centripedally along the ventral body surface onto the walls of the

preoral chamber (Fig. 5). These bands occupy the internal crests of the inter-coxal folds between the lobes of the preoral chamber and may act to maintain the shape of the preoral chamber. Muscle fibers (*5*) arise from each cartilage-like band and associated cuticle and pass to adjacent and subadjacent bands. It is noteworthy that the inter-coxal portion of the anteriormost pair of bands appears to have been modified, or replaced, by the epistomal horns, which pass between the chelicerae and the coxae of the first leg pair (Figs. 2, 4). In fact, like the connective tissue bands, each epistomal horn is associated with a muscle (*20*) that arises from the endosternite (Figs. 2, 4). The epistomal horns wrap around the posterior margin of the chelicerae and join the body of the epistome, whereupon the sclerite assumes the appearance of a connective tissue band, gives rise to muscle fibers (*5*), and defines the lateral margins of the labrum or anterior lobe of the complex (Fig. 4). Apparent dilator muscles (*73*) arise from the posteromedial coxal margins of legs 1–4 and pass centripedally to insert in a ring around the deeper, narrower region of the preoral chamber (Fig. 4). The attachment of these muscles separates the roughly circular fibers of the preoral sphincter from those of the foregut (*8*) (Figs. 2, 3) and may indicate the site of the true mouth.

Foregut: The foregut is the cuticle-lined region of the digestive tract that connects the preoral chamber and midgut (Figs. 2C, 3). The foregut is essentially C-shaped in lateral perspective (Fig. 2). The narrow ''esophageal'' portion of the foregut passes anteriorly through the brain. The longitudinally folded lumen is surrounded by circular constrictor muscles (*8*) and is supplied with one well-developed dilator muscle arising from the endosternite (Figs. 2, 7: *7*). A second dilator described and illustrated by Lankester et al. (1885) was never observed and was probably based on a misinterpretation of dorsoventral muscles that arise form the anteroventral surface of the cephalothorax, pass dorsally along the lateral surfaces of the crop, but continue dorsally to insert on the carapace (Fig. 2: *2*). The foregut then expands, both in the diameter of the lumen and thickness of circular muscles, and turns dorsally and then posteriorly (Figs. 2, 5C). The lumen walls become progressively more heavily sclerotized as the

foregut approaches the midgut, and the last portion (proventriculus or gizzard) is apparently specialized for grinding. The foregut is separated from the midgut by a strongly developed valve (Fig. 2).

DISCUSSION

Evolutionary morphology of axial muscles in Chelicerata.—*The box-truss axial muscle system:* Comparative anatomical studies of crustaceans (e.g., Cephalocarida, Malacostraca, Mystacocarida, Branchiopoda: Hessler 1964), myriapods (e.g., Pauropoda: Verhoeff 1934, Tiegs 1947), hexapods (Diplura: Manton 1972; Microcoryphia: Birket-Smith 1974) and, perhaps, trilobites (Cisne 1981) have revealed a common box-truss axial muscle system (Fig. 9A). This system consists of bilateral dorsal and ventral longitudinal elements that attach to each somite, a bilateral set of dorsoventral muscles within each somite that passes from the tergite to the ventral body wall, a bilateral set of posterior oblique elements that arises ventrally in association with dorsoventral elements and inserts dorsally on a more posterior somite, and a bilateral pair of anterior oblique elements that also arises ventrally with a dorsoventral elements but inserts dorsally on a more anterior somite. The ventral longitudinal, dorsoventral, anterior oblique and posterior oblique elements all attach to a transverse endoskeletal bar within each somite (Fig. 9A). Axial muscles of arachnids appear to correspond to elements of the box-truss system (Fig. 9C); that is, the dorsal longitudinal muscles and endosternite plus ventral longitudinal muscles correspond to the dorsal longitudinal and ventral longitudinal elements, respectively; dorsal endosternal suspensors and dorsoventral muscles of the opisthosoma appear to correspond to the dorsoventral elements; and the dorsoposterior endosternal suspensors and, perhaps, ''transverse'' muscles of the opisthosoma (e.g., Amblypygi: Shultz 1999: muscle 22; Araneae: Whitehead & Rempel 1959: muscle 89; Scorpiones: original observation) can be homologized with posterior oblique elements. No muscles corresponding to the anterior oblique elements are known in arachnids (Fig. 9C). However, it is unclear from these comparisons whether the relative simplicity of arachnids is a primitive antecedent of the box-
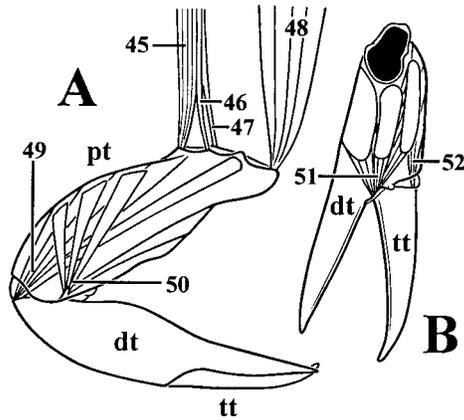
Figure 5.—Skeletomuscular anatomy of the chelicerae. A, Medial view of the right chelicera showing insertions of extrinsic muscles (45–48) and proximal intrinsic muscles (49, 50). B, Distal articles of the right chelicera showing intrinsic muscles that operate the chela (51, 52). The figure shows a dorsal view of a fully flexed chelicera. Numbers correspond to muscles listed in Table 1. *Abbreviations:* pt, protomerite or first cheliceral article; dt, deutomerite or second cheliceral article; tt, tritomerite or third cheliceral article.

