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THE RELATIONSHIP OF THE CHELICERATE ARTERIAL SYSTEM TO THE EVOLUTION OF THE ENDOSTERNITE

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ABSTRACT

Comparative anatomical studies are carried out on representatives of the Arachnida, Merostomata, and Pycnogonida with respect to (a) circulatory morphology, and (b) the morphological significance of the muscles which insert on the endosternite. A morphological relationship of the chelicerate arterial system to the endosternite is demonstrated, and evidence is brought forth that this is a primitive relationship in chelicerates. A comparative analysis of the chelicerate endosternite provides evidence that it has evolved by fusion of an arterial membrane with the connective tissue of serial, paired, transverse and dorsoventral muscles. A hypothetical model of the primitive chelicerate endosternite is reconstructed.

Specimens dissected and/or sectioned include representative genera of each arachnid order; the xiphosuran, *Limulus*; and seven genera of pycnogonids. The endosternites of merostomes and arachnids are interpreted to be homologous structures, and the transverse suspensor muscles of the endosternite are hypothesized to be homologous to the transverse muscle fibers of the pycnogonid horizontal vascular septum.

In all apulmonate arachnids which have endosternites (orders Palpigradida, Acarida, Opilionida, Ricinuleida, and Pseudoscorpionida) the endosternite is demonstrated to be continuous with a perineural vascular membrane which encloses a periganglionic arterial sinus. It is demonstrated that palpigrades possess the most primitive endosternite of all the known extant chelicerates. In the nonpalpigrade apulmonate arachnids, there has been a tendency toward reduction of the endosternite and a corresponding tendency toward development of an elaborate apodemal endoskeleton. The most extreme degree of development of an apodemal endoskeleton occurs in solpugids, and in this order the mesodermal endosternite has been reduced to absence.

Limulus (Class Merostomata) also possesses a perineural vascular membrane and an endosternite. Only in the immature *Limulus* is the endosternite continuous with the arterial system; by the adult stage the anatomical connection between the two is vestigial.

In all pulmonate arachnids (orders Scorpionida, Thelyphonida, Schizomida, Amblypygida, and Araneida) the adult arterial system includes a pair of enlarged arteries (thoracic sinuses) which lie dorsad to the subesophageal ganglionic mass. Since the larval *Limulus* possesses a similar pair of thoracic sinuses (Kingsley, 1893) which during later ontogeny hypertrophy and surround the central nervous system, giving rise to a periganglionic arterial sinus, it is hypothesized that the thoracic sinuses of adult pulmonate arachnids represent a neotenous condition. In the pulmonate arachnid orders, there is no anatomical connection between the adult arterial system and endosternite, except in the lungless spider, *Orthonops gertschi* (family Caponiidae), where an anatomical connection exists in the adult.

The existence in pycnogonids of a perivisceral arterial membrane is demonstrated, and in the light of this the circulatory blood movements in pycnogonids are reinterpreted. The perineural portion of this membrane is interpreted to be homologous to the perineural vascular membrane of merostomes and arachnids. In pycnogonids, the perivisceral arterial membrane is continuous with the double-layered horizontal vascular septum (of Dohrn, 1881) which separates dorsal and ventral portions of the trunk hemocoel. It is suggested that this septum is homologous to the hypothetical progenitor of the endosternite of merostomes and arachnids. Moreover, it is suggested that the primitive function of the chelicerate endosternite may have been vascular rather than skeletal.

It is hypothesized that neoteny has been involved in the origin of arachnids from merostomes, and in the origin of apulmonate arachnids from pulmonates. The Palpigradida is regarded as the closest apulmonate order to the ancestral apulmonate stock. The Pulmonata and Apulmonata are both regarded as natural monophyletic catagories. The Pulmonata is regarded as having emerged from the arachnid ancestors of modern scorpions. The ancestral apulmonate stock diverged to give rise both to modern palpigrades and to the nonpalpigrade apulmonates.

INTRODUCTION

The development of this research started with some observations I made of a noteworthy relationship of the arterial system to the endosternite in opilionids. The anterior aorta in these arachnids is continuous with a vascular membrane which envelops the entire central nervous system and its nerve trunks. Thus, the nervous system is enclosed within a periganglionic arterial blood sinus. The same vascular membrane is also continuous with the endosternite. A detailed observation showed that this is a histological continuity of connective tissue; the endosternite is actually a thickened portion of the perinueral vascular membrane.

Subsequently, I observed that a similar perineural arterial membrane, with the same relation to the endosternite, exists in all three suborders of the Opilionida, and I interpret this similarity to be homology. Although Kaestner (1968) mentioned the perinueral arterial membrane in opilionids, and Appelt (1900) observed that the endosternite in *Phalangium opilio* is continuous around its borders with a membrane which surrounds the brain, the actual relation of the arterial system and endosternite has never been mentioned by any author.

A perineural vascular membrane, similar to that in opilionids, has been reported for *Limulus* (Milne-Edwards, 1872; Petrunkevitch, 1922; Kaestner, 1968) and in the Acarida (Hughes, 1959; Evans, 1961), though none of these authors mentioned a relationship of this membrane to the endosternite. My own dissection of *Argas persicus*, a tick, showed that the perineural vascular membrane, is, in fact, continuous with the endosternite. I found that the same relationship exists also in an immature *Limulus*, though in the adult the endosternite has become a separate, detached structure with only a vestigial connection to the arterial system. Apparently, this relationship in the young *Limulus* was almost discovered by Snodgrass (1952), who commented:

> In a larval specimen of *Limulus* 2 cm. in length, the endosternum is a thin membrane . . . . In a specimen 5 mm. in length, the "plate" is a delicate membrane resting close upon the nerve mass beneath it . . . .

These discoveries led me to the opinion that the chelicerate endosternite is a structure of mesodermal origin, contrary to the opinions of some other arthropodologists: e.g., Bernard (1892a, b; 1894c; 1896); Comstock (1948); Chamberlin (1931); Fox and Fox (1964). In this way, I was motivated to undertake an investigation of the endosternite and its relation to the arterial system in the subphylum Chelicerata.

The endosternite is an internal skeleton composed of connective tissue. It occurs in all chelicerates, with the exception of solpugids and a few groups of mites. It is serially metamerized, though in the cephalothorax it is centralized as a common tendon for the attachments of many skeletal muscles. In the abdomen, the endosternite is uncentralized (i.e., it occurs independently in each of one or more segments). The morphological significance of the endosternite became a controversial issue after the appearance of Lankester's (1881) hypothesis that *Limulus* in an arachnid, and especially after Patten's (1889, 1899) hypothesis that *Limulus* is a prevertebrate. The most comprehensive treatments of the nature and origin of the endosternite, from the standpoint of comparative morphology, were those of Schimkewitsch (1893, 1894) and of Pocock (1902). Both of these authors supported the view that the evolution of the endosternite is most satisfactorily reconstructed by means of a theory of the hypertrophy and fusion of muscle tendons. However, neither of them recognized the role of the circulatory system in endosternite development, and accordingly they failed to reconstruct the phyletic history by which the metameric cephalothoracic elements gave rise to a centralized skeletal structure lying horizontally above the subesophageal ganglionic mass.

My own analysis of the endosternite musculature in chelicerates indicated that it is necessary to distinguish the muscles which insert upon the endosternite from those which originate from it. Muscles which insert upon the endosternite have the function of moving or tensing it when they contract; these are the suspensors of the endosternite, and there are two types: the dorsoventral suspensors and the transverse suspensors (Figs. 1, 2). Primitively, one pair of each of these took part in the development of the endosternite in each of the six appendage-bearing segments, as shown by the fact that in palpigrades the endosternite is formed by the six appendage-bearing cephalothoracic segments. The dorsoventral suspensors are bisected by the endosternite, which lies in a horizontal plane, and are thus divided into dorsal suspensors and ventral suspensors. Dorsal suspensors originate from the carapace, while ventral suspensors originate from the sternum. The transverse suspensors are bisected medially by the endosternite, and thus they are divided into right and left counterparts. They originate from the pleural region of the body wall: either from the lateral extremities of the carapace, or else from pleural sclerites (epimera) which lie between the appendicular coxae.

The suspensor muscles of the endosternite insert upon it by way of tendons which are histologically continuous with its connective tissue matrix. They cannot be separated from the endosternite without tearing either the muscle tendon or else part of the endosternite itself. Their points of origin are never on movable appendages such as coxae or endites.

Muscles which originate from the endosternite always insert upon movable structures (e.g., stomodeum, lorum, or appendages). In specimens which have been preserved in alcohol, the muscle origins can be pulled cleanly away from the endosternite, with forceps, exposing a smooth, white surface of attachment on the endosternite surface.

In all the apulmonate arachnids (i.e., those which lack book lungs) the endosternite is continuous all around its borders with a perineural vascular membrane which encloses a periganlionic arterial sinus. This sinus receives blood directly from the aorta. The perineural vascular membrane ensheathes all nerve trunks arising from the central nervous system, and it is reflected posteriorly over the entire length of the postcerebral intestine as a peri-intestinal vascular membrane which encloses a peri-intestinal arterial sinus. (I have observed the peri-intestinal vascular membrane in opilionids, in mites, and in pycnogonids. However, I have not attempted a comparative study of it, for it is not involved directly with the morphology of the endosternite, nor have I confirmed the presence of this membrane in all groups of chelicerates studied in this paper.) The peri-intestinal and perineural vascular membranes constitute collectively a perivisceral arterial membrane which is present also in pycnogonids. The perivisceral arterial membrane is composed of vascular connective tissue like that of the heart and aorta, with which it is con-

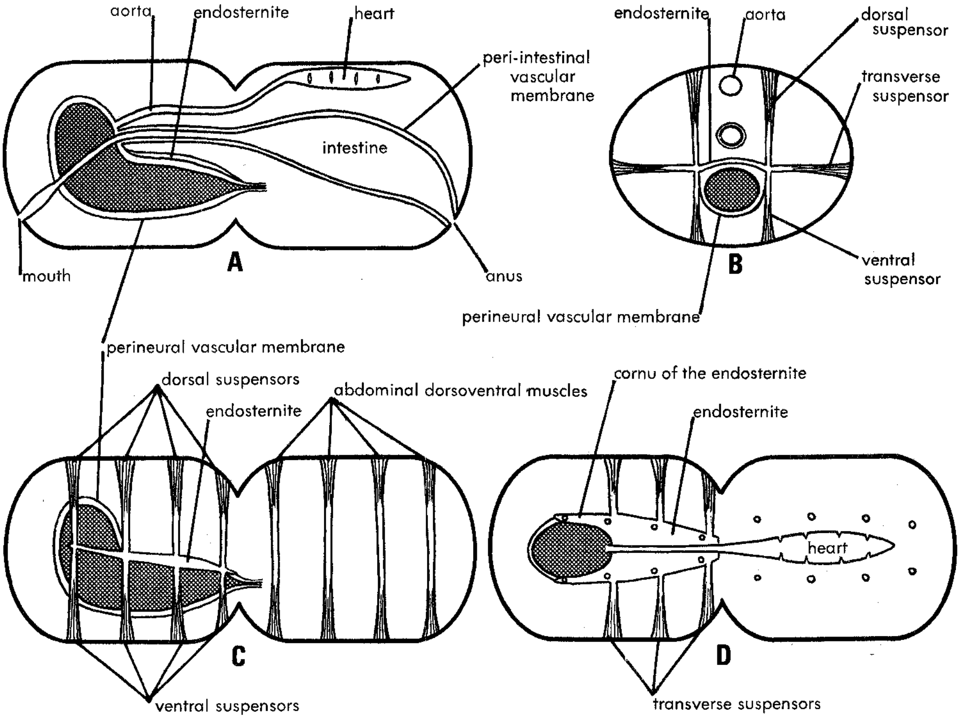


Fig. 1.–TYPICAL APULMONATE ARTERIAL SYSTEM. This condition exists in all chelicerates which lack book lungs. It exists in the arachnid orders Palpigradida, Opilionida, Acarida, Pseudoscorpionida, Ricinuleida, Solpugida, and in the lungless spiders. It exists also in the merostome, *Limulus*, and a similar, homologous condition exists in the Pycnogonida. The central nervous system is shown in dark stipple. Note that blood is pumped into a periganglionic arterial sinus which surrounds the central nervous system. A: midsagittal view; B: transverse section through the subesophageal ganglionic mass; C: lateral view of the endosternite and dorsoventral muscles, seen from the left; D: dorsal view of the endosternite and transverse suspensors; the circles represent the positions of dorsoventral muscles.

tinuous. The endosternite, in the apulmonate arachnids, is a thickened portion of the perineural vascular membrane.

In all the pulmonate arachnids (i.e., those which breathe with book lungs) the perineural arterial development stops short at the stage (as in the larval *Limulus*) in which a pair of thoracic sinuses lie on top of the subesophageal ganglionic mass (Kingsley, 1893). The endosternite of pulmonates develops independently of the arterial system, notwithstanding the primitive association of the two which persists in all other chelicerates which have endostenites. The arrested arterial development peculiar to pulmonate arachnids is an ontogenetic specialization which apparently has arisen through neoteny. The possibility that this has actually occurred will be discussed in greater detail later.

MATERIALS AND METHODS

All specimens were chosen for this study on the basis of availability. Some groups of chelicerates are rare, in which case specimens for dissection must be obtained either from specialists, or else from curators of museum collections. Dr. J. W. Hedgpeth gave me

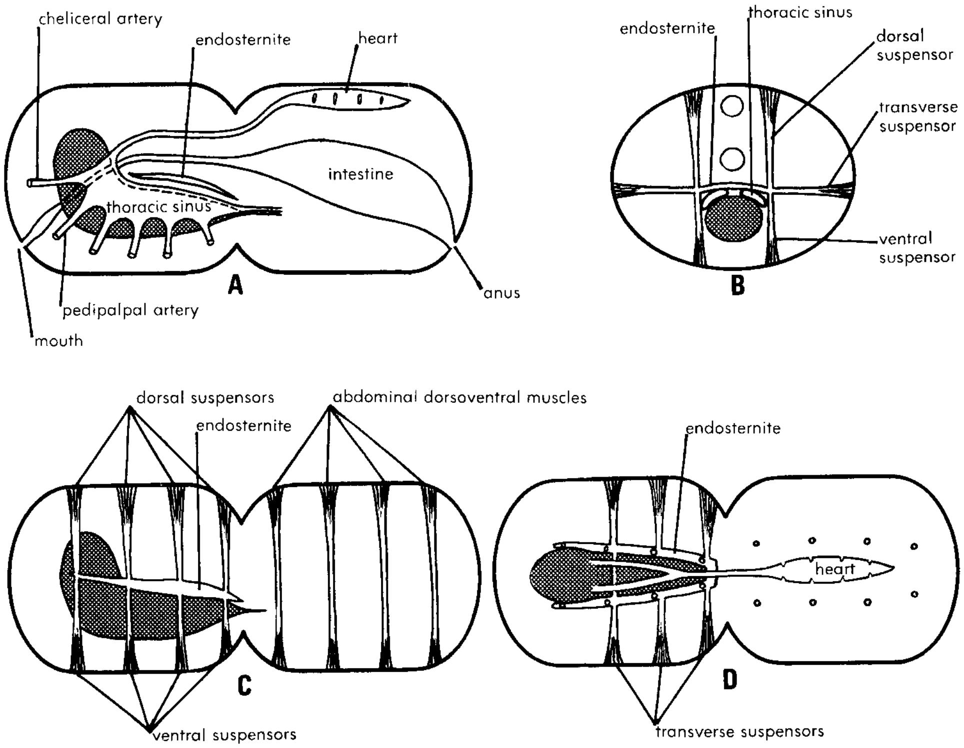


Fig. 2.–TYPICAL PULMONATE ARTERIAL SYSTEM. This condition exists in all arachnids which possess book lungs. It exists in the orders Scorpionida, Thelyphonida, Schizomida, Amblypygida, and Araneida (except lungless spiders). The central nervous system is shown in dark shading. Note that blood is pumped into a paired thoracic sinus which lies on top of the subesophageal ganglionic mass. A: sagittal view, with the left side of the arterial system superimposed, as seen from the left; B: transverse section through the subesophageal ganglionic mass; C: lateral view of the endosternite and dorsoventral muscles, seen from the left; for clarity the circulatory system is omitted; D: dorsal view of the endosternite and transverse suspensors; the circles represent the positions of dorsoventral muscles; for clarity the thoracic sinuses have been omitted, though a heart and aorta are shown. For a dorsal view of the thoracic sinus arterial system, see Figure 19B.

specimens of the following pycnogonids: *Colossendeis scotti, Pycnogonum rhinoceros, Endeis* sp., *Decolopoda australis, Nymphon charcoti, Pentanymphon antarcticum,* and *Ammothea striata.* Dr. Willis J. Gertsch gave me specimens of the following arachnids: *Prokoenenia wheeleri, Trithyreus pentapeltis, Cryptocellus boneti,* and *Orthonops gertschi.* From Dr. D. P. Abbott, I obtained *Garypus californicus*; from Dr. R. W. Mitchell, *Cryptocellus osorioi*; from Dr. L. E. Eighm, *Siro acaroides*; and from Miss M. J. Moody, a Costa Rican amblypygid, *Tarantula* sp. I purchased specimens of *Pycnogonum littorale, Argas persicus,* and *Limulus polyphemus* from General Biological, Inc. (Turtox), Chicago, Illinois.

Dr. E. T. Roche prepared serial cross sections of *Siro acaroides*; the microtome sectioning of this arachnid was made practical by the prior removal of the exoskeleton. All other specimens used in this study were dissected in 70% ethanol, using a Spencer stereoscopic dissection microscope with objectives of 1X, 4X, and 8X, and with oculars of 12X and 20X. Most specimens were cut midsagittally, with a sharp razor blade, and anchored to a Syracuse watchglass with paraffin. Other specimens were cut parasagittally, to the left of the midline, anchored in paraffin on the right side, and dissected from the left side. A few specimens were cut transversely and dissected from the anterior or posterior surface. Illumination was reflected from two sides, and in order to enchance detail, the tissues were stained, as required, with Shaeffer's washable blue Skrip ink.

OBSERVATIONS AND FINDINGS

The Apulmonate Arachnid Orders:
Palpigradida
Opilionida
Acarida
Pseudoscorpionida
Ricinuleida
Solpugida

Order Palpigradida—Most arachnologists regard palpigrades as the most generalized of the living arachnids, i.e., with the greatest number of primitive features, and with fewest specializations (Roewer, 1934). The carapace is metamerized externally, and there are five cephalothoracic sternites, the anteriormost of which belongs to the cheliceral segment. This is the only living order in which there is a distinct cheliceral sternite (Snodgrass, 1952). *Sternarthron zitteli*, stated to be a fossil palpigrade of Upper Jurassic age, possesses six cephalothoracic sternites (Petrunkevitch, 1955). Palpigrades bear close resembalance to the superorder Uropygida (schizomids and thelyphonids), and most arachnologists agree that modern palpigrades have emerged from the ancestral stock that gave rise to the non-scorpion pulmonate orders. However, palpigrades are not pulmonates, for they do not possess book lungs. Some palpigrades possess three pairs of abdominal "lung-sacs" which some investigators have interpreted as respiratory organs. Rucker (1901) believed that lung-sacs were the phyletic antecedants of both book lungs and tracheal spiracles.

The earliest published description of the internal anatomy of a palpigrade is that of Rucker (1901), who said of the circulatory system of *Prokoenenia wheeleri* only that ". . . the simplest condition possible exists." She said that a heart is lacking, although Börner (1904) described a heart with four pairs of ostia in *Eukoenenia mirabilis*. The endosternite of *E. mirabilis* has been described by Börner (1904), but the most detailed studies have been those of Millot (1942b, 1943, 1949b). Millot described six pairs of ventral suspensors of the endosternite; this number is regarded as primitive, since presumably there was one pair of dorsoventral muscles in each of the six appendage-bearing segments of the cephalothorax of ancestral arachnids. Only four pairs of suspensors persist on the dorsal side of the endosternite. In addition to the dorsal and ventral suspensors, Millot described five pairs of transverse suspensors (he called them "lateral suspensors") which originate from the sides of the carapace and extend horizontally to their insertions on the lateral margins of the endosternite (Fig. 4B and C).

I have examined *Prokoenenia wheeleri*, of central Texas, and I have found that the central nervous system is invested by a perineural vascular membrane which encloses a periganglionic arterial sinus (Fig. 3), as in the other apulmonate chelicerates. This membrane is continuous with the borders of the endosternite. The same membrane is continuous also with a dorsal vessal, probably an aorta, in the cephalorthorax. I did not trace this vessel into the abdomen to confirm the presence of a heart, but my diagram of a generalized palpigrade (Fig. 4) shows a heart because Börner (1904) described one in *E.*

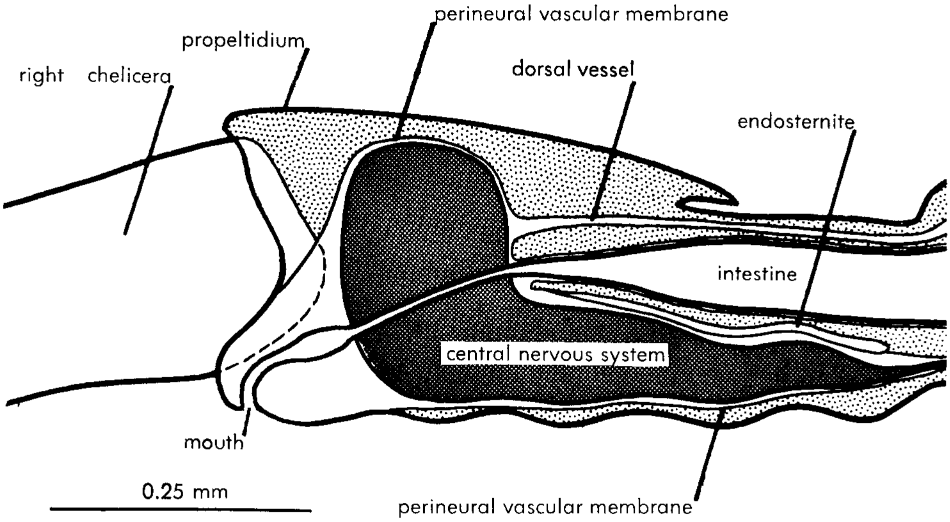


Fig. 3.—Midsagittal view of the caphalothorax of *Prokoenenia wheeleri* (order Palpigradida), seen from the left. The central nervous system is shown with dark shading.

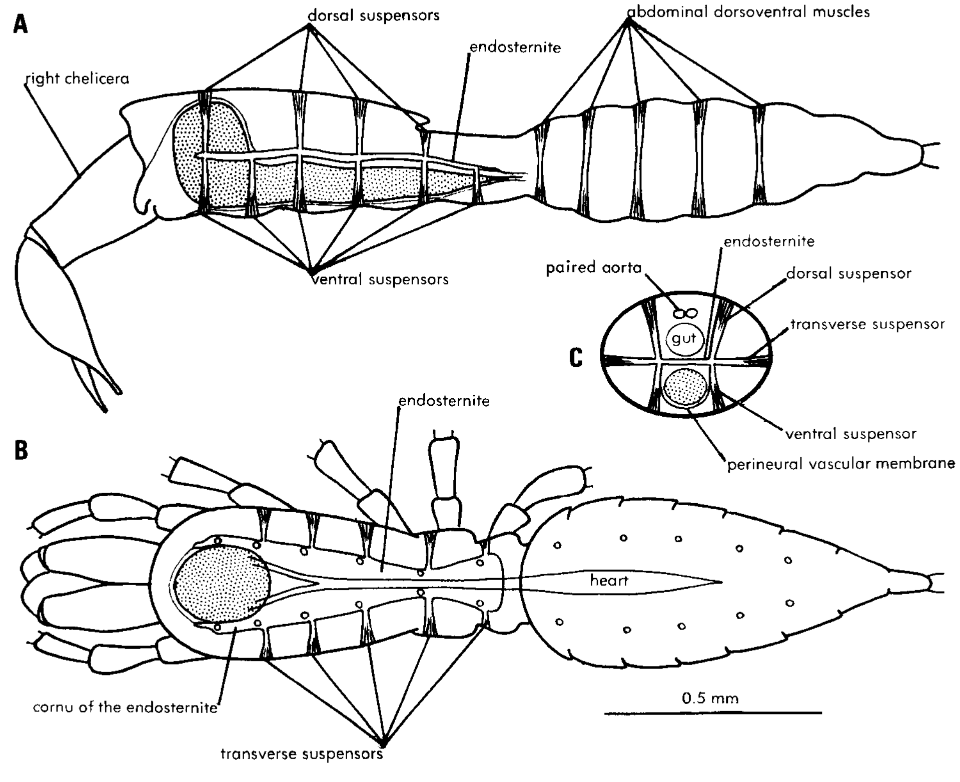
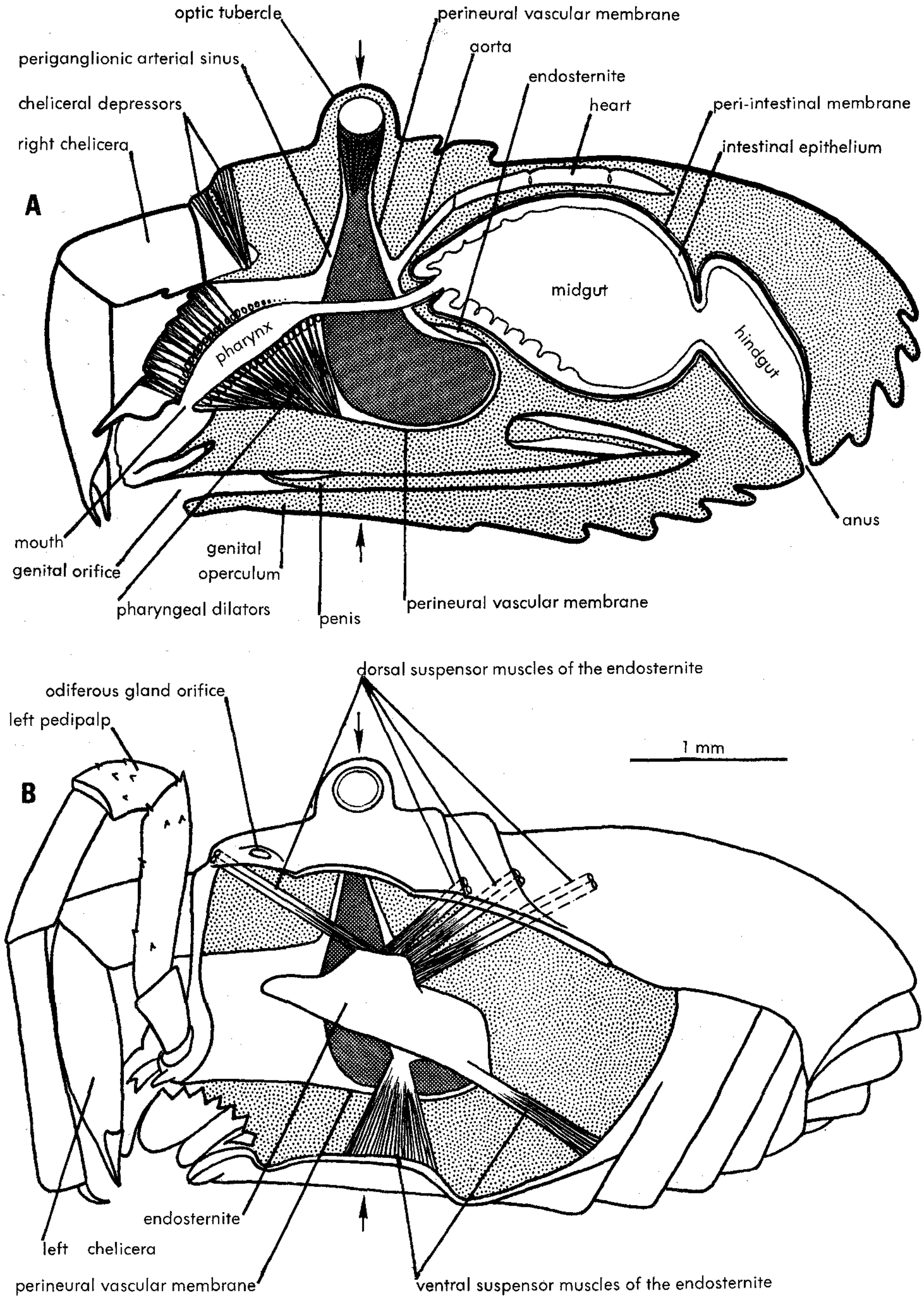


Fig. 4.—The arterial system and endosternite of a generalized palpigrade, adapted from Millot (1943), Börner (1904), Rucker (1901), and my own Fig. 3. A: lateral view, seen from the left, showing the dorsoventral muscles; B: dorsal view, showing the endosternite and its transverse suspensors; the circles represent the positions of the dorsoventral muscles; C: transverse view through the subesophageal ganglionic mass. The central nervous system is stippled.

mirabilis. The endosternite of *P. wheeleri*, and the suspensor muscles which insert upon it, correspond exactly to the condition described by Millot (1943) for *E. mirabilis*. The dorsal and ventral suspensors of the palpigrade endosternite appear to represent cephalothoracic dorsoventral muscles which are serially homologous to those of the abdomen. The palpigrade endosternite is more primitive than that of any other extant arachnid (Fig. 4), and it could almost serve as a model of the endosternite in a hypothetical ancestral arachind (Figs. 26D, 27F).

Order Opilionida—The perineural vascular membrane is most easily observed (and its relationship to the endosternite most readily discerned) in any of the common harvestment of the order Opilionida, e.g., *Leiobunum exilipes* (Figs. 5, 6). None of the morphol-



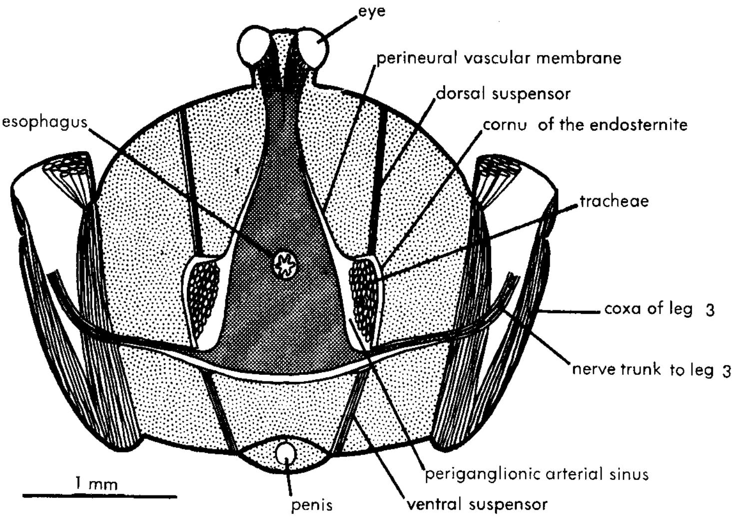


Fig. 6.–Transverse section through *Leiobunum exilipes* (order Opilionida), seen from the anterior. The plane of the section is indicated by the arrows in Fig. 5.

ogists of the last century left a published record of having observed this membrane in opilionids. The earliest students of opilionid anatomy, Treviranus (1816) and Tulk (1843), both of whom observed *Phalangium opilio*, made no mention at all of the endosternite. Apparently the first investigator to identify an endosternite in the Opilionida was Leydig (1862) who interpreted it as a chitinous derivative of the exoskeleton. In 1882, Rössler advanced the hypothesis that the opilionid endosternite is composed of a modified connective tissue, and in 1893 and 1894, Schimkewitsch adopted the same point of view in his descriptions and illustrations of the endosternite of *Opilio parietinus*. During the present century, the only published mention of the perineural membrane and endosternite of opilionids has been that of Appelt (1900) and Kaestner (1933, 1968). Appelt observed that "... the borders of the endosternite make transition into a tough membrane which embraces the whole nervous system." He did not report that he observed the continuity of this membrane with the aorta, for which reason it seems unlikely that he discerned the vascular significance of the membrane, although he stated the possibility that movements of the endosternite may facilitate the heart in the circulation of blood. Kaestner (1968) stated that the opilionid aorta "... opens as a funnel that surrounds the brain."

I have examined the arterial system and endosternite of *Leiobunum exilipes* (suborder Palpatores), a phalangid which is abundant in central California. The arterial system consists of a heart and an anterior aorta which is continuous with a perineural vascular membrane. This membrane surrounds a periganglionic arterial sinus which receives blood from the aorta. Also, the perineural vascular membrane is continuous with a peri-intestinal vascular membrane which surrounds a peri-intestinal arterial sinus (Fig. 5A). A lateral view of the endosternite of *L. exilipes* is shown in Fig. 5B. It is saddle-shaped,

Fig. 5.–A: midsagittal section through *Leiobunum exilipes* (order Opilionida), seen from the left; B: lateral view of same, with part of the body wall removed so as to show the endosternite and suspensor muscles. The central nervous system is shown with dark shading. The arrows indicate the plane of the cross section in Fig. 6.

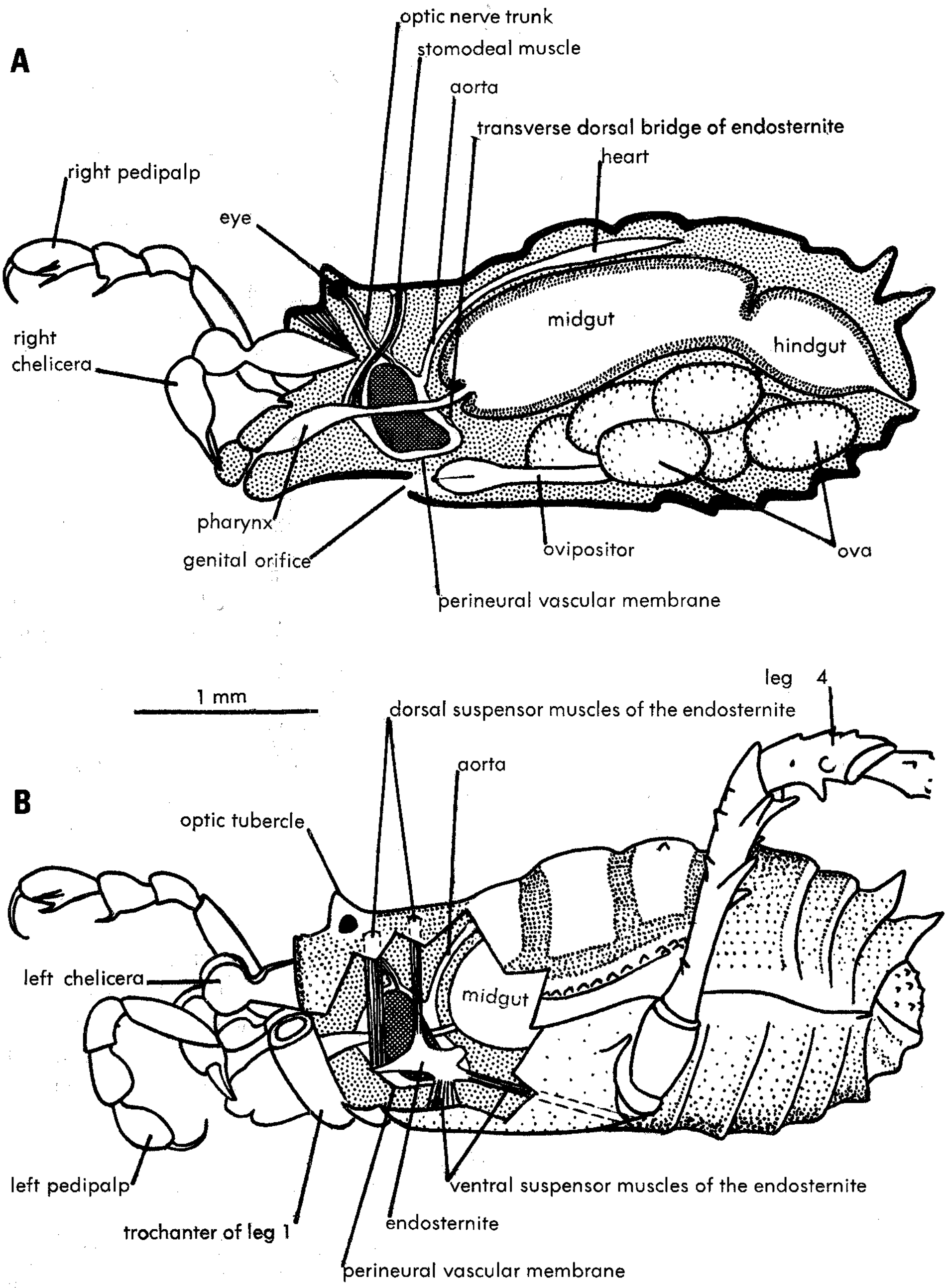


Fig. 7.–A: midsagittal section through a laniatore opilionid (family Gonyleptidae), seen from the left; B: lateral view of same, with part of the body wall removed so as to expose the endosternite and suspensor muscles on the left side. The central nervous system is shown with dark shading.

consisting of a median portion which lies above the subesophageal ganglionic mass, and a pair of cornua that extend anteriad along the sides of the supraesophageal ganglionic mass (Fig. 6). All around its border, the endosternite is continuous with the perineural vascular membrane. A close examination showed that this is a histological continuity of connective tissue; the endosternite is morphologically a thickened portion of the perineural vascular membrane. Four pairs of suspensor muscles insert onto the dorsal surface of the endosternite at its lateral margins, and two pairs insert onto the ventral surface. Transverse suspensors are lacking in all the opilionids I have examined.

The suborder Laniatores includes, among other families, the Gonyleptidae, which is confined in its distribution to Latin America (pers. comm., C. J. Goodnight). Fig. 7A and B shows that the gonyleptid possesses a perineural vascular membrane which is essentially similar to that of a palpatorid; the endosternite, however, is considerably reduced, its dorsal portion being represented by a thin, transverse band across the posterior end of the subesophageal ganglionic mass. The reduced condition of the gonyleptid endosternite closely resembles that of the other nonpalpigrade apulmonates, and is accompained by

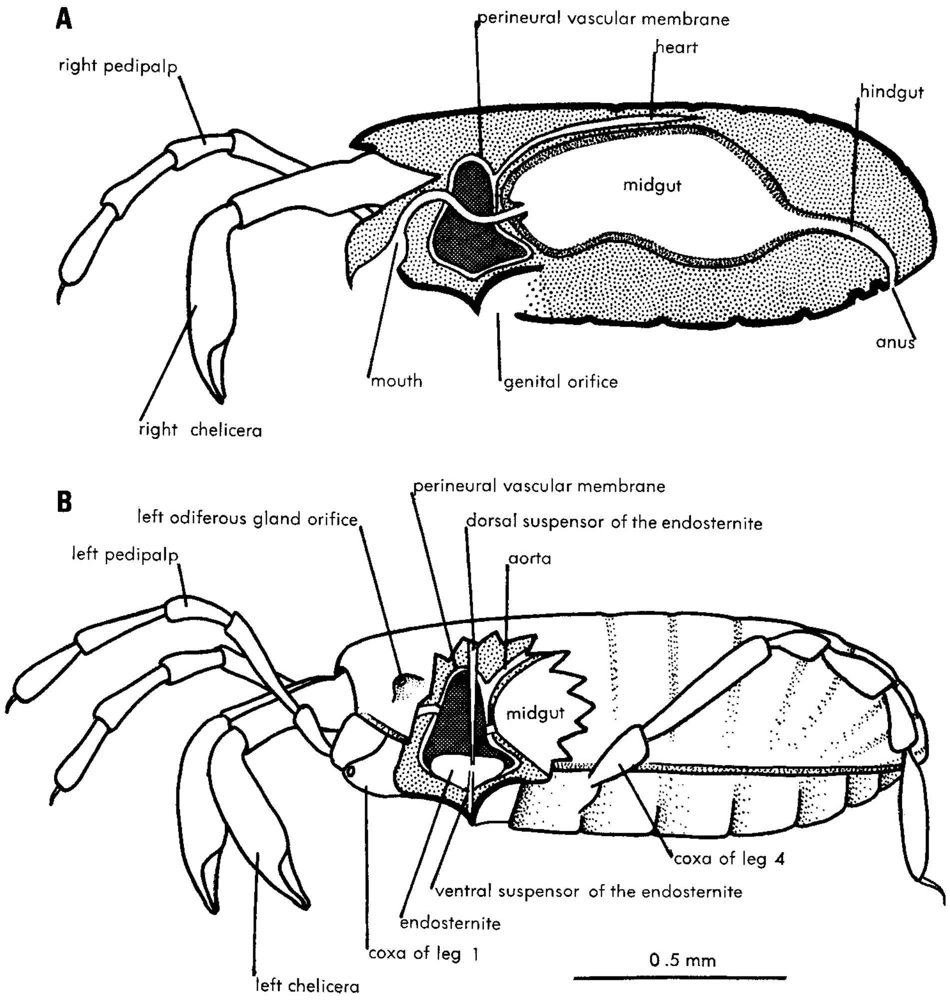


Fig. 8.–A: midsagittal view of a cyphophthalmid opilionid, *Siro acaroides*, seen from the left; B: lateral view of same, with part of the body wall removed so as to expose the endosternite and suspensor muscles on the left side. The central nervous system is shown with dark shading.