truss system or a derived reduction of the box-truss system.

Based on information obtained in the present study, I propose that the abdominal axial muscle system in *Limulus* retains all essential components of the box-truss system, including the anterior oblique elements (Fig. 9B), and that the box-truss system is the plesiomorphic condition in Chelicerata. Specifically, the dorsal longitudinal elements of the box-truss system are retained as muscles *27–30* and perhaps *31–35* (Fig. 7); the ventral longitudinal elements are retained as muscles *19, 20, 23* and *24* (Fig. 7); the dorsoventral elements are retained as muscles *13* and *17* (Fig. 7); the posterior oblique muscles are retained as muscles *21, 22* and perhaps *25*; and the anterior oblique muscles are retained as muscle series *26*. Most of these comparisons are probably non-controversial, except for the anterior oblique muscles (*26*). Specifically, all relevant muscles in *Limulus* other than *26* are already accepted as axial muscles, and the necessary evolutionary transformation of a portion of the posterior oblique elements into muscle series *22* (i.e., anterior migration of the ventral attachments from each abdominal somite to

the dorsal surface of the endosternite) has been documented in ontogeny (see Scholl 1977: Figs. 3, 5). However, muscle series *26* is generally considered a group of extrinsic opercular muscles, not axial muscles, and this inconsistency must be addressed.

Lankester et al. (1885) and many subsequent authors have referred to muscle series *26* as ''branchio-thoracic'' muscles and considered them to be extrinsic opercular muscles, although the anteriormost member of this series (26_{VIII}) was recognized for the first time in the present study. My conclusion that these are actually axial muscles is based on the following lines of evidence: 1) One muscle (26_{XIV}) is associated with a somite that lacks appendages during all stages of development (Scholl 1977). 2) The ventral entapophyses, which give rise to the long tendons on which these muscles insert, are invaginations of the body wall rather than the appendages. This is particularly evident in the ventral entapophysis associated with 26_{XIV} which is continuous with the postopercular sternum (Fig. 7). 3) The bases of the ventral entapophyses and the adjacent region of the abdominal floor serve as attachment sites for muscles that are clearly axial rather than appendicular in origin (Fig. 7: *24, 25*). 4) The muscles insert on the cardiac lobe medial to the axial furrow, not lateral to the furrow like all appendicular muscles (Fig. 1: *53–57*), including those associated with the genital operculum (Fig. 1: 96_{VIII}, 101_{VIII}). I suggest that members of muscle series *26* may have been misinterpreted as extrinsic opercular muscles due to the erroneous assumption that the postgenital opercula are formed by medial fusion of the paired appendages, an evolutionary process that would be expected to obliterate the ventral body wall between them and its associated axial muscles. In fact, however, the abdominal floor is present externally between each postgenital operculum as a triangular fold (e.g., Snodrass 1952) and internally serves as an attachment site for the unambiguous axial muscles described above.