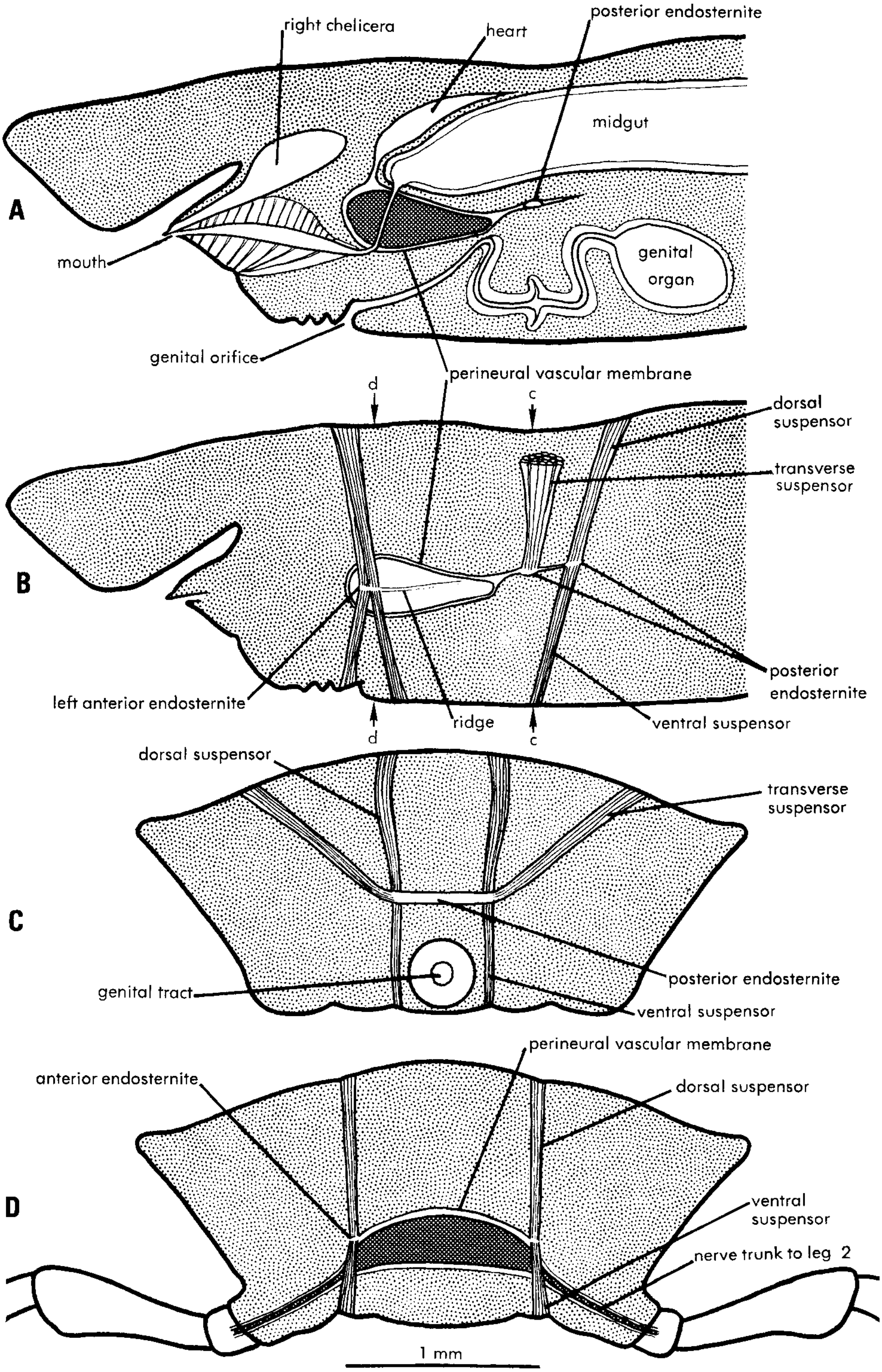
the presence of a strongly developed system of intercoxal apodemes. Only two pairs each of dorsal and ventral suspensors insert onto the gonyleptid endosternite (Fig. 7B). Sorensen (1879), in his classic treatise on the anatomy of the Gonyleptidae, made no mention of the endosternite, nor of the perineural vascular membrane.

The suborder Cyphophthalmi includes only a single family, Sironidae, of mite-sized opilionids. No previous studies of the endosternite or circulatory system have been made in this suborder. The presence of a perineural vascular membrane in *Siro acaroides* (Fig. 8) was confirmed by me, both from dissections and from serial cross sections. The endosternite of *S. acaroides* is vestigial, being represented by a pair of lateral thickenings of the perineural vascular membrane. The right and left sides are not continuous, except by way of the perineural vascular membrane; there is no dorsal, median portion connecting the right and left sides, as there is in other opilionids. The only muscles inserting onto the endosternite are a single pair of dorsoventral suspensors, though several appendicular and pharyngeal muscles originate from it.

Order Acarida–Hughes (1959) stated that in mites " . . . the brain is invested by a thin connective tissue sheath." This sheath is the perineural vascular membrane, and I have found it to be present in all the mites I have examined. There is general agreement among acarologists that most mites do not possess a functional heart (e.g., André, 1949); nevertheless, in all my observations I have found that a dorsal vessel or its vestige is present, and this is continuous with the perineural vascular membrane. Bonnet (1907) described a heart in the ixodid thick, *Hyaloma*, and Evans (1961) stated that the hearts of ixodids have two pairs of ostia. Winkler (1888a, b) described and illustrated a heart with a single pair of ostia in gamasid mites of the suborder Mesostigmata, and Baker and Wharton (1952) reported that a simple heart is present in the suborder Holothyroidea. Schaub (1888) in his sagittal view of *Hydrophantes dispar* (a water mite) showed a membrane which completely envelops the central nervous system, though he did not show an endosternite or a heart. However, Mitchell (1957), who described the musculature of *Hydryphantes*, mentioned a "transverse ligament" to which muscles attach, and I infer that this is an endosternite. Both Steding (1923) and Vitzthum (1940) described and illustrated an endosternite in the genus *Halarachne*; moreover, Vitzthum affirmed the existence of an endosternite in the Notostigmata, the Holothyroidea, the Gamasina, the argasid ticks, the Trombidiformes, and the Sarcoptiformes, but he stipulated that certain groups of mites lack an endosternite (e.g., the Uropodina and the Tetrapodili).

For the purposes of this research I have focused my attention upon the fowl tick, *Argas Persicus* (suborder Metastigmata). I chose this form because of its availability, and because of its large size compared to other members of the order. In the fowl tick, I found that a perineural vascular membrane is well developed; it is continuous with an endosternite and with a dorsal aorta leading from the heart (Figs. 9, 26H). This confirms the report of Borradaile, et al. (1961) that " . . . in the tick, *Argas*, there is a single-

Fig. 9.–A: midsagittal view through the cephalothoracic region of *Argas persicus*, the fowl tick (order Acarida), seen from the left; B: lateral view of same, showing the endosternite and its suspensor muscles, seen from the left; C: transverse section through the transverse suspensor of the posterior endosternite, as seen from the anterior, with the posteriormost pair of dorsoventral suspensor muscles behind it; the plane of the section is indicated in Fig. B by the arrows, cc. D: transverse section through the anterior endosternite, showing the attachment of the anteriormost pair of dorsoventral suspensor muscles, as seen from the anterior; the plane of the section is indicated in Fig. B by the arrows, dd.


A
right chelicera
heart
posterior endosternite
midgut
mouth
genital organ
genital orifice
perineural vascular membrane
B
d
c
dorsal suspensor
transverse suspensor
posterior endosternite
left anterior endosternite
ridge
ventral suspensor
C
dorsal suspensor
transverse suspensor
posterior endosternite
genital tract
ventral suspensor
D
perineural vascular membrane
anterior endosternite
dorsal suspensor
ventral suspensor
nerve trunk to leg 2
1 mm

chambered pulsating vessel with a pair of ostia and an aorta running forward to a periganglionic sinus."

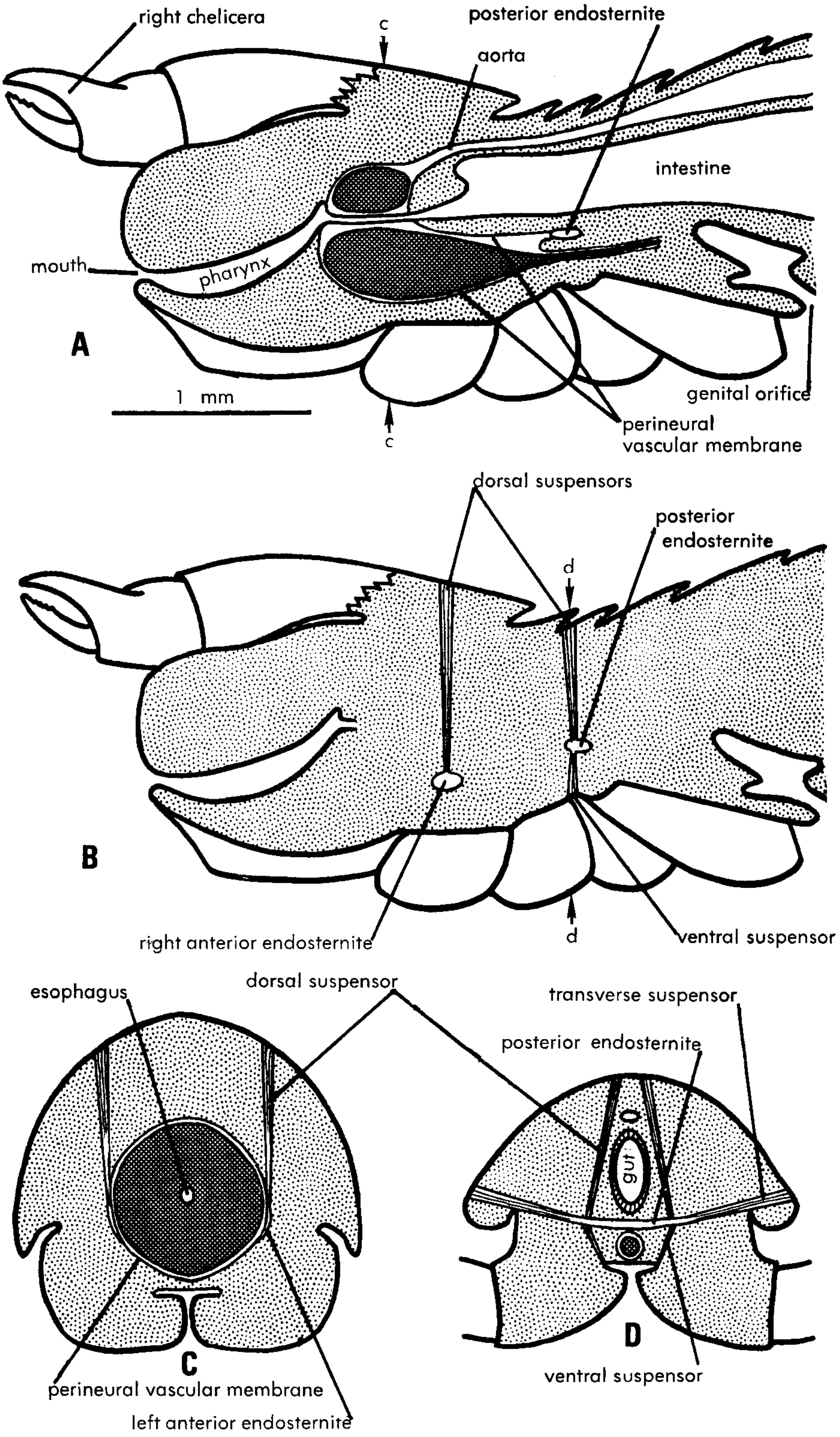
The endosternite of *A. persicus* is divided into anterior and posterior parts: the anterior endosternite consists of a pair of thickened portions of the perineural vascular membrane on the right and left sides of the brain. This condition resembles that of the cyphophthalmid endosternite (described above). Each side receives the insertions of two pairs of dorsoventral muscles (Fig. 9B and D). Extending posteriad from the anterior endosternite, on each side of the central nervous system, is a skeletal ridge of thickened perineural vascular membrane which receives the origins of many appendicular muscles, mainly coxal rotators. Morphologically, this ridge must be regarded as part of the anterior endosternite; it is labeled in Fig. 9B. The posterior endosternite is formed principally by the tendonified medial portion of a single transverse muscle (Fig. 9A, B, C). It is continuous with a posterior extension of the perineural vascular membrane. Immediately posterior to the transverse band of the posterior endosternite, a single pair of dorsoventral muscles is bisected by the perineural vascular membrane, which forms a horizontal membranous septum for a short distance behind the transverse band (Fig. 9B). Hence, the endosternite of this tick (anterior plus posterior portions) involves three pairs of dorsoventral muscles and one pair of transverse muscles. In the past, certain authors (e.g., Pagenstecher, 1862) have confused the true dorsoventral muscles with coxal elevators. The latter are powerful muscles, originating on the carapace, which extend ventrad to insert on coxal apodemes, whereas the true dorsoventral muscles originate on the carapace and sternum and insert on the endosternite.

I have studied wholemount slides (prepared by I. M. Newell) of *Caloglyphus* sp., an astigmatic mite (suborder Sarcoptiformes), which show an endosternite that is more extensively developed than in ticks. It is continuous with a perineural vascular membrane which receives a dorsal vessel, though a functional heart is said not to be present in the Sarcoptiformes. The endosternite of this mite is more similar to that of a harvestman than is the tick endosternite.

Order Pseudoscorpionida—Morphological treatments of the pseudoscorpion date back as far as the *Vermischte Schriften*, by Treviranus (1816), who examined *Chelifer* sp. The earliest investigation of the internal anatomy is that of Menge (1855), who examined various genera, though description of the circulatory structures was not attempted until 1880, by Daday, in *Chernes hahnii*. A general treatment of internal morphology was prepared in 1888, by Croneberg, who based his report upon earlier findings, and upon his own observations of *C. hahnii.*

Croneberg (1888), in describing the brain of *C. hahnii*, distinguished an "inner neurilemma" from an "outer neurilemma," and I infer that the latter is a vestige of the perineural vascular membrane. In his Fig. 17, he showed that the "outer neurilemma" is

Fig. 10.—Generalized diagram of the endosternite and perineural vascular membrane in pseudoscorpions, based upon my observations of *Microcreagris* sp. and *Garypus californicus*, and upon the descriptions of Vachon (1949) in *Chelifer cancroides*, and of Croneberg (1888) in *Chernes hahnii.* A: midsagittal view of the cephalothoracic region, seen from the left; B: lateral view of the endosternites, showing the dorsal and ventral suspensor muscles, as seen from the left; C: transverse section through the anterior endosternite, seen from the anterior; the plane of the section is indicated in Fig. A by the arrows, cc. D: transverse section through the posterior endosternite, seen from the anterior; the plane of the section is indicated in Fig. B by the arrows, dd. The central nervous system is shown with dark shading.


right chelicera
c
posterior endosternite
aorta
intestine
mouth
pharynx
A
1 mm
c
genital orifice
perineural
vascular membrane
dorsal suspensors
posterior
endosternite
d
B
right anterior endosternite
d
ventral suspensor
esophagus
dorsal suspensor
transverse suspensor
posterior endosternite
gut
C
perineural vascular membrane
left anterior endosternite
D
ventral suspensor

continuous with a dorsal vessel which I take to be the anterior aorta. Although Croneberg made no comment about this relationship, he did say that the aorta extends forward until it reaches the posterior face of the supraesophageal ganglionic mass.

The pseudoscorpion endosternite has been described by Vachon (1949), based mainly upon *Chelifer cancroides*. The endosternite of this arachnid, like that of *Argas persicus* (the fowl tick), is divided completely into separate anterior and posterior portions. The anterior endosternite is paired, lying on the right and left sides of the supraesophageal ganglionic mass (Fig. 10B, C). A single pair of dorsal suspensor muscles inserts into the anterior endosternite, and several pairs of appendicular and pharyngeal muscles originate from it. The posterior endosternite has been described by Vachon as "... a simple transverse, tendinous band." He illustrated it in both lateral and dorsal views, and Croneberg (1888) illustrated it in transverse view. A single pair of dorsoventral suspensor muscles inserts onto the posterior endosternite, and at least three pairs of appendicular muscles originate from it. According to Vachon (1949), the anterior and posterior endosternites are derived each from three segments: he said that the anterior endosternite is derived from the pedipalpal and the first and second walking-leg segments, whereas the posterior endosternite is derived from the third and fourth walking-leg and the first abdominal segments.

I have examined the arterial system and endosternite of *Microcreagris* sp. and of *Garypus californicus*. In both of these genera, I found a perineural vascular membrane (Fig. 10A, C) which is similar to that already described for other apulmonate arachnids. It is somewhat fragmentary, however, and it exists apparently as a vestige which may no longer have a vascular function. It is most plainly developed in those regions where it is continuous with the endosternites. Weygoldt (1969) in his midsagittal view of the anterior end of an embryonic *Neobisium* sp. (his Fig. 92) illustrated a membrane which is continuous with the posterior endosternite, and I believe this is the same membrane (the perineural vascular membrane) which I have observed in *Microcreagris* sp. and *G. californicus.*

The endosternites of these two pseudoscorpions correspond exactly to the earlier descriptions of Croneberg (1888) and Vachon (1949). The anterior endosternite, lying on each side of the brain, is continuous with the perineural vascular membrane; I interpret it as the morphological equivalent of the lateral horns (the anterior cornua) of the more completely developed endosternites of other arachnids. The posterior endosternite resembles the posterior portion of the tick endosternite because, morphologically, it is the tendinous, medial axis of a transverse muscle which originates, on both sides, from the carapace (Fig. 10A, D).

The pseudoscorpion endosternite, despite its morphological similarity to the argasid endosternite, is more reduced (i.e., more vestigial) than the latter: the anterior endosternite of the pseudoscorpion receives the insertion of only a single pair of dorsoventral muscles, whereas that of the argasid tick has two such insertions on each side. Moreover, the endosternal ridge, of the anterior endosternite of the tick, is not developed in the pseudoscorpion. The apodemal endoskeleton is more highly developed in pseudoscorpions than it is in argasic ticks. I believe this supports my hypothesis that there is a general correlation in all apulmonate arachnids between the extent of apodemal development and the degree of reduction of the mesodermal endosternite.

Order Ricinuleida—The first morphological treatment of the Ricinuleida was that of Hansen and Sorensen (1904), who dealt primarily with the external anatomy of various

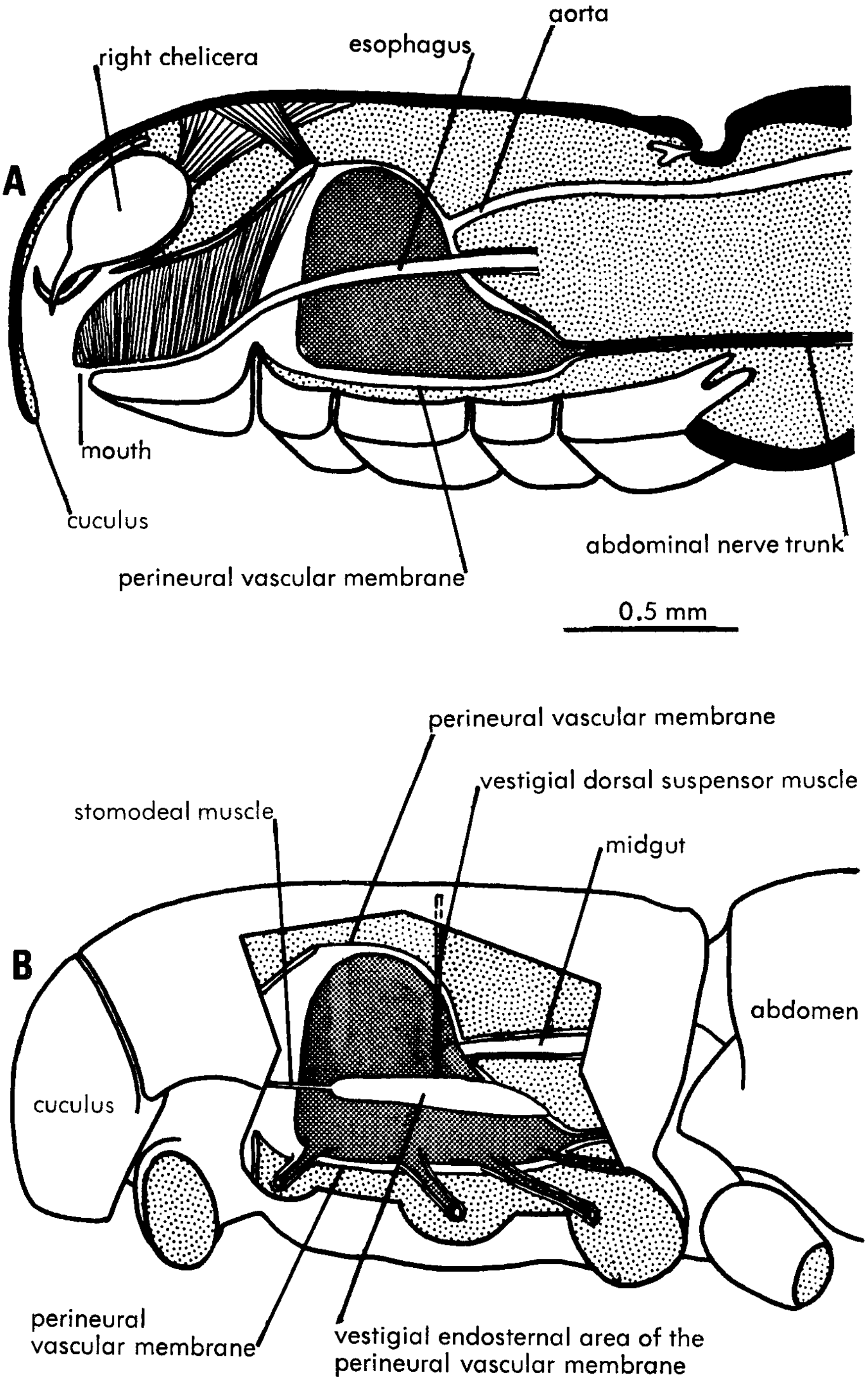


Fig. 11.–A: midsagittal view of the cephalothoracic region of *Cryptocellus boneti* (order Ricinuleida), seen from the left; B: lateral view of same, showing the vestigial endosternal area of the perineural vascular membrane; the central nervous system is shown with dark shading.

species of *Ricinoides*. The internal anatomy was not studied in detail until Millot (1945a, b, c) dissected *R. feae*. He described a reduced heart and an anterior aorta which becomes lost at the posterior surface of the supraesophageal ganglionic mass. He noted a thin "fibro-muscular sheet" associated with the brain and commented that this may represent the vestige of an endosternite.

I have examined two species of *Cryptocellus* (Fig. 11): *C. boneti*, from Morelos, México, and *C. osorioi*, from caves in San Luis Potosí, México. I find in both of these species of *Cryptcellus* the typical apulmonate condition of the arterial system: the central nervous system is invested with a perineural vascular membrane which is continuous with the aorta. Associated with this membrane, there is a certain region which I call the endosternal area (Fig. 11B). For the following two reasons, I interpret this area as a vestigial endosernite: (1) arising from the endosternal area is a pair of strands of connective tissue; these strands are probably non-contractile, but they attach to the carapace and appear to be vestiges of dorsal suspensor muscles; (2) a pair of stomedeal muscles originates from the anterior portion of the endosternal area.

The apodemal endoskeleton in ricinuleids is more strongly developed than in pseudoscorpions, but less so than in solpugids; the development of the mesodermal endosternite seems to be inversely proportional to the development of the apodemal endoskeleton, as is also the case in the other apulmonate arachnids.

Order Solpugida—In 1896, Bernard observed in *Galeodes* that "... the anterior end of the heart is produced into an aorta, which ... appears to discharge the blood direct on the central nerve-mass." My own dissections of *Eremobates* sp. (Fig. 12) confirm this report; the central nervous system is enveloped by a perineural vascular membrane which encloses a periganglionic arterial sinus. The order Solpugida is unique in that all its members lack a mesodermal endosternite (Bernard, 1896; Giltay, 1925; Millot, 1949a). In its place, solpugids possess a highly developed apodemal endoskeleton. An apodemal arch arises from the floor of the tritosternal segment (Bernard, 1896; Millot and Vachon, 1949b). This arch passes over the dorsal surface of the subesophageal ganglionic mass, where it serves as a functional analogue of the mesodermal endosternite.

The solpugid endoskeleton was studied first by Kittary (1848) in *Galeodes*, and later by Dufour (1862) in *Galeodes*, Bernard (1896) in *Galeodes*, Sorensen (1914) in *Daesia, Solpuga, Galeodes, Rhagodes*, and especially by Roewer (1934) in various genera. Unfortunately, Bernard's erroneous interpretation is this structure was adopted as valid by certain influential arachnologists, such as Comstock (1948). Bernard attempted to homologize all arachnid endosternites with the apodemal endoskeleton of the solpugid, which he regarded as a primitive arachnid. Apparently, he was motivated by a determination to demonstrate unequivocally that arachnids cannot at all be closely related to *Limulus*, which he regarded as a crustacean (Bernard, 1892a, b). Bernard's interpretation of the arachnid endosternite is not in agreement with that of Pocock (1902), nor or Millot (1949a), nor of my own. Millot said that the interpretation of the solpugid tritosternal apodeme (incontestably an ectodermal structure) as a homologue of the scorpion endosternite, is an indefensible conception. Moreover, he pointed out that embryologists universally recognize the mesodermal origin of the endosternite (p. 287):

> L'apodème tritosternal des Solifuges a été parfois homologué à l'endosternite des Scorpions et, par son intermédiaire, à celui des autres Arachnides. Cette conception ne paraît pas défendable. L'apodème tritosternal, incontestablement ectodermique, ne peut être comareé à l'endosternite dont l'origine mésodermique est reconnue par tous les embryologistes.

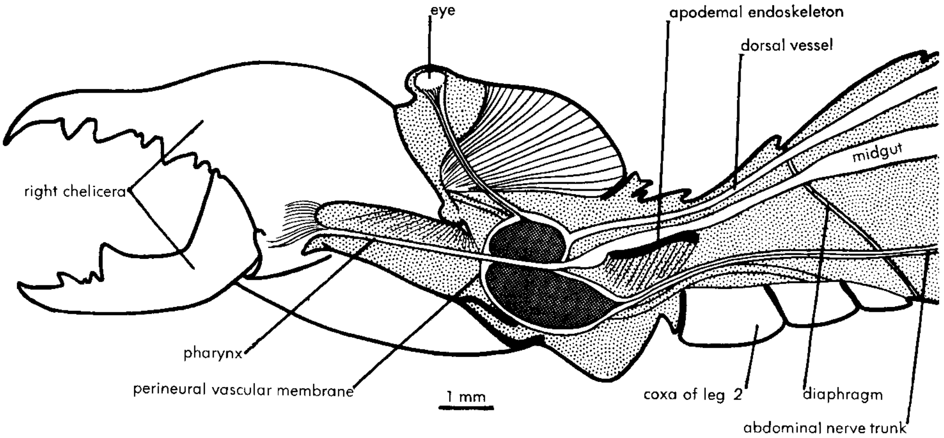


Fig. 12.–Midsagittal view of the cephalothoracic region of *Eremobates* sp., a solpugid, seen from the left. Note that a mesodermal endosternite is lacking. An apodemal invagination of the exoskeleton, derived from the tritosternum, forms a functional analogue of the endosternite. The central nervous system is shown with dark shading.

The Pulmonate Arachnid Orders:
Scorpionida
Thelyphonida
Schizomida
Amblypygida
Araneida

Order Scorpionida–The circulatory system of scorpions has been described by various investigators, including Newport (1843) in *Androctonus* and *Buthus*, Houssay (1886, 1887) in *Androctonus* and *Buthus*, Schneider (1892) in *Buthus*, Petrunkevitch (1922) in *Centrurus*, and Buisson (1925) in *Buthus*. According to these authors, the arterial system conforms to the general pattern that exists in other pulmonates (Fig. 13): a paired aorta gives rise to a paired thoracic sinus which lies on top of the subesophageal ganglionic mass. The thoracic sinuses give rise to appendicular arteries and to a series of circumneural arteries which surround the central nervous system. At their posterior ends, the thoracic sinuses give rise to a common, median, unpaired supraneural artery which carries blood posteriad into the abdomen.

The endosternite of the scorpion has been described by Beck (1885) in *Androctonus* and *Buthus*, by Bernard (1894c) in *Palamnaeus*, by Schimkewitsch (1894) in *Androctonus*, and by Pocock (1902) in *Palamnaeus, Iurus, Bothriurus*, and *Centruroides*. It consists of a pair of longitudinal rods which join each other posteriorly, where they also join a transverse muscular partition, the diaphragm, which separates the cephalothoracic and abdominal cavities. The endosternite is circumneural at its posterior end, where it joins the diaphragm; i.e., it forms a complete transverse ring around the posterior end of the subesophageal ganglionic mass (Fig. 14A; see also Fig. 26C).

The morphology of the scorpion endosternite is neither simple nor primitive; its complexity lies partly in its involvement with the diaphragm, which Bernard (1894c) regarded as the derivative of an ancient intersegmental septum. He regarded the scorpion dia-

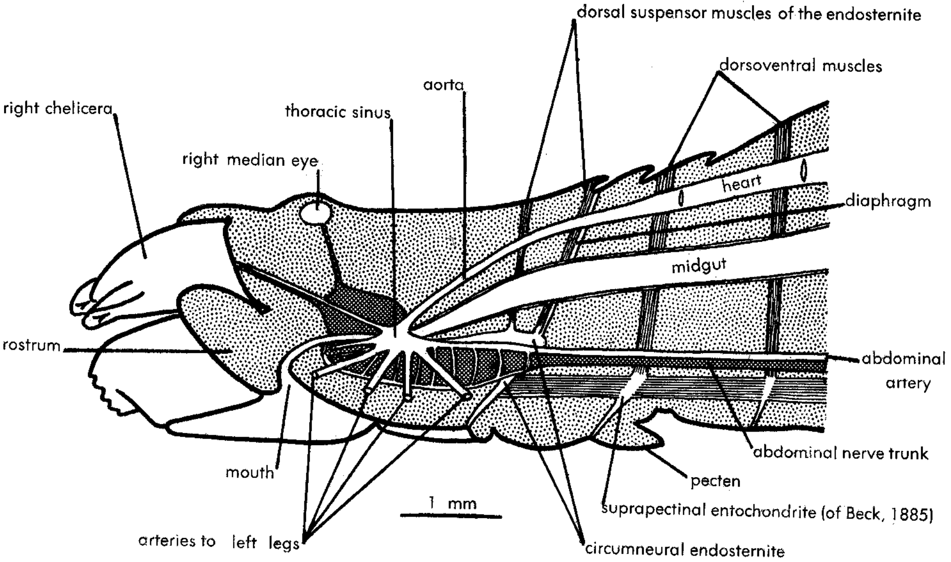


Fig. 13.–The arterial system and endosternite of a generalized scorpion, based upon my observsations of *Centruroides* sp., and upon the diagrams of Schnieder (1892), Petrunkevitch (1922), Beck (1885), Schimkewitsch (1894), and Pocock (1902).

phragm to be homologous to that of solpugids. In scorpions, the diaphragm is muscularized by a layer of dorsoventral fibers. Beck (1885) described three pairs of serial, dorsal suspensor muscles of the cephalothoracic endosternite; she named them respectively the anterior, median, and posterior dorso-plastron muscles. The posterior pair of these originates from the first mesosomatic tergite and extends ventrad for a short distance behind the diaphragm; it passes through the diaphragm and continues ventrad in front of it to an insertion on the posterior end of the circumneural endosternite. This condition apparently is homologous to that in thelyphonids and amblypygids, where the posterior end of the endosternite receives the insertions of the first pair of abdominal dorsoventral muscles (Figs. 15, 16B, 18). The median (penultimate) dorsal suspensor of the scorpion is adherent to the anterior surface of the diaphragm; this muscle is actually part of (derived from) the diaphragm musculature. I believe this fact gives a clue to the evolutionary origin of the chelicerate dorsoventral muscles: they are derived from the muscle fibers on primitive intersegmental transverse septa which internally separated the trunk segments of prechelicerate ancestors.

Beck also described three pairs of transverse suspensors (her epimero-plastron muscles) which insert onto the cephalothoracic endosternite (Fig. 14A; see also Fig. 26C).

In addition to the cephalothoracic endosternite, scorpions possess also an abdominal endosternite (Beck's suprapectinal chondrite) at the anterior end of the mesosoma (Beck, 1885) (Fig. 14B). Morphologically, this is a transverse muscle, for on either end it is contractile, with origins on the body wall. It differs from the cephalothoracic endosternite, however, in that it lies under the nervous system rather than over it. It is fused with the connective tissue of a single pair of dorsoventral muscles, and Lankester (1885) believed it to be homologous to one of the mesosomatic entochondrites of *Limulus*.

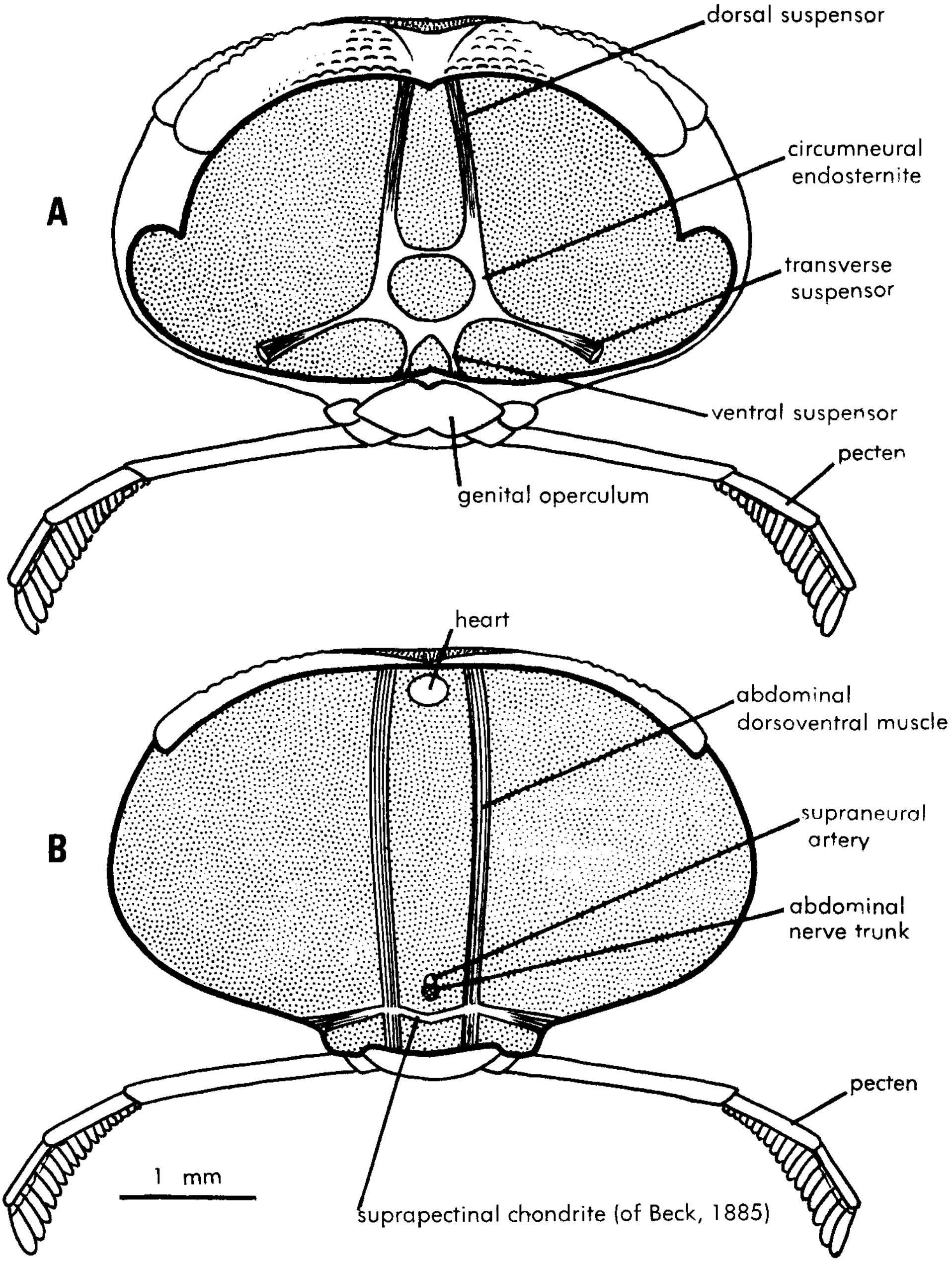


Fig. 14.–A: transverse section through the circumneural portion of the endosternite of *Centruroides* sp. (order Scorpionida), showing the muscles which insert upon it, as seen from the anterior; B: transverse section through the suprapectinal endosternite of same.

I have examined the arterial system and endosternite of *Centruroides* sp., and my observations correspond exactly to the descriptions of the authors cited above.

Order Thelyphonida—I have examined the endosternite and arterial system of *Mastigoproctus giganteus*. I find that the arterial system conforms to the basic pattern for pulmonate arachnids. The endosternite corresponds to the earlier descriptions of Tarnani (1890) in *Thelyphonus asperatus*, Pocock (1902) in *Mastigoproctus giganteus*, Börner (1904) in *T. caudatus*, and Millot (1949c) in *M. giganteus*. However, the published drawings do not distinguish dorsoventral suspensors from transverse suspensors, and they compound confusion by showing the two kinds as though they were serial homologs. The thelyphonid endosternite consists of a pair of longitudinal rods which join

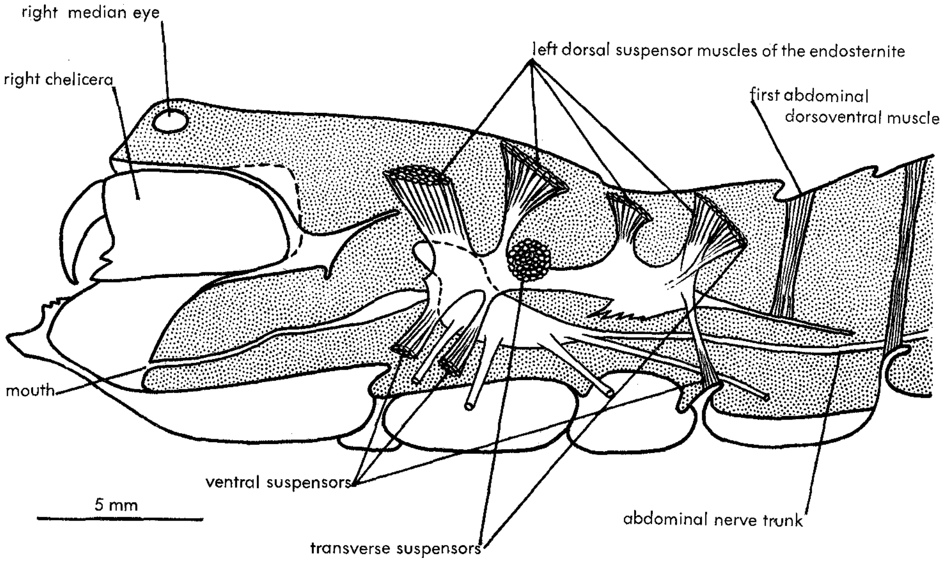


Fig. 15.—Sagittal view of the cephalothoracic region of *Mastigoproctus giganteus*, a whip scorpion (order Thelphonida), showing a superimposed lateral view of the left side of the endosternite and central nervous system.