Given these arguments, I hypothesize that *Limulus* retains the abdominal elements of a box-truss system like that observed in other arthropod groups, although certain elements have been modified (Fig. 9). The principal evolutionary transformations required by this hypothesis are anterior migrations of portions
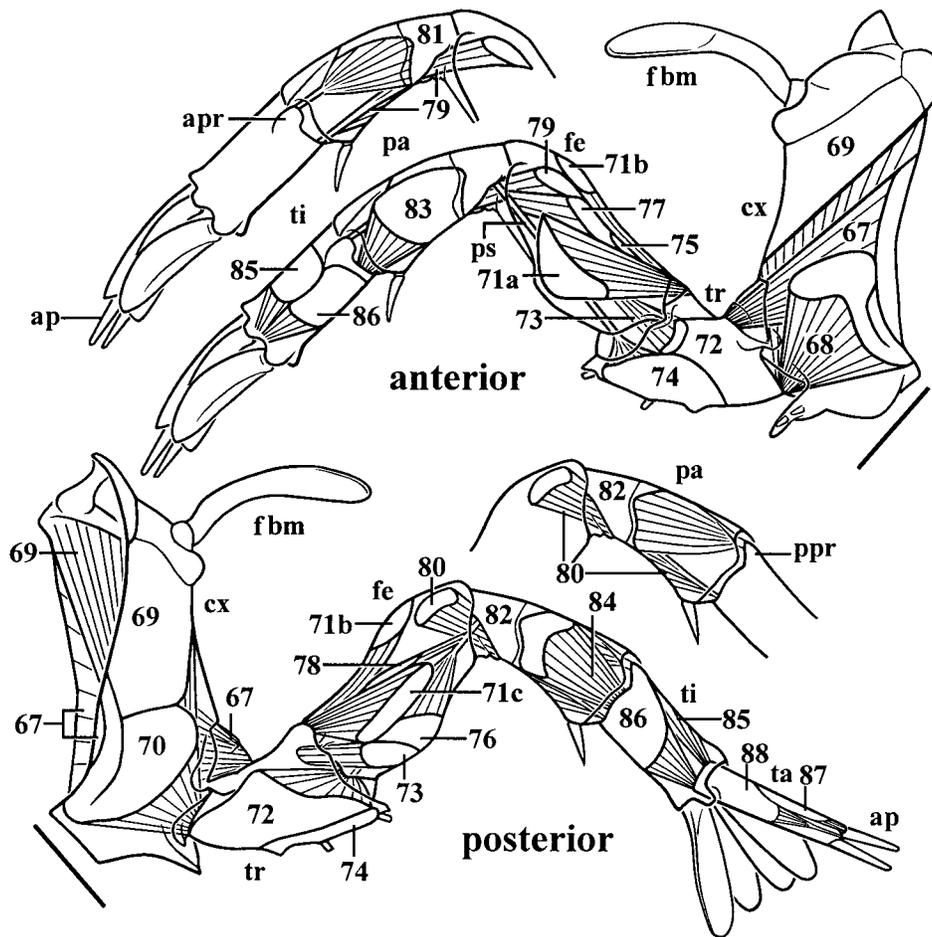
Figure 6.—Muscular anatomy of the intrinsic muscles of leg 5 from anterior and posterior perspectives. Insets show deeper muscles with superficial muscles removed. The lines near the coxae indicate the mid-sagittal plane of the intact animal. *Abbreviations:* ap, apotele; apr, anterior process of tibia; cx, coxa; fbm, flabellum; fe, femur; pa, patella; ppr, posterior process of tibia; ps, patellar sclerite; ta, tarsus; ti, tibia; tr, trochanter.

of the ventral attachments of the posterior oblique elements to the dorsal surface of the endosternite and anterior migration of the dorsal attachments of the anterior oblique elements to the carapace. These transformations would likely be associated with the evolutionary elimination of all tergal articulations except the carapace-tergum hinge (summarized by Anderson & Selden 1997), as they would allow the muscles to retain a function in moving the body. If this scenario is correct, the box-truss axial muscle system should probably be regarded as synapomorphic for Arthropoda and plesiomorphic for Chelicerata (Edgecombe et al. 2000), and the losses re-

sulting in simplification of the box-truss system, especially the loss of all anterior oblique elements, would be synapomorphic for Arachnida.