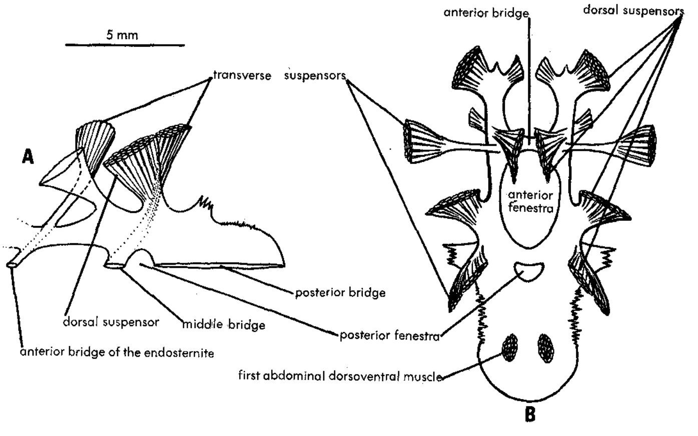


Fig. 16.—A: Dorsomedial view of the right half of the posterior end of the endosternite (cut midsagittally) of *Mastigoproctus giganteus*, showing the dorsal and transverse suspensor muscles, as seen from the left. Note that the anterior and middle cross-bridges are morphologically part of the transverse suspensors. Also note that the posterior transverse suspensor is anatomically integrated with the posterior dorsal suspensor. B: dorsal view of the endosternite.

each other at their posterior ends by a bridge which extends horizontally posteriad to the second abdominal segment. The endosternite receives the insertions of four pairs of dorsal suspensors, three pairs of ventral suspensors, and two pairs of transverse suspensors. The positions of the anterior and posterior transverse suspensors are marked respectively by anterior and middle bridges which join the right and left sides of the endosternite (Fig.16). The space enclosed by these two bridges forms the anterior fenestra, and behind the middle bridge there is a smaller posterior fenestra which separates it from the posterior bridge. The right and left extremities of the anterior transverse suspensor originate from the lateral margins of the cephalothorax, but the posterior transverse suspensor is deflected dorsomedially so as to become anatomically and functionally indistinguishable from the posteriormost pair of dorsal suspensors (Fig. 16A). A close examination of the transverse suspensors shows that the connective tissue fibers which strengthen them run across the respective bridges; hence, the anterior and middle bridges may be interpreted as morphological components of (as derived from) the transverse muscles.

Order Schizomida–Except for their small size, schizomids are very similar to thelyphonids, externally and internally. Millot (1942a) split the heterogeneous order Pedipalpi, and put schizomids, thelyphonids and amblypygids into respective orders of their own. Later, however, Millot (1949c) and Kaestner (1968) reunited the schizomids and thelyphonids as families of the order Uropygida. Nothwithstanding this, there is a current trend to separate schizomids and thelyphonids (Petrunkevitch, 1955; Savory, 1964), and to recognize both as separate orders.

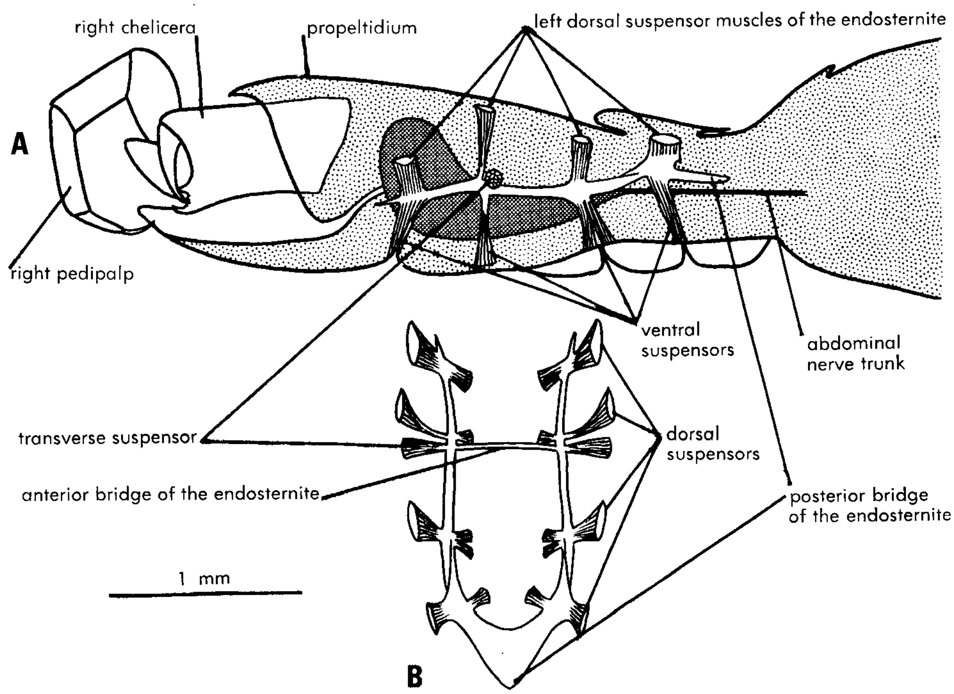


Fig. 17.–A: midsagittal view of the cephalothoracic region of *Trithyreus pentapeltis* (order Schizomida), showing a superimposed lateral view of the left side of the endosternite; B: dorsal view of the endosternite.

The earliest study of the schizomid arterial system is that of Börner (1904) who described a heart with five pairs of ostia in *Trithyreus cambridgei.* I have examined *T. pentapeltis*, and I find that the arterial system conforms to the basic pattern which is typical of other pulmonate arachnids.

A description of the endosternite of *T. cambridgei* was given by Börner (1904). My own observations of *T. pentapeltis* confirm Börner's findings. The schizomid endosternite is morphologically very similar to that of a thelyphonid, except that it lacks the middle bridge and accordingly has only one central fenestra. There are four pairs of dorsal suspensors which are matched below by four pairs of ventral suspensors (Fig. 17). The histological continuity of these dorsoventral muscles through the endosternite is readily apparent, even by gross observation: it can be seen clearly that the dorsal and ventral suspensors are continuous with each other by a tendinous tract of connective tissue fibers which passes vertically through the endosternite. A transverse muscle passes horizontally through the endosternite immediately behind the second dorsoventral suspensors, and at right angles to them (Fig. 17B). The right and left extremities of this muscle, which originate from the lateral margins of the carapace, are continuous with each other by a tendinous bar which constitutes the anterior cross-bridge (Börner's "verdere Querbrücke") of the endosternite of *Trithyreus.*

Order Amblypygida—The circulatory system of amblypygids has been described by Blanchard (1852) in *Tarantula palmata.* The arterial system conforms to the basic pattern for pulmonate arachnids. The endosternite has been described by Börner (1904) in *T. palmata*, and by Millot (1949d) in *Damon medius.* I have examined the endosternite of *Tarantula* sp, from Costa Rica. Its endosternite (Fig. 18), while bearing certain resemblances to that of thelyphonids, is shaped more like that of an orthognath spider. It has four pairs of dorsal suspensors and three pairs of transverse suspensors. On the ventral side, there are two pairs of non-contractile tendinous processes which represent the first and fourth ventral suspensors (i.e., they match the first and fourth dorsal suspensors). According to Millot (1949d, Fig. 325) in the endosternite of *Damon medius* the first pair of ventral suspensors are contractile. As in thelyphonids, the endosternite extends posteriad to the second abdominal segment. However, it lacks the anterior and middle bridges, and accordingly it has no fenestrations; in this way, it resembles the cephlothoracic endosternite of spiders.

Order Araneida—Except for lungless spiders, the circulatory system of spiders corresponds to the basic pattern depicted in Fig. 19: a paired anterior aorta gives rise to a paired thoracic sinus which lies on top of the subesophageal ganglionic mass. Appendicular arteries arise from the sinus on each side, and a series of circumneural arteries surrounds the central nervous system. An unpaired abdominal artery extends posteriad from the thoracic sinus. All of this has been described and illustrated by Schneider (1892) in *Tegenaria*, and in various other genera by Causard (1896). As in all nonscorpion pulmonate arachnids, there is no apparent morphological continuity of the arterial system with the endosternite.

An endosternite is universally present in spiders (Comstock, 1948), although there is variety in its shape and relative size throughout the order. I have studied the endosternites of various spiders: among those of the suborder Orthognatha, I have examined the brown tarantula, *Eurypelma californicum* (cf. Firstman, 1954), and the trapdoor

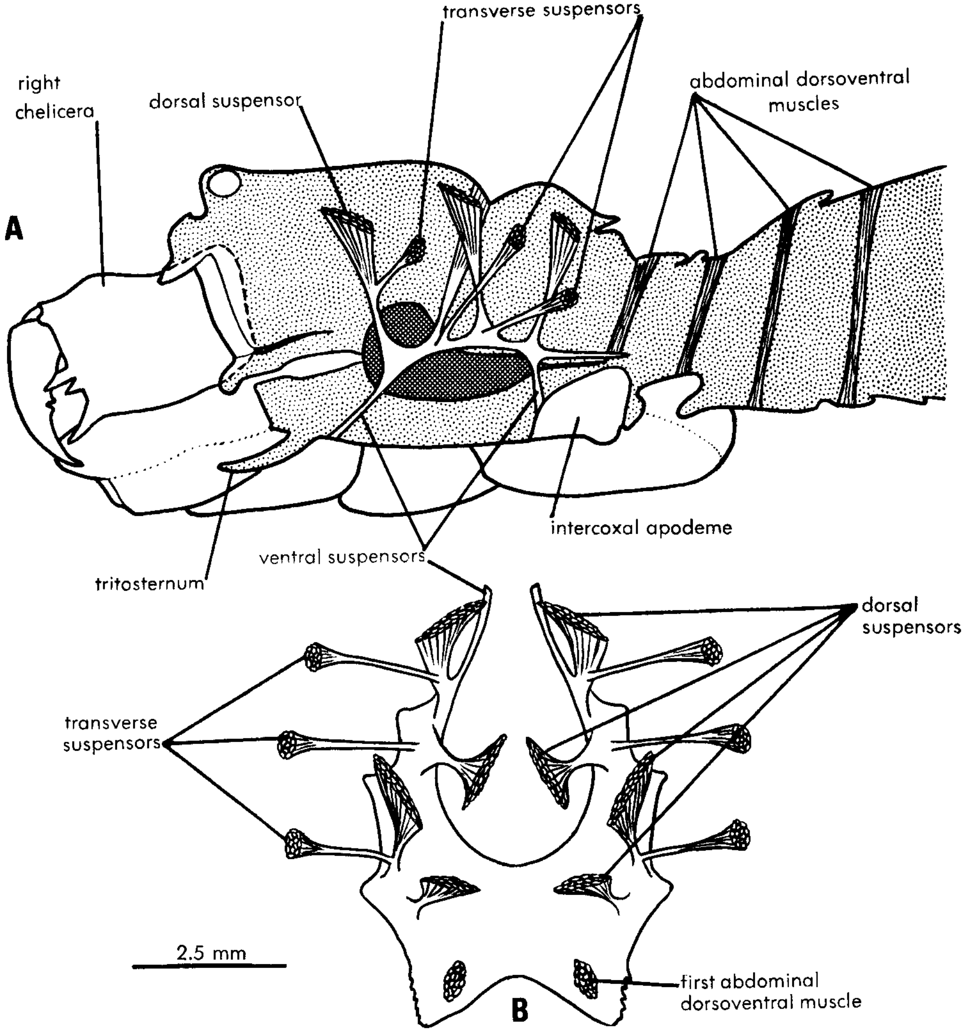


Fig. 18.—A: midsagittal view of the cephalothoracic region of *Tarantula* sp. (order Amblypygida), showing a superimposed lateral view of the left side of the endosternite; B: dorsal view of the endosternite.

spider, *Bothriocyrtum californicum*. Among the spiders of the suborder Labidognatha, I have examined representatives of the following genera: *Latrodectus* (family Theridiidae), *Argiope* (family Araneidae), *Gnaphosa* (family Gnaphosidae), *Ctenus* (family Ctenidae), *Phiddipus* (family Salticidae) and *Orthonops* (family Caponiidae). On the basis of my observations, I make the following generalizations with regard to the endosternite: the cephalothoracic endosternite of spiders is centralized into a single, metamerized, unfenestrated structure which receives the origins of rostral, stomodeal, gastric, coxal and pedicellar muscles. On its dorsolateral margins it receives the insertions of four pairs of dorsal suspensor muscles, and one to three pairs of transverse suspensors.

In the true spiders (suborder Labidognatha), there are no ventral suspensors (Fig. 20A); however, in the tarantulas and their allies (suborder Orthognatha), each dorsal suspensor is continuous through the endosternite with a noncontractile tendon that ex-

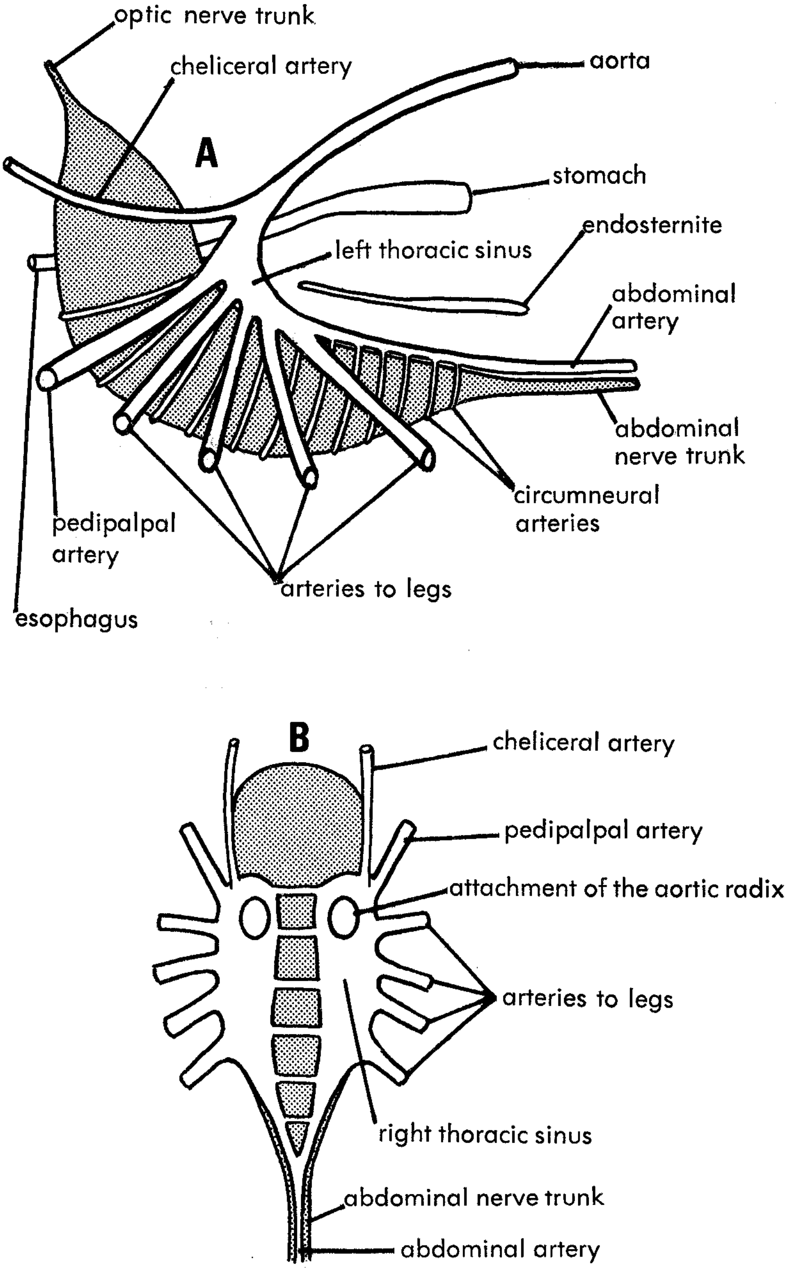


Fig. 19.–Generalized diagram of the arterial system of a spider, based on Schneider (1892) and Causard (1896); A: lateral view of the central nervous system, showing the left thoracic sinus, as seen from the left, with the endosternite shown in midsagittal section; B: dorsal view of same, with the endosternite omitted.

tends from the ventral surface of the endosternite to an attachment on the sternum (Fig. 20B). When Pocock (1902) saw this in the tarantula, he realized that each ventral tendon, plus its dorsal counterpart, represents a cephalothoracic dorsoventral muscle. Thus, he became convinced that the connective tissue of the dorsoventral muscles has become an integral part of the endosternite, and that the bisected dorsoventral muscles have given rise to both conditions in spiders: (1) as in the orthognath spiders, where each ventral suspensor is a non-contractile tendinous process, and (2) as in the true spiders, where ventral suspensors have disappeared altogether. Schimkewitsch (1893, 1894) had already suggested that the endosternite (he called it an aponeurotic membrane) is formed by the coalescence of muscle tendons, based on his observations of spiders, thelyphonids, opilionids, scorpions and *Limulus*.

The suspensor muscles which originate from the cervical apodeme of spiders I interpret as transverse suspensors, for these bear the same morphological relation to the endosternite as the transverse suspensors of other nonscorpion pulmonate arachnids (Figs. 26F, 27I). Hence, according to this view, the transverse suspensors of spiders are peculiar,

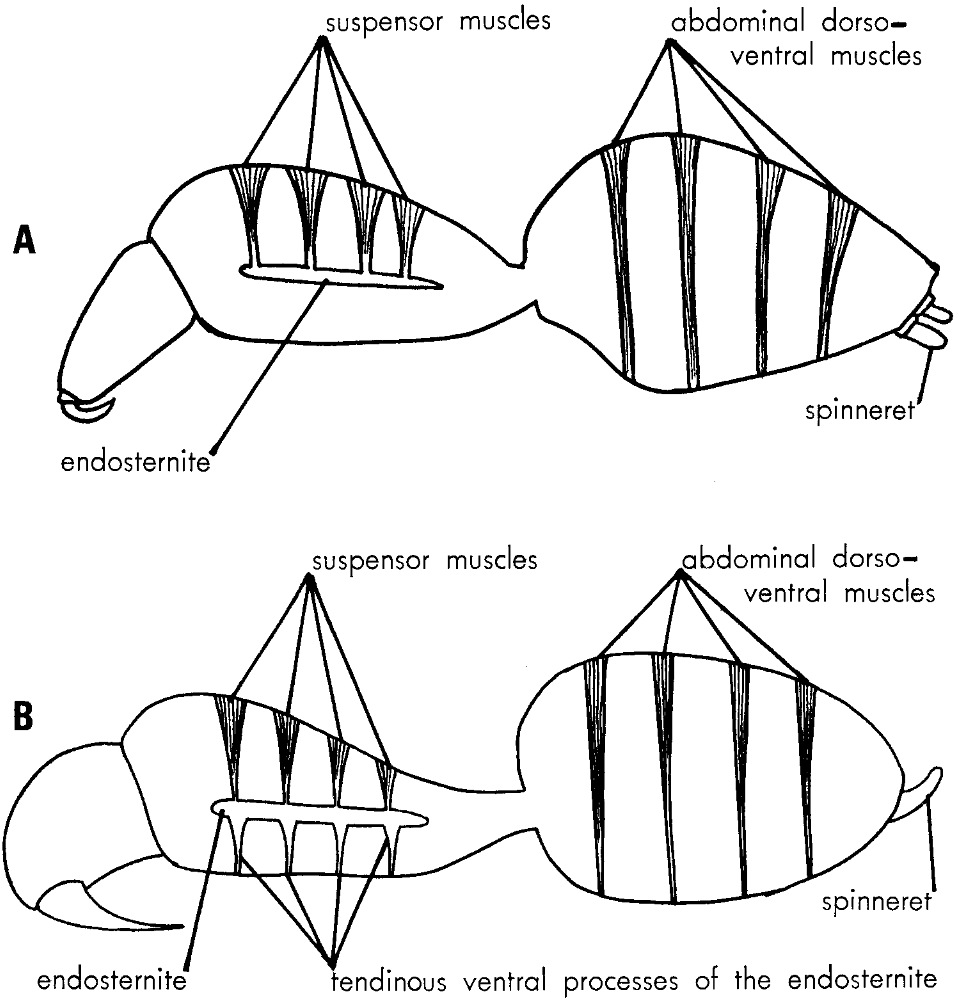


Fig. 20.–Schematic depictions of the serial homology of the dorsoventral muscles of spiders. A: a true spider (suborder Labidognatha); note that the dorsal suspensors of the endosternite are incomplete dorsoventral muscles. B: a mygalomorph spider (suborder Orthognatha); note that the dorsoventral suspensors of the endosternite are morphologically complete, but ventral to the endosternite they are non-contractile.

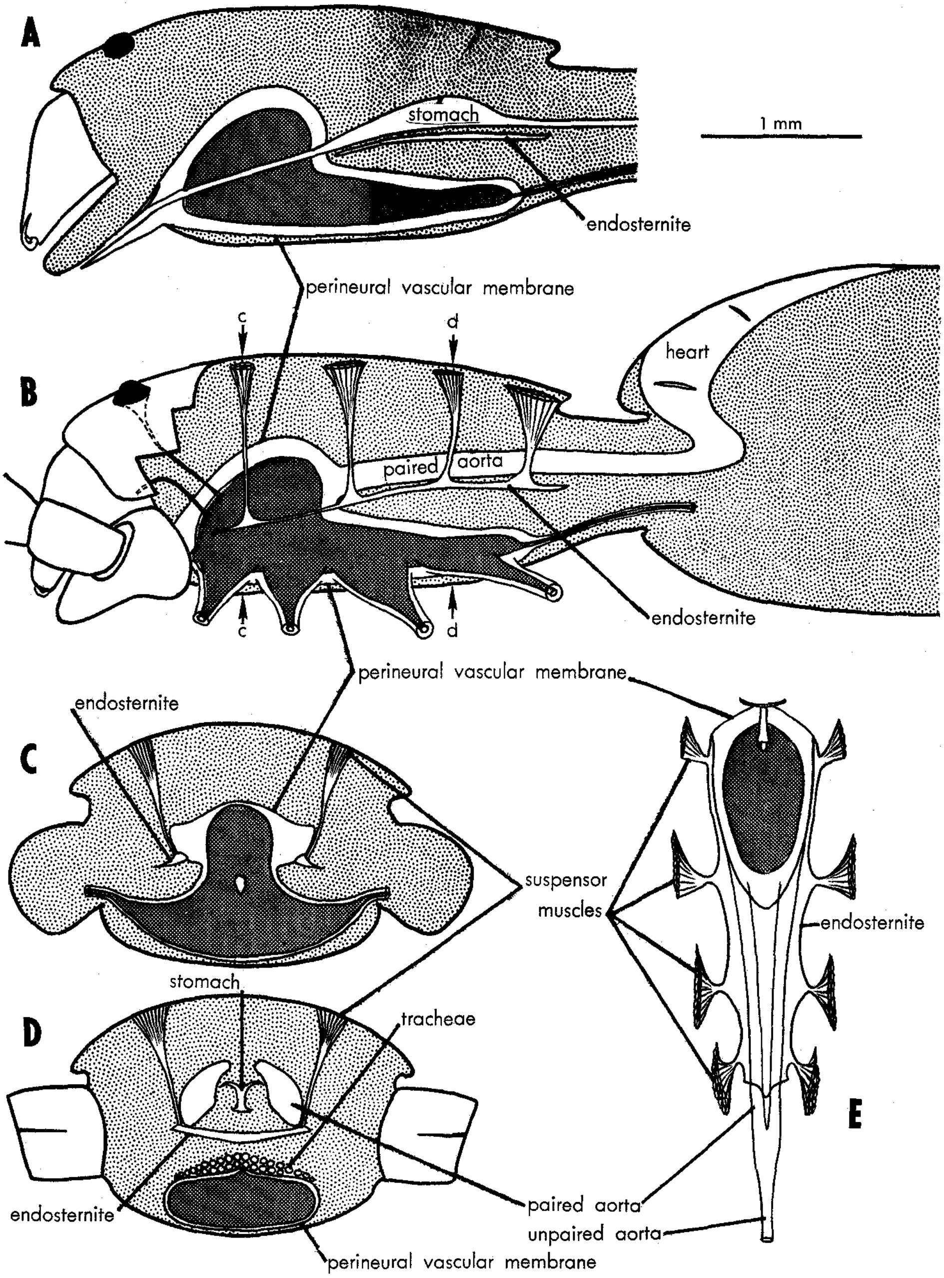


Fig. 21.—A lungless spider, *Orthonops gertschi* (order Araneida, family Caponiidae). A: midsagittal view of the cephalothorax, seen from the left. B: lateral view on the left side of the endosternite, showing the arterial system and the central nervous system. C: transverse section through the anteriormost pair of dorsal suspensor muscles, showing that the anterior cornua of the endosternite are continuous with the perineural vascular membrane; the plane of the section is indicated in Fig. B by the arrows, cc. D: transverse section through the suspensor muscles of the third walking-leg segment; the plane of the section is indicated in Fig. B by the arrows, dd. E: dorsal view of the endosternite. The central nervous system is shown with dark shading.

compared to those of other arachnids, because they are deflected dorsomedially, so as to originate from the cervical apodeme rather than from the lateral extremities of the carapace. In most of the spiders I have examined, there is only one apparent pair of transverse suspensors, located in the segement of the second walking leg. However, in the genus *Ctenus*, I find two pairs of transverse suspensors; the posteriormost of these has merged with the posterior pair of dorsal suspensors, as in thelyphonids. In the jumping spider, *Phiddipus*, I find three distinct pairs of transverse suspensors. In the lungless spiders of the family Caponiidae, where a cervical apodeme is lacking, transverse suspensors are absent altogether.

I have examined the arterial system and endosternite of the lungless *Orthonops gertschi* (family Caponiidae). This spider possesses an arterial system which is periganglionic, as in apulmonate arachnids. The central nervous system is invested by a perineural vascular membrane which is continuous with a paired aorta (Fig. 21). The anterior cornua of the endosternite are anatomically continuous with the perineural vascular membrane; this is the only spider species in which the endosternite is known to be continuous with an arterial membrane. The same circumstances probably exist also in the other lungless families (Telemidae, Symphytognathidae) but I have not examined these.

Class Merostomata, Subclass Xiphosura

Borradaile, et al. (1961) pointed out that "... a unique feature of *Limulus* is the complete investment of the ventral nervous system by an arterial vessel which corresponds to the supraneural vessel of the scorpion." It has been known since the last century that the central nervous system of the horseshoe crab is ensheathed completely by a perineural vascular membrane which is continuous with the left and right radices of the paired anterior aorta (Fig. 22). The complex circulatory system of *Limulus* has been described by Alphonse Miln-Edwards (1872), Owen (1873), Patten and Redenbaugh (1899), Petrunkevitch (1922), Lameere (1933), and Fage (1949a). It is noteworthy that the larval *Limulus* passes through a thoracic sinus stage of arterial development which corresponds to that of the adult scorpion (Kingsley, 1893) (Fig. 34). The implication which follows this is that in the pulmonate arachnids a selection pressure has foreshortened the development of the arterial system (I interpret this as neotenous developmental retardation), probably related to some physiological contingency of breathing atmospheric air with book lungs. Levi (1967) has compared circulatory development in spiders, with regard to their respiratory adaptations.

I have examined the arterial system and endosternite of *Limulus polyphemus*. All of my observations verify the descriptions of the authors cited above. The arterial system of *Limulus* includes a perineural vascular membrane which surrounds a periganglionic arterial sinus (Fig. 22). This sinus receives the radices of the paired dorsal aorta.

The endosternite of the horseshoe crab was first described by Straus-Dürckheim (1829), to whom the arachnid similarities seemed immediately obvious. Later, it was described in greater detail by various investigators, principally Lankester (1881a; 1884; 1885) and his student, Benham (1885), and by Patten and Redenbaugh (1899). My own observations of the endosternite of *L. polyphemus* confirm the observations of these authors. The cephalothoracic endosternite of *Limulus* is roughly rectangular, located horizontally above the central nervous system (Figs. 22, 23). It receives the insertions of three pairs of dorsal suspensors and one pair of ventral suspensors. In addition, there are two pairs of transverse suspensors (the lateral tergo-proplastral muscles, of Benham,

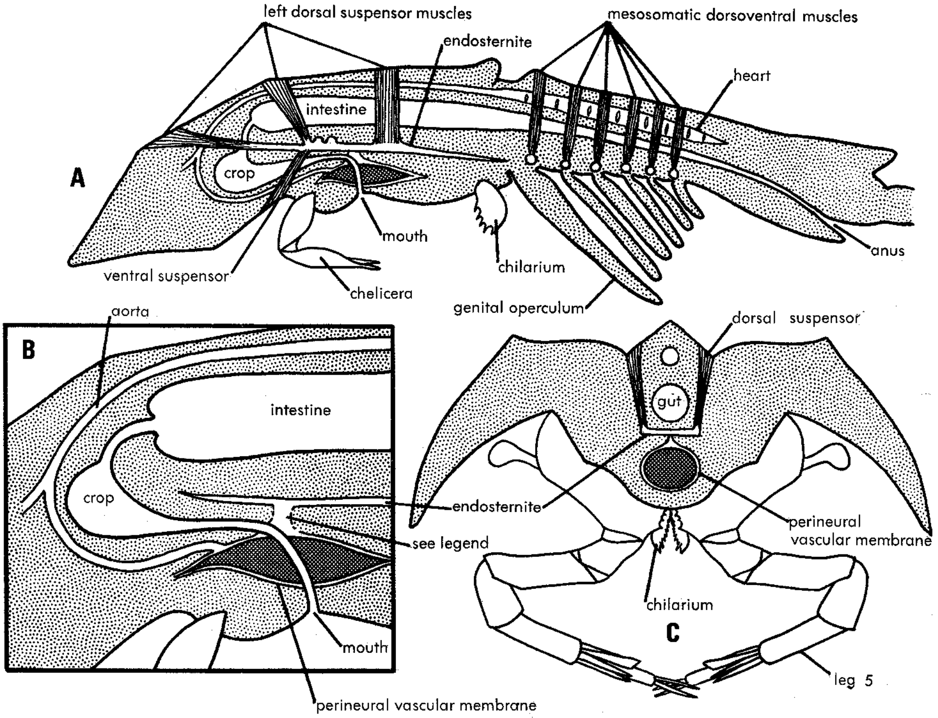


Fig. 22.—A: midsagittal view of *Limulus polyphemus* (class Merostomata), showing the endosternites and the muscles which insert upon them, seen from the left. The muscles of the left side have been superimposed. The white circles in the mesosoma represent the locations of the mesosomatic endosternites. The two bumps on the dorsal surface of the cephalothoracic endosternite represent the positions of the transverse suspensors. B: an enlarged detail, midsagittal, with musculature omitted; the region indicated by "see legend" contains strands of connective tissue, in the adult, representing the vestigial connection of the perineural vascular membrane to the endosternite. C: transverse section through the subesophageal ganglionic mass, showing the cephalothoracic endosternite and one pair of dorsal suspensors, seen from the anterior.

1885); these I interpret as homologous to the transverse suspensors of arachnid endosternites.

Six abdominal endosternites are also present in *Limulus* (the mesosomatic entochondrites of Benham, 1885). Morphologically, each of these is a tendonified transverse muscle which is contractile at its lateral extremities (Fig. 23). Each one receives the insertion of a single pair of dorsal suspensors. The anatomical configuration of these abdominal endosternites, in relation to the muscles which insert on them, gives the impression that they are serially homologous to the metameric elements of the cephalothoracic endosternite, and that they represent a primitive stage of endosternite evolution, for this is the way that Lankester (1885) interpreted them. I do not doubt that the mesosomatic dorsoventral muscles are serially homologous to those of the cephalothorax, but the transverse muscles differ from those of the cephalothorax in that: (1) they lie under the nervous system instead of over it, and (2) they attach distally to movable structures (the book gills) instead of the body wall. Lankester resolved the first problem, to his own satisfaction, by hypothesizing that the nerve cords (which he presumed were primitively in a lateral position) moved medially to their present position on the midline during a time when the endosternite was in a formative stage of evolutionary development. He assumed that the endosternites were derived from subepidermal connective tissue of the ventral floor, and that the cephalothoracic endosternite (which presumably is older) had arisen far enough from the ventral floor that it came to lie over the relocated nervous system, while the younger abdominal endosternites were still under it.

Although Snodgrass (1952) feels that Lankester's hypothesis is overly contrived, I do not feel that the question of the morphological significance of the mesosomatic endosternites of *Limulus* has been resolved one way or another. However, I am inclined to the opinion that the mesosomatic transverse muscles of *Limulus*, because they attach distally to movable appendages, are not serially homologous to those which have been instru-

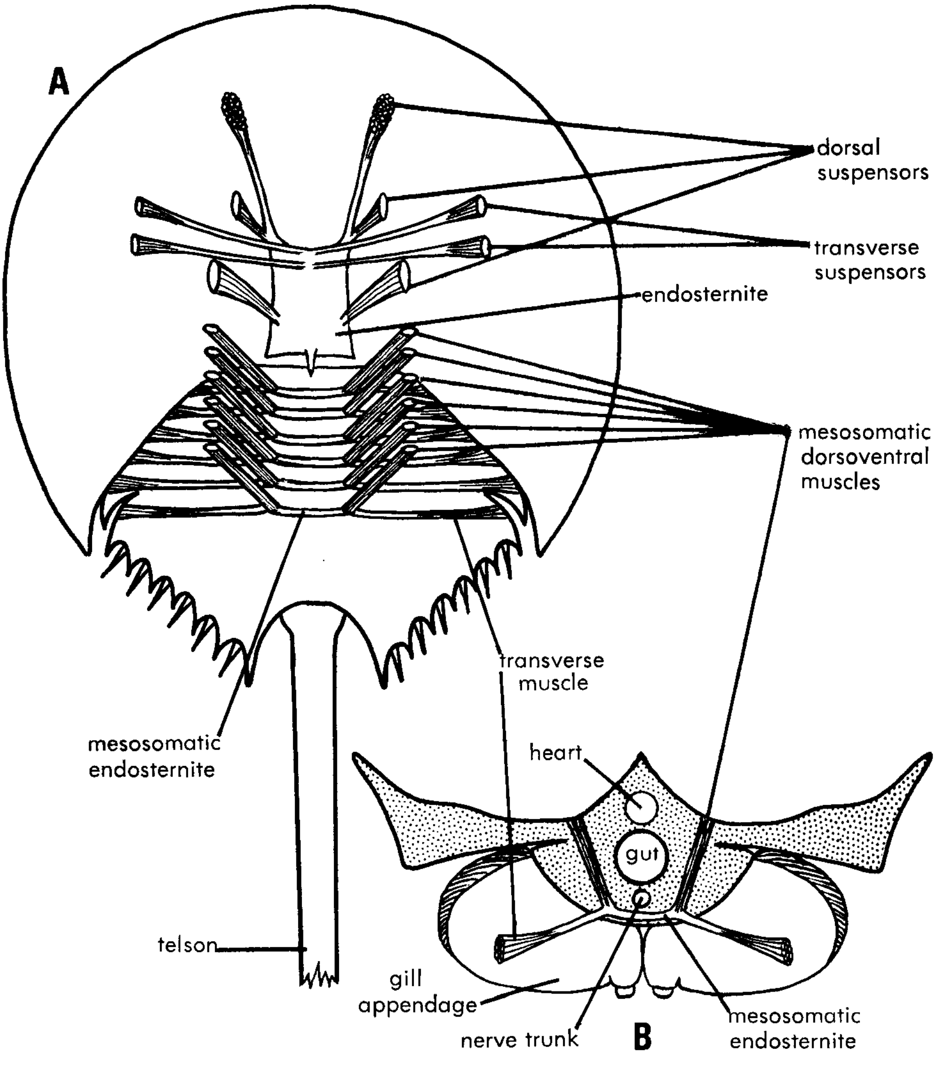


Fig. 23.—A: dorsal view of *Limulus polyphemus*, showing the endosternites and the muscles which insert upon them. B: transverse section through the mesosoma, showing one of the mesosomatic endosternites, seen from the anterior.

mental in the formation of the cephalothoracic endosternite. In accordance to the comparative evidence put forth in this paper, I believe the transverse suspensors of the cephalothoracic endosternite are derivatives of serial transverse muscles which lay primitively over the nervous system. In this connection, Snodgrass (1935, 1952) pointed out that in insects there are serial transverse muscles which lie over the nervous system (Fig. 28).

Class Pycnogonida

The Pycnogonid Arterial System—Early observations of circulation in pycnogonids were made Johnston (1837), Henri Milne-Edwards (1840), Quatrefages (1845), and Van Beneden (1846). None of these authors described a heart, although Van Beneden saw some of the movements of blood beneath the dorsal integument of a living specimen of *Nymphon*. Cole (1910) similarly described circulatory movements which he observed in living specimens of *Endeis*. A heart was described in *Nymphon* by Zenker (1852), in *Endeis* by Krohn (1885), and in *Colossendeis* and certain other genera by Hoek (1881). A detailed description of the pycnogonid circulatory apparatus, based principally upon *Endeis* and *Nymphon*, was given by Dohrn in 1881. He agreed with Hoek in describing the heart as a tube which attaches dorsally to the integument and ventrally to the gut. It was Dohrn who first pointed out that the pycnogonid hemocoel is divided longitudinally by a double-walled, horizontal, vascular septum which separates dorsal and ventral blood cavities; blood in the dorsal cavity is directed anteriad, whereas blood in the ventral cavity flows posteriad. The ventral surface of the heart is continuous with this septum along its midline; rhythmic undulations of the septum coincide with the cardiac systole and diastole, and these undulatory movements create the pressures which aspirate blood in and out of the paired appendages. The concept of Dohrn's horizontal vascular septum has been reviewed and diagrammed by Cole (1910).

My own dissections of pycnogonids include the following species: *Pycnogonum littorale, P. rhinoceros, Endeis* sp., *Colossendeis scotti, Decolopoda australis, Nymphon charcoti, Pentanymphon antarcticum*, and *Ammothea striata*. These dissections show the presence of a perivisceral arterial membrane, continuous with the aorta, which envelops the intestine and the central nervous system (Figs. 24, 25). As in *Limulus* and the arachnids, this membrane encloses a perivisceral arterial blood sinus. The membrane is continuous with the double-walled horizontal septum (described above) that extends laterad to the body wall, separating the venous hemocoel into dorsal and ventral cavities. The horizontal septum is partially muscularized by means of transverse muscle fiber bands that originate on the exoskeleton; it extends horizontally through the coxae into the walking legs (the legs protrude laterally from the trunk), separating their lumina into dorsal and ventral venous channels.

The horizontal vascular septum (of Dohrn) is present in all the pycnogonids I have examined, although the exact vertical position of its horizontal plane, with respect to the gut, differs from family to family. Whereas in *Colossendeis* it is situated immediately beneath the heart, in *Endeis* it extends laterad from the sides of the gut, and in *Pycnogonum* it extends from the base of the gut; in all casses it is a continuation of the perivisceral arterial membrane (Fig. 27A, B, C). Between the two layers of the horizontal septum there lies a thin arterial blood sinus which is continuous with the rest of the perivisceral blood sinus.

Loman (1917) studied the blood circulation in *Nymphon*. He described the aorta as bifurcating to go around the optic nerve ("läuft ringförmig um den Augennerv") and

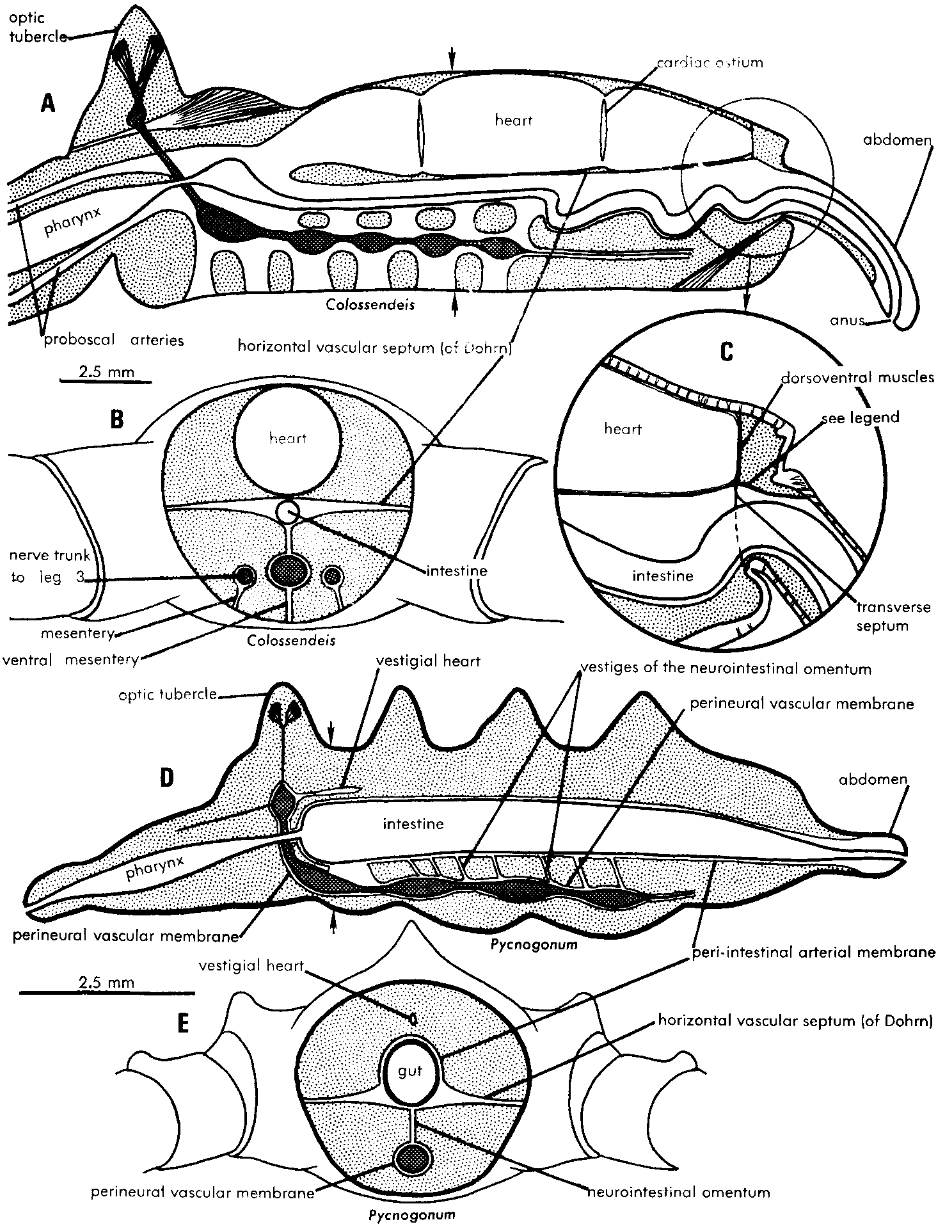


Fig. 24.—A: midsagittal view of *Colossendeis scotti* (class Pycnogonida), seen from the left. The full length of the proboscis is not shown. The oval windows above the nerve cord are perforations in the neurointestinal omentum; the ovate windows below the nerve cord are perforations in the ventral mesentery. B: transverse section through the plane indicated by the arrows in Fig. A. C: an enlarged detail of Fig. A. The structure indicated by "see legend" is the uppermost membrane (the top) of Dohrn's horizontal vascular septum; it is thickened at this point and it receives the insertions of cardiac muscles which extend dorsoventrally from the dorsal integument. D: midsagittal view of *Pycnogonum littorale*. E: transverse section through the plane indicated by the arrows in Fig. D. The central nervous system is shown with dark shading. The venous hemocoel is stippled; the heart, arterial system and gut are unshaded.