Endosternal evolution in Chelicerata: First-man (1973) proposed a primitive axial muscle system for Chelicerata that was remarkably similar to the box-truss model. He hypothesized that the primitive system was ladderlike with a ''rung'' of connective tissue (transverse endoskeletal bar) positioned transversely within each somite and connected to longitudinally adjacent transverse bars by ventral longitudinal muscles. Each transverse bar was also suspended from the exoskeleton by bilat-

Figure 7.—Dorsal view of the endosternite (est), ventral surface of the abdomen, and the base of the telson. The appendages, carapace, tergum and most other heavily sclerotized structures have been removed, but the dorsal entapophyses (de) have been cut at their attachments to the tergum and are depicted as "floating" at their intact anatomical positions. The ventromedial surface of the abdomen is composed of pliable cuticle arranged in transverse folds. A series of subneural plastrons (snp) bridge the crests of a pair of adjacent folds (compare Fig. 2). A, The left side shows the middle tract of the posterior oblique muscles (22). The right side shows the lateral tract of ventral longitudinal muscles (24) and posterior oblique muscles (25). Only one member of the anterior oblique muscles (26_{XI}) is shown, the others have been cut near their ventral attachments. The posterior end shows the arrangement of muscles that insert on the ventrolateral processes of the telson (39–44). B, Same perspective as in A, but the medial invaginated portion of the carapace-tergum hinge (if) "floats" above the other elements to show the attachments of muscles 27–29. The left side shows the arrangement of the posteriormost anterior oblique muscle (26_{XIV}), the right side shows muscles that span the dorsal entapophyses (30), and the posterior end shows the arrangement of muscles that insert on the dorsal process of the telson (31–38). C, Same perspective showing the position of the gut and its muscles (7–10). The crop and rectum have been cut horizontally and the intermediate portions of the gut have been removed to show the underlying endoskeleton and muscles (compare Fig. 2). The right side depicts the dorsoventral muscles (17) and the medial tracts of ventral longitudinal muscles (19, 20) and posterior oblique muscles (21). The left side shows the middle tract of ventral longitudinal muscles (23) and the dorsal interconnections between opercular chondrites (diac). Arabic numerals correspond to muscles listed in Table 1. Roman numerals correspond to the postoral somite with which the indicated muscle or structure is associated. *Abbreviations:* de, dorsal

eral dorsoventral suspensor muscles and from the lateral exoskeleton by transverse suspensor muscles. As in the box-truss model, the endosternite would have evolved by fusion of the transverse bars and the tendinified longitudinal muscles of the first seven postoral somites. Thus, Firstman's model departed from the box-truss model only in predicting a series of intra-segmental transverse muscles in chelicerates rather than intersegmental posterior oblique muscles and, apparently, in regarding the ''branchio-thoracic'' muscles (*26*) as extrinsic appendicular muscles rather than axial muscles.

Upon applying his model to the axial system in *Limulus*, Firstman (1973) concluded that the endosternite retained six pairs of endosternal suspensor muscles, namely, the dorsal, transverse and ventral suspensors of somites III, the dorsal and transverse suspensors of somite IV, and the dorsal suspensors of somite V. However, observations from the present study are not consistent with Firstman's (1973) interpretation. First, he overlooked or omitted several endosternal and axial muscles in *Limulus*, specifically, one dorsal suspensor (*13*$_I$) (Figs. 1, 7), all axial muscles that arise from the endosternite and insert on more posterior structures (Fig. 7: *14*, *19*, *20*, *22–24*), and the anterior oblique muscles (*26*) (Figs. 1, 7). Second, Firstman implied in his figures that transverse suspensors were present in the abdominal somites of *Limulus*, although he recognized in the text that these muscles (probably *102* and *103*: Fig. 8) inserted on the opercula rather than the lateral body wall and doubted their homology with the transverse suspensors of the endosternite. Third, he did not provide specific criteria for assigning muscles to particular somites (e.g., position with respect to other muscles). Fourth, he appeared to assign suspensor muscles to the ''dorsal'' and ''transverse'' series based on whether the muscle had a dorsoventral or transverse orientation rather than some more precise criterion, such as placement with respect to other muscles that could be assigned unambiguously to specific somites. [Recent studies of
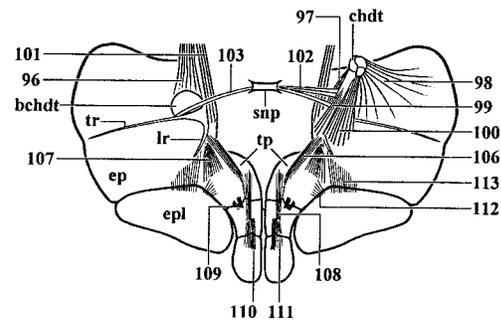

Figure 8.—Dorsal view of the first postgenital operculum with the posterior surfaces and respiratory lamellae removed. The appendage is shown in its fully retracted position, so the inner surface of the anterior surface faces dorsally. The subneural plastron (snp) of somite VIII is the only other structure depicted; the pliable ventral cuticle in which the opercula are embedded has been removed. The anatomical relationship between the appendage and the other abdominal structures can be envisioned by superimposing this figure on appropriate elements of Fig. 7. Numbers correspond to muscles listed in Table 1. *Abbreviations:* bchdt, site where the base of the appendicular chondrite attaches to the anterior plate; chdt, dorsal terminus and shaft of chondrite; ep, inner surface of the anterior plate; epl, exopodial lobe; lr, longitudinal ridge; snp, subneural plastron of somite IX; tp, telopod; tr, transverse ridge.

arachnid anatomy suggest that muscles Firstman homologized as ''transverse suspensor muscles'' represent different kinds of muscles in different chelicerate taxa, such as ventral suspensors in scorpions (pers. obs.) and posterior oblique muscles in Pedipalpi (Shultz 1993, 1999)].

In contrast, current evidence from *Limulus* suggests that the endosternal suspensors acknowledged by Firstman are members of a single metameric series representing somites II through VI. This is consistent with embryological evidence (Scholl 1977) and with the pattern of suspensor insertions on the carapace, which shows one suspensor associated with each set of extrinsic appendicular muscles (Fig. 1: *13*$_{II}$–*13*$_{VI}$). Firstman apparently overlooked one dorsal suspensor muscle that