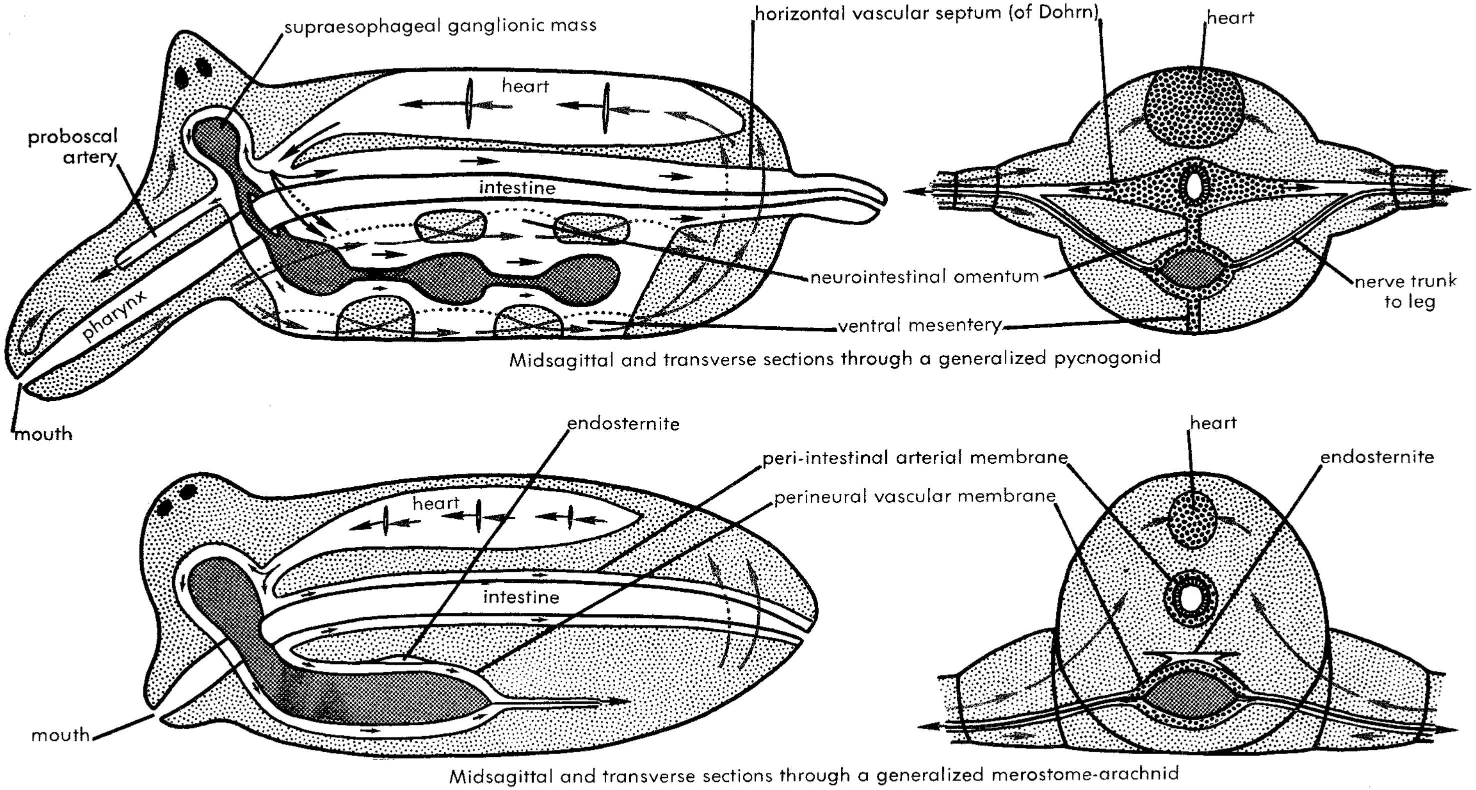


Fig. 25.—Blood flow diagrams comparing the basic circulation of a generalized pycnogonid with that a a generalized merostome-arachnid. The central nervous system is shown with dark shading. The venous hemocoel is shown with black stipples; the heart, arterial system and gut are unshaded. Red arrows represent the direction of arterial flow (the arterial system is restricted to the perivisceral arterial sinus), and blue arrows represent venous flow. Red stipples represent arterial flow which is perpendicular to the plane of the page. Oval windows above the pycnogonid nerve cord represent perforations in the neurointestinal omentum; ovate windows beneath the pycnogonid nerve cord

extending anteriad as an artery into the proboscis. On the contrary, my own observations convince me that, in fact, the aorta envelops the entire central nervous system and gut as a perivisceral membrane which encloses a perivisceral arterial blood sinus (Figs. 24, 25, 27). The peri-intestinal and perineural portions of this sinus are continuous with each other by a double-walled neuro-intestinal omentum, and the perineural portion extends ventrad to the trunk floor as a double-walled ventral mesentery. Also, each nerve trunk to the legs is anchored to the ventral floor by a mesentery. Sanchez (1959) described and illustrated all of this in *Endeis spinosa*. She said that the perivisceral membrane continues also beneath the hypodermis of the integument so as to enclose a hemocoel cavity with parietal and splanchnic lining, in the manner of a true coelom. However, Sanchez dismissed all notions that this cavity may, in fact, be a true coelom.

According to my observations of the circulatory anatomy of pycnogonids, I describe blood movements differently from any previous descriptions (Fig. 25). There are two hemocoelic spaces:

(1) a *perivisceral arterial sinus* fed by the aorta, supplies blood to the viscera and to the proboscis and appendages; at the distal extremities of this sinus, blood passes into

(2) a *venous hemocoel*, which is subdivided by the horizontal septum into two compartments:

  (a) beneath the horizontal septum, the right and left *ventral venous hemocoels* communicate with each other by large foramina in the neuro-intestinal omentum and in the ventral mesentery. The ventral venous hemocoels are continuous, through openings at the extremities of the horizontal septum with

  (b) the *pericardial cavity*, which lies above the horizontal septum. Blood contained within the pericardial cavity bathes the heart and enters its lumen through paired ostia in the cardiac wall.

Since there are no respiratory organs in pycnogonids, it follows that external respiratory gas exchanges occur across the integument between the sea and the blood contained within the venous hemocoels; once inside the heart, freshly aerated blood is pumped into the perivisceral arterial sinus to supply the nervous system and gut. This understanding of pycnogonid circulation provides, I believe, a historical basis for understanding the morphology of the perineural and peri-intestinal arterial membranes in the other chelicerate classes. I hypothesize that remote common ancestors of the Merostomata and Arachnida possessed a perivisceral arterial system homologous to that of modern pycnogonids (Fig. 27).

A heart is lacking in all species of the genus *Pycnogonum*. In the large *P. rhinoceros*, and even in *P. littorale*, I find just behind the brain some loosely organized connective tissue, associated with the perineural vascular membrane, which I take to be a functionless vestige of the heart (Fig. 14D). A perivisceral arterial membrane is present in *Pycnogonum*, but the ventral mesentery is lacking and the neuro-intestinal omentum is reduced to fine strands, faintly visible (Fig. 14D); these persist only as sheaths surrounding the fine autonomic nerve trunks which pass dorsad on the midsagittal plane from the central nervous system to the alimentary canal. How does an animal of the size of *Pycnogonum* survive without a heart? Probably the peristaltic contractions of the extensive digestive caeca (these movements can be observed through the integument of a living specimen) are of sufficient force to effect blood movements.

The Pycnogonid Endosternite—In *Colossendeis*, the posteriormost portion of Dohrn's horizontal septum is chondrified (thickened slightly) as a tough membrane to which cardiac muscles attach (Fig. 24C). I believe this condition supports the idea that Dohrn's horizontal septum is potentially skeletogenous. It is a major thesis of this paper that a homolog of Dohrn's septum in ancient merostomes and arachnids (or in the common ancestor of both) has established the horizontal plane of the endosternite; this plane lay between the intestine and the central nervous system. According to this interpretation, the transverse muscle bundles of the pycnogonid horizontal septum are homologous to the transverse muscles of the endosternites of merostomes and arachnids (Fig. 27).

DISCUSSION

Origin of Dorsoventral Muscles

According to my general observations (and general inference from the literature I have seen), serial dorsoventral muscles occur in all chelicerates except pycnogonids. By definition, a dorsoventral muscle is one which attaches dorsally to a tergite or carapace and ventrally to a sternite or sternum in the same segment. They are always paired muscles (except in ticks, where there are median, unpaired dorsoventral muscles, as well as paired ones), serially arranged along the length of the trunk of the body. The abdominal dorsoventral muscles function as compressors, where they doubtless serve a vascular function in regulating abdominal blood pressures. In mites without hearts, it is known that dorsoventral muscles function to maintain circulation of blood (Mitchell, 1957; Evans, 1961). The cephalothoracic dorsoventral muscles of *Limulus* and all arachnids are interrupted (bisected) by the endosternite, so as to form its dorsal and ventral suspensors. Only in ticks have I seen cephalothoracic dorsoventral muscles which are not integrated with the endosternite.

The scorpion diaphragm helps, I believe, to throw light on the original condition of dorsoventral muscles in arachnids, for it is muscularized dorsoventrally along its entire width, and the median (penultimate) pair of dorsoventral suspensors of the cephalothoracic endosternite are a part of this diaphragm musculature. If Bernard's hypothesis, that the diaphragm is a persistent intersegmental septum held over from prechelicerate ancestors, be true, then it is reasonable to hypothesize that all dorsoventral muscles have originated in this way (i.e., as a specialization of septal musculature).

The exact manner in which cephalothoracic dorsoventral muscles became involved with the chelicerate endosternite is a problem which cannot be resolved until the nature of the trunk musculature in the immediate ancestors of arthropods is better known. Since dorsoventral muscles are very common in many groups of polychaete worms (pers. comm., Donald P. Abbott), it seems to me reasonable to hypothesize that dorsoventral musculature is a primitive arthropodan feature, derived from polychaete ancestors. Serial dorsoventral muscles are lacking in pycnogonids and in the onychophoran, *Peripatus* (personal observation). While I do not gainsay the possibility that this is a primary absence in both of these, and that dorsoventral muscles may have arisen independently and convergently in the other arthropod groups, it seems to me more conservative a hypothesis that ancestral arthropods had dorsoventral muscles, and that the absence of these muscles in pycnogonids and in *Peripatus* are cases of secondary loss. In pycnogonids, I suggest that such loss has been correlated with heavy sclerotization of the integument, and with the development of a rigid, inflexible trunk.

Origin of Transverse Muscles

The transverse suspensor muscles appear to be a more primitive feature of the chelicerate endosternite than the dorsoventral suspensors, for their occurence in living merostomes and arachnids is more archaic (i.e., in a more vestigial state). If *loss of muscles* be regarded as a specialized evolutionary development, then chelicerates in general can be said to be less specialized in the direction of loss of dorsoventral suspensors than they are in the loss of transverse suspensors. Only palpigrades, among living arach-

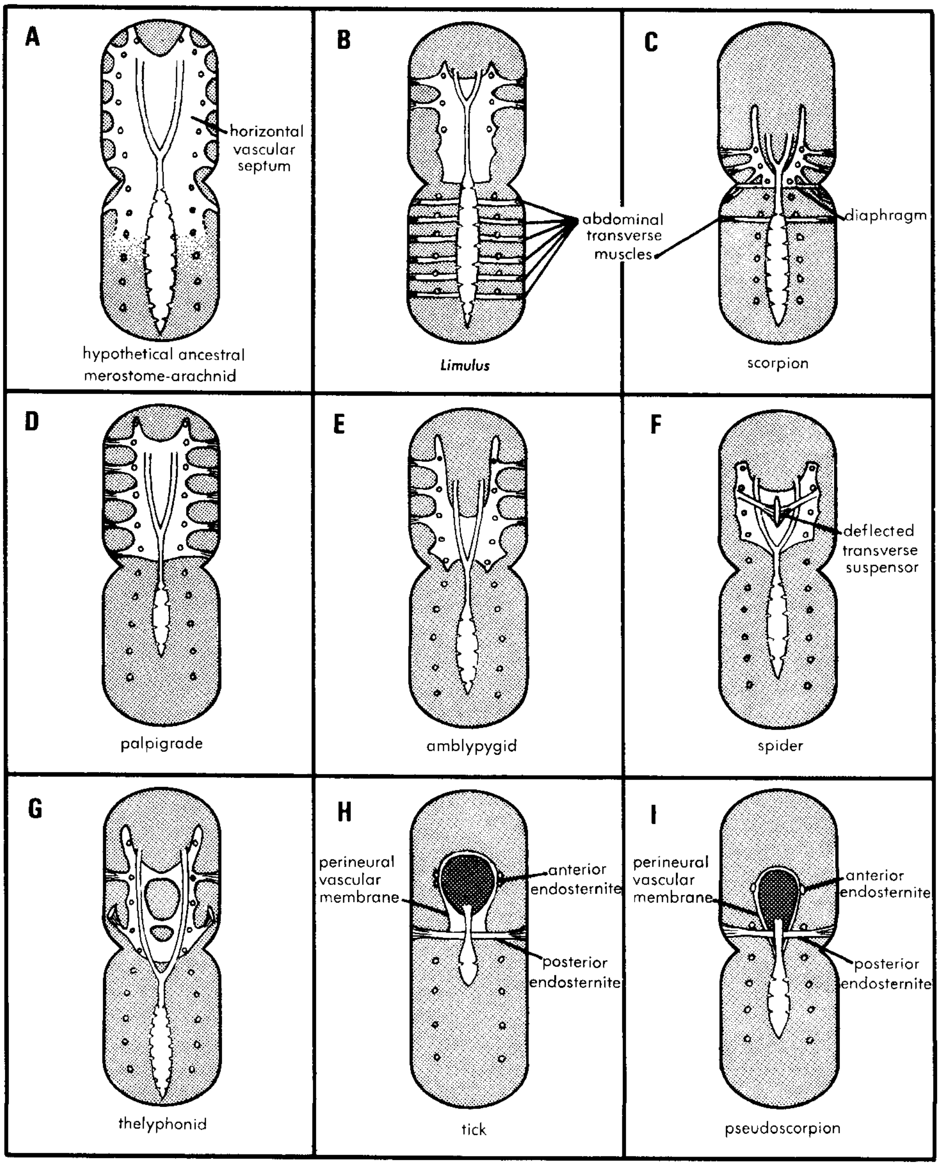


Fig. 26.–Sterograms depicting adaptive radiation of the transverse musculature of the cephalothoracic endosternite in chelicerates. All views are dorsal, with the heart and aorta shown in position over the endosternite. Circles represent the locations of the dorsoventral muscles. The abdominal transverse muscles of *Limulus* and the scorpion are shown. The central nervous system (shown only for the tick and pseudoscorpion) is shaded darkly.

nids, possess as many as five pairs of transverse suspensors of the endosternite. Scorpions possess three pairs, and the nonscorpion pulmonates have from one to three pairs. In the nonpalpigrade apulmonates, where the endosternite has tended toward reduction, the number of persistent transverse muscles never exceeds one pair, if they are present at all (Fig. 26).

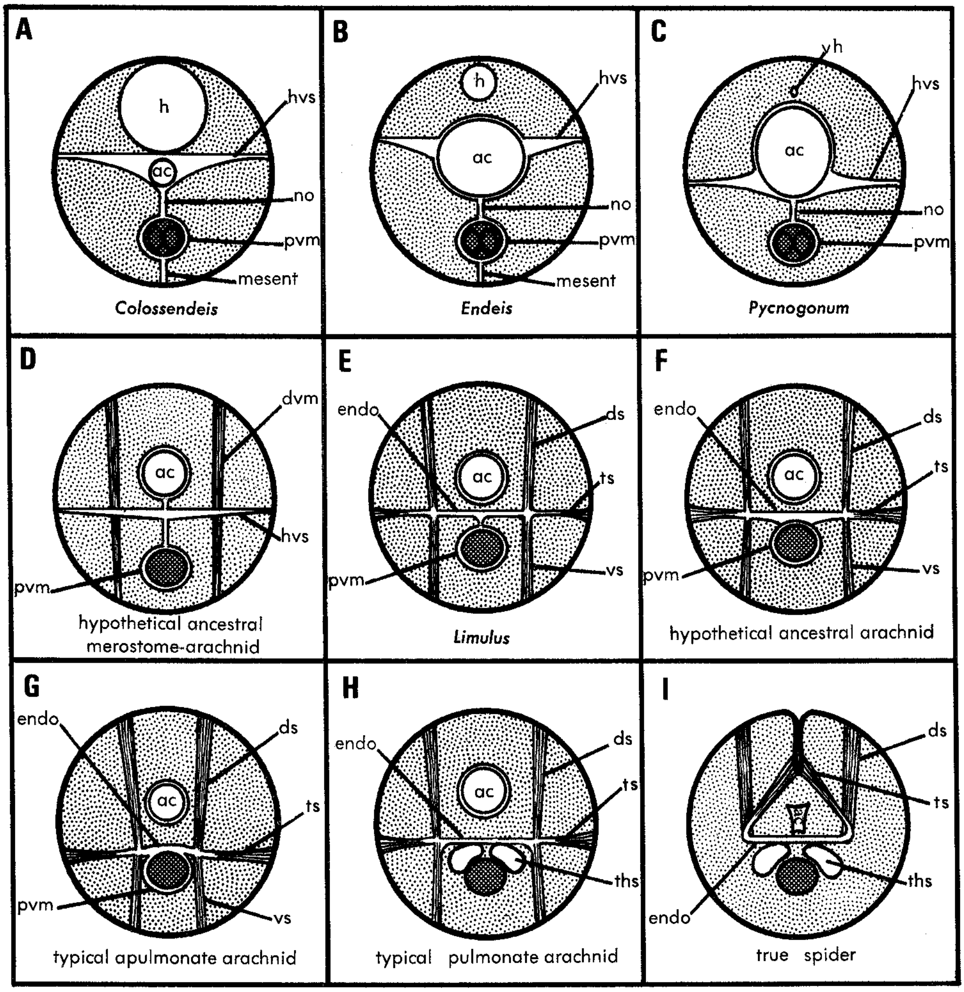


Fig. 27.–Schematic cross-sections of actual and hypothetical chelicerates. A, B, and C are three representative pycnogonids, showing that the horizontal plane of Dohrn's septum can occupy different positions with respect to the gut. D: hypothetical common ancestor of the Merostomata and Arachnida, showing a transversely muscularized horizontal septum (the precursor of the endosternite) lying in a plane between the gut and nervous system. E: the merostome, *Limulus*. F: hypothetical ancestral arachnid, with an endosternite similar to that of modern palpigrades. G: a typical apulmonate. H: a typical pulmonate. I: a typical true spider, with ventral suspensor muscles lacking, and with the transverse suspensors deflected dorsomediad so as to originate from the cervical apodeme. Sections D through I are in a plane through the subesophageal ganglionic mass. The central nervous system is shown with dark shading. Symbols are as follows: ac, alimentary canal; ds, dorsal suspensor muscle; dvm, dorsoventral muscle; endo, endosternite; h, heart; hvs, horizontal vascular septum; mesent, mesentery; no, neurointestinal omentum; pvm, perineural vascular membrane; ths, thoracic sinus; ts, transverse suspensor muscle; vh, vestigial heart; vs, ventral suspensor muscle.