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appendicular chondrites; dprt, dorsal process of telson; esph, esophageal portion of foregut; est, endosternite; if, intersegmental fold of carapace-tergum hinge; post, postopercular sternum; snp, subneural plastron; ve, ventral entapophysis; vlprt, ventrolateral process of telson.
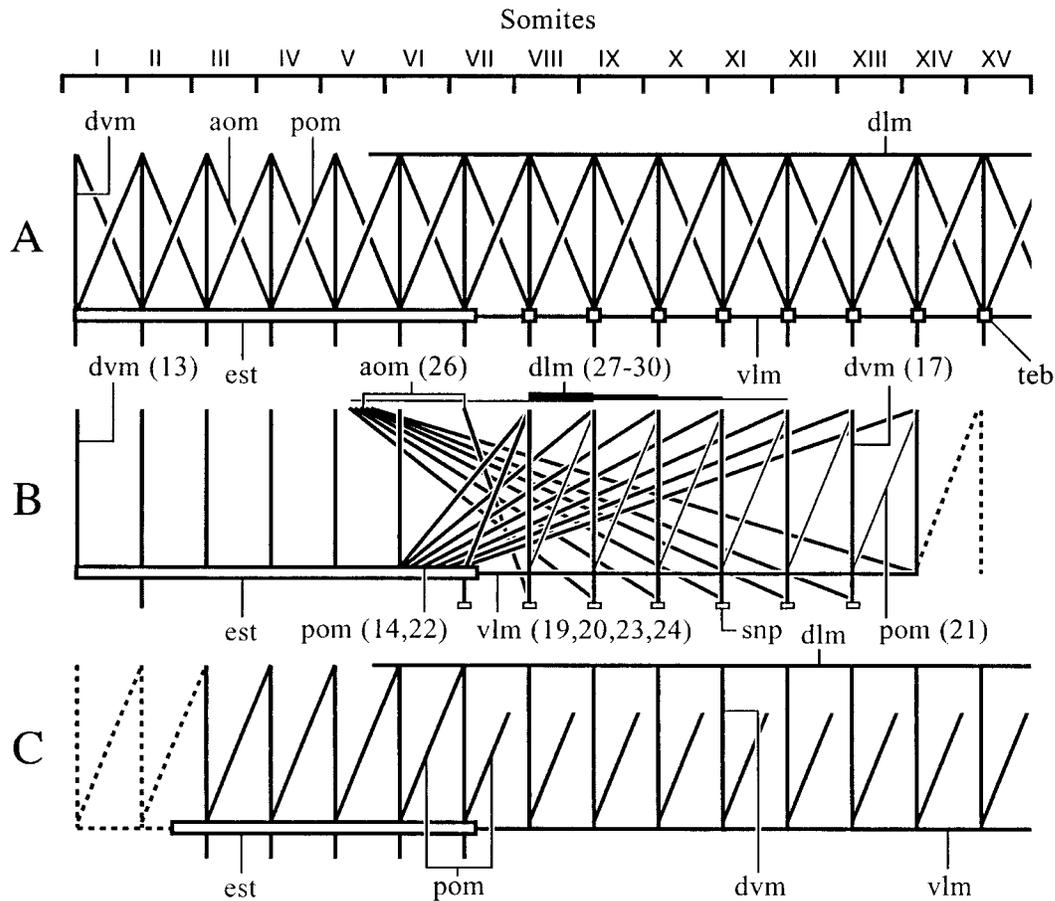
Figure 9.—Diagrammatic medial views of hypothetical axial muscle systems in chelicerates showing how the box-truss axial muscle system of other arthropods may have been modified in *Limulus* and arachnids. A, Hypothetical ancestral chelicerate condition showing primitive box-truss axial-muscle system and the chelicerate endosternite. B, Arrangement of axial muscles in *Limulus* labeled to show proposed homologies with the box-truss axial-muscle system in "A." Note simplification of prosomal elements and anterior displacement of dorsal attachments of aom and ventral attachments of pom. The dotted lines at the posterior indicate muscles present in the larva but not in adult. C, Hypothetical ancestral arachnid condition showing loss or modification of anterior elements, loss of aom in all somites, and displacement of opisthosomal pom attachments from tergites to pleural regions. Abbreviations: aom, anterior oblique muscle; dvm, dorsoventral muscle; est, endosternite; pom, posterior oblique muscle; teb, transverse endoskeletal bar; vlm, ventral longitudinal muscle.

appears to be associated with the cheliceral somite (Figs. 1, 7: 13_I). This muscle arises and inserts more posteriorly than would be expected from its metameric position due to posterior migration of the entire cheliceral somite during development (Scholl 1977) (Fig. 3). With the recognition of 13_I, *Limulus* appears to have a single metameric series of six dorsal endosternal suspensors (13_I–13_VI), one for each of the six original prosomal somites.

When these conclusions are interpreted in the framework of the box-truss model, several evolutionary and phylogenetically relevant insights emerge. First, anterior oblique muscles are absent from the endosternite in both xiphosurans and arachnids, and this might represent a synapomorphy for these two lineages. However, given the extreme reduction of all axial muscles in pycnogonids (Firstman 1973), it is possible that this feature is synapomorphic for Chelicerata. Second, posterior oblique muscles are absent from the first five

somites of the endosternite in *Limulus* but are present for somites III-V in at least some arachnids (i.e., Araneae, Amblypygi, Thelyphonida) (Shultz 1991, 1993, 1999). Thus absence of posterior oblique endosternal suspensors in *Limulus* and all Asian species of horseshoe crabs (Yamasaki et al. 1988) is probably a synapomorphy of extant Xiphosura. Third, the apparent absence of endosternal components associated with somites I and II is a possible synapomorphy of Arachnida, given that they are present in *Limulus*. It should be noted, however, that these endosternal components may have been retained but modified and incorporated into the epipharyngeal complex of arachnids in a variety of ways (Shultz 1993, 2000). Fourth, the presence of a postcerebral pharynx supplied with dilator muscles that arise from the endosternite may be a plesiomorphic condition for Arachnida rather than a derived feature of Araneae and Amblypygi alone as is widely thought (e.g., Wheeler & Hayashi 1998). A muscularized postcerebral pharynx is clearly present in *Limulus* (Figs. 2, 7C) and has been reported but not confirmed in a palpigrade by Rucker (1901). An unmuscularized postcerebral pharynx (cuticle-lined ''esophagus'' only) and endosternal foramen instead of pharyngeal dilator muscles are present in Uropygi (Millot 1949; Shultz 1993).

Monophyly of Arachnida.—The vast majority of phylogenetic analyses of Chelicerata have concluded that Xiphosura and Arachnida are sister groups among extant chelicerates and that each group is monophyletic. This conclusion is strongly and consistently supported by phylogenetic analyses of morphological evidence (Weygoldt & Paulus 1979; Shultz 1990; Edgecombe et al. 2000), molecular evidence (Regier & Shultz 1997, 1998; Shultz & Regier 2000; but see Colgan et al. 1998; Giribet & Ribera 2000) and combined evidence (Wheeler & Hayashi 1998; but see Edgecombe et al. 2000). Morphological synapomorphies supporting the monophyly of Arachnida include 1) reduced pleural fold (doublure) in the prosomal carapace (Shultz 1990); 2) slit sensilla (Weygoldt & Paulus 1979; Shultz 1990); 3) anterodorsal rotation of anterior prosoma resulting in anteroventrally directed mouth (Weygoldt 1979); 4) absence of appendages on somite VII in adults (Shultz 1990); 5) absence of cardiac lobe or glabella on carapace (original observation); 6) single medial genital opening rather than bilaterally paired genital openings (paired genital openings in all extant xiphosurans: Yamasaki et al. 1988; single median opening in arachnids: Clarke 1979, original observations); 7) absence of appendages on somite XIII (Shultz 1990; but see Dunlop 1998); 8) loss or reduction of postcerebral crop and proventriculus (present study); 9) absence of anterior oblique axial muscles (present study); 10) pleural rather than tergal attachments of opisthosomal posterior oblique axial muscles (present study); and 11) endosternal suspensors of somites I and II absent or detached from the endosternite (present study). However, alternative phylogenetic systems have been proposed. Van der Hammen (1985, 1989) suggested that Xiphosura, Scorpiones and Opiliones be placed within a clade (Myliosomata) based on presence of a ''coxisternal'' feeding apparatus, a feature that actually appears to be primitive for all extant arthropods, including myriapods and hexapods (Popadic et al. 1998; Scholtz, Mittmann & Gerberding 1998). Dunlop (1998) suggested that scorpions are more closely related to xiphosurans than to tetrapulmonate arachnids (Araneae, Amblypygi, Uropygi), because the tetrapulmonates retain primitive lamellate respiratory structures on the genital somite but scorpions and xiphosurans have lost them (see Weygoldt 1998 for an alternative view). Each dissenting view is derived from interpretation of a single character system and the devaluation or dismissal of all characters that do not support its conclusions. Given the explicit enumeration of arachnid synapomorphies offered here and elsewhere, workers who maintain that xiphosurans be placed among arachnids should provide explicit justification for their position and specific reasons for rejecting the accumulating evidence that excludes xiphosurans from Arachnida.

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