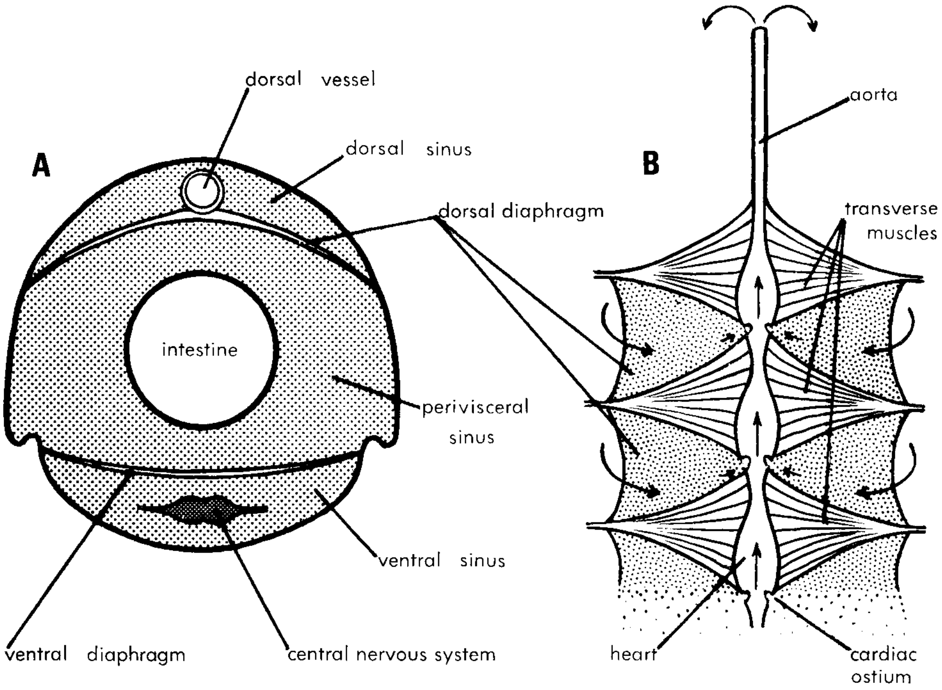


Fig. 28.–A: diagramatic transverse section through an insect, showing the circulatory membranes and sinuses. B: dorsal view of the heart and dorsal diaphragm of an insect, showing the dorsal transverse muscles. Arrows indicate the direction of blood flow. Redrawn from Snodgrass (1935).

There is comparative evidence that the transverse muscles of chelicerates have arisen from primitive septal musculature. The pycnogonid horizontal vascular septum could be homologous to a similar septum of hypothetical prechelicerate ancestors; its transverse muscle fibers could be the progenitors of the transverse suspensors of the endosternite (Fig. 27). This hypothesis is supported by the following facts:

1. The pycnogonid horizontal vascular septum is muscularized transversely, a condition which allows its undulatory movements. The septum extends along the entire length of the trunk (cephalothorax), and thus its musculature is predisposed toward serial metamerization.
2. The plane of the pycnogonid horizontal septum can be variably located (Fig. 27A, B, C) with regard to the position of the gut: in *Colossendeis*, it lies essentially over the gut; in *Endeis*, it straddles the sides of the gut; in *Pycnogonum*, it lies at the base of the gut. In a hypothetical merostome-arachnid ancestor, it would have needed to lie under the gut (Fig. 27D) and over the central nervous system.
3. In *Colossendeis*, the skeletogenous nature of the horizontal vascular septum suggests that it is an incipient endosternite. At its posterior end, the horizontal septum (which is already muscularized transversely) traverses a transverse septum which is muscularized dorsoventrally (Fig. 24C). This situation suggests a prototype of the endosternite musculature.

Snodgrass (1935) has described horizontal diaphragms in insects (Fig. 28) and these have a vascular function, for they separate blood sinuses. There are two principal horizontal septa in insects: (1) a dorsal diaphragm, separating the pericardial and perivisceral hemocoels, and (2) a ventral diaphragm, separating the perivisceral and perineural hemocoels. Both of these diaphragms are muscularized by transverse fibers. The ventral diaphragm holds a particular interest because it lies in a plane which separates the intestine from the central nervous system, and thus it suggests the hypothetical chelicerate condition depicted in Fig. 27D. Although I do not intend here to suggest homologies between the Insecta and the Chelicerata, I think that the mere presence in insects of a

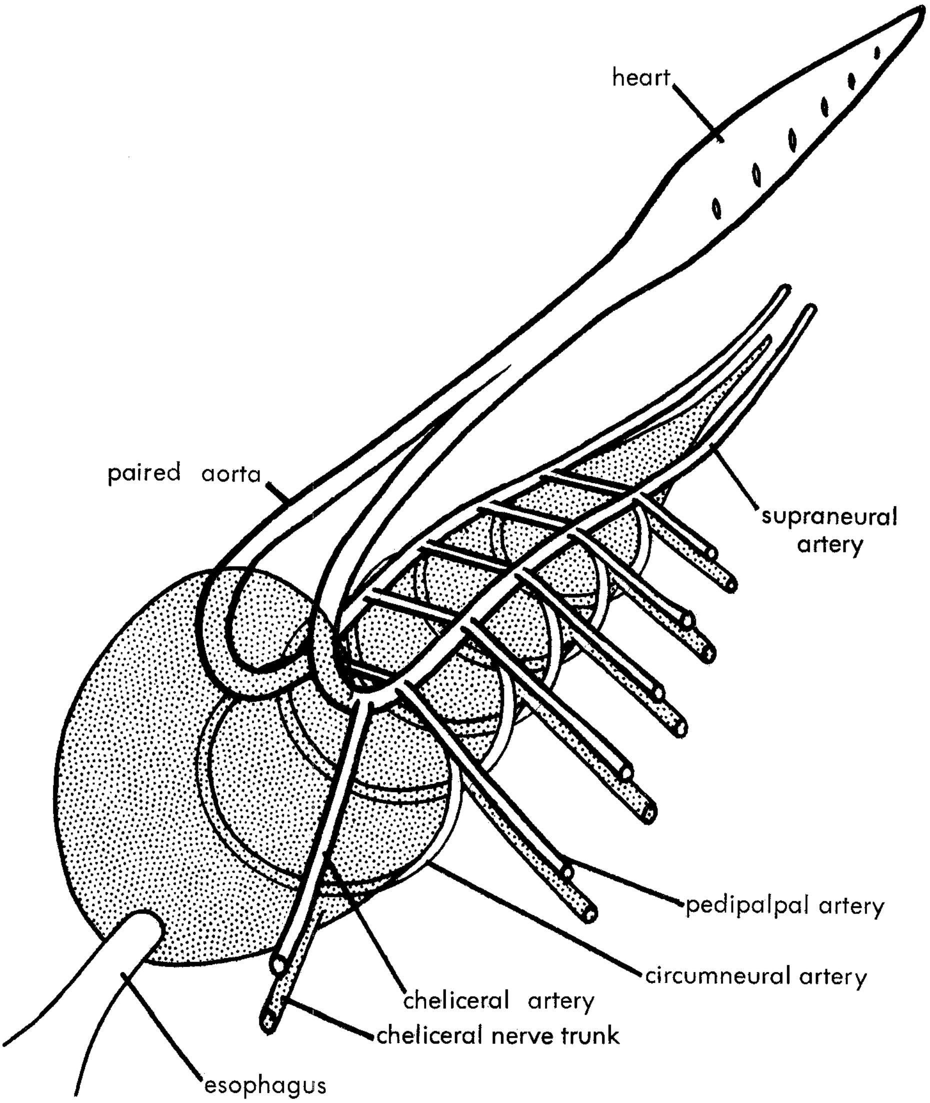


Fig. 29.–Hypothetical arterial system of a prechelicerate, showing a paired supraneural artery. The view is anterodorsolateral. A ghost of the central nervous system (stippled) is shown in position. See Fig. 34A.

transversely muscularized horizontal septum, lying in a plane between the gut and the nervous system, supports my hypothesis that a similar condition could have existed in primitive chelicerates.

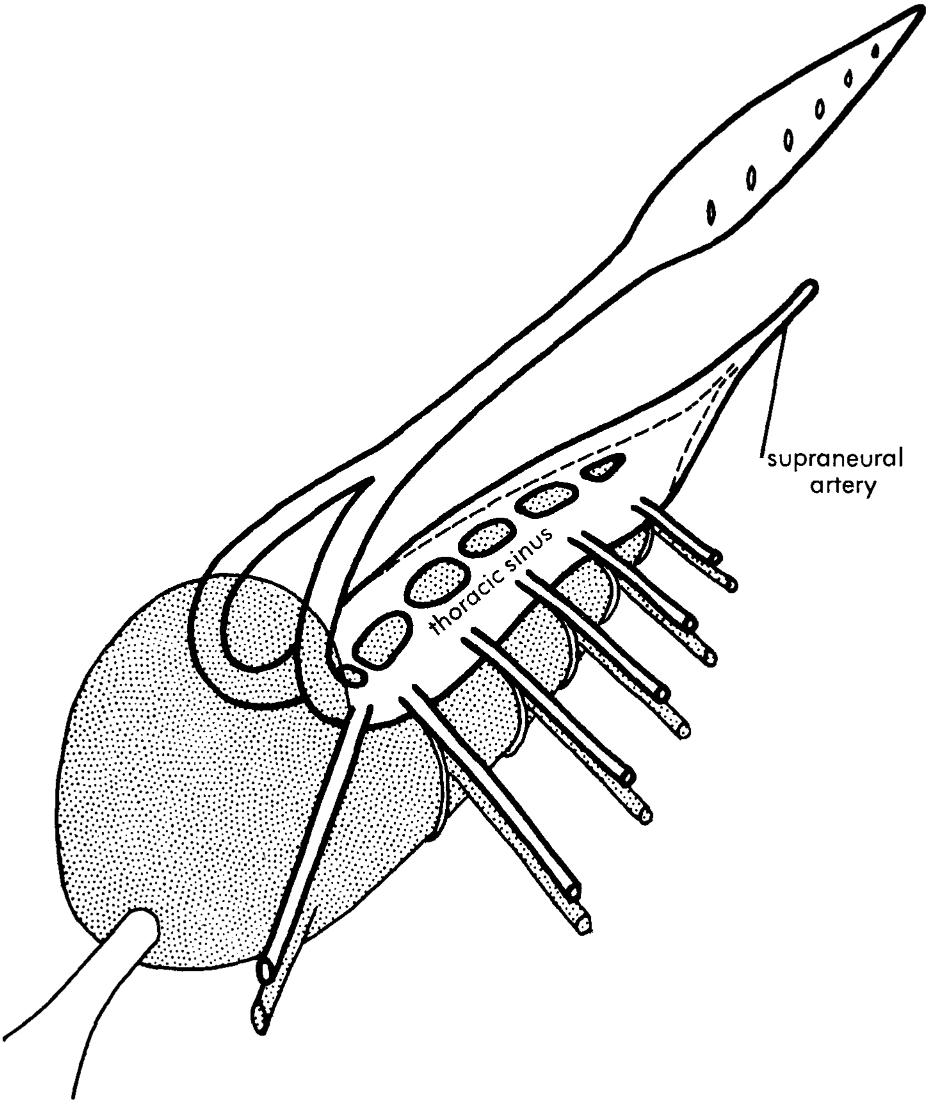


Fig. 30.—The thoracic sinus stage of arterial development. This stage persists in the adults of all pulmonate arachnids. See Fig. 34B.

The Evolution of Arterial Membranes

In pycnogonids, in *Limulus*, and in apulmonate arachnids, the arterial system is perivisceral. From this evidence, it seems likely that the same state of being existed also in ancestral chelicerates. In the light of the ontogeny of *Limulus*, discussed earlier, the

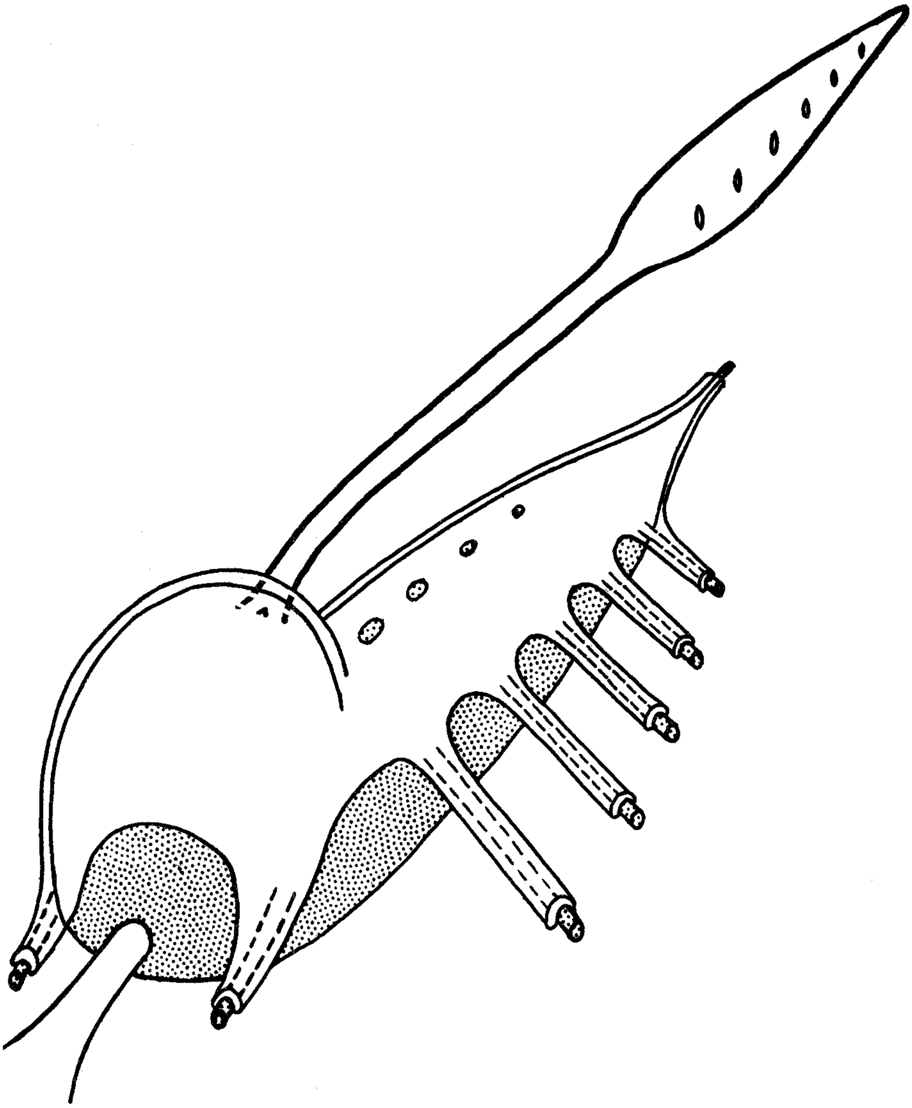


Fig. 31.–A stage of arterial development intermediate between the thoracic sinus and the periganglionic sinus. See Fig. 34C.

periganglionic arterial sinus probably emerged through a series of stages of arterial evolution, as depicted in Figs. 29 to 34:

1. A paired supraneural artery (Figs. 29, 34A) probably existed in prechelicerate ancestors. This type of condition is presaged by the neural circulation in certain polychaetes; e.g., *Nereis cultrifera* (Karandikar and Thakur, 1946).
2. Hypertrophy of the supraneural arteries, and expansion of their lumina, as depicted in Figs. 30, 34B, produced a thoracic sinus condition, such as occurs in all pulmonate arachnids. However, the thoracic sinuses of pulmonate arachnids are here regarded as a neotenous retardation of the developmental process because *Limulus*

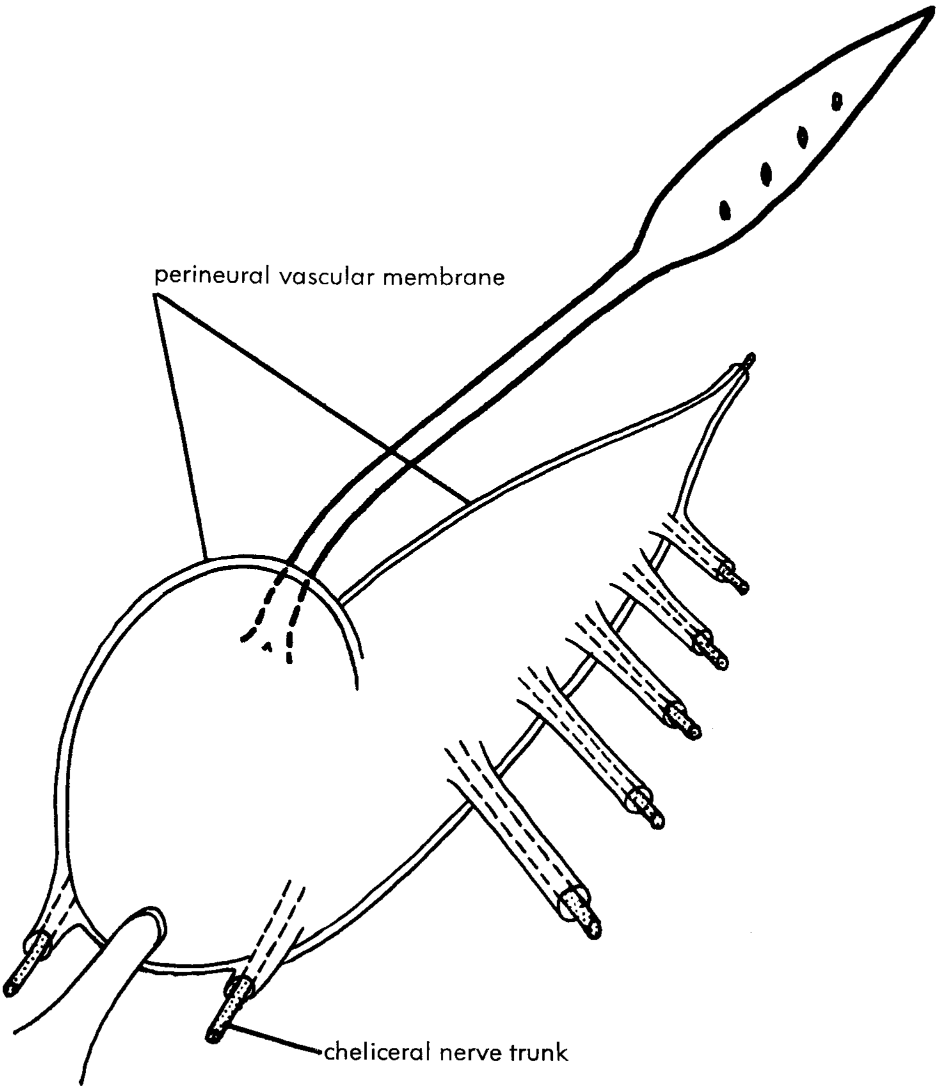


Fig. 32.–The definitive periganglionic stage of arterial development. This condition exists in all adult chelicerates which lack book lungs. See Fig. 34D.

passes through a larval stage in which it has a paired thoracic sinus, and because lungless spiders still possess the genetic machinery to carry their development on (in the absence of book lungs) to the full periganglionic sinus condition.

3. Figs. 31 and 34C depict an intermediate condition between the paired thoracic sinus and the full periganglionic sinus. This stage does not exist in any adult chelicerate, but it occurs in the larva of *Limulus* (Kingsley, 1893).
4. The definitive periganglionic arterial sinus (Figs. 32, 34D) is enclosed by a perineural vascular membrane which ensheathes all the nerve trunks arising from the central nervous system. This membrane, which consists of connective tissue, is the substratum for the phylogenetic development of the endosternite.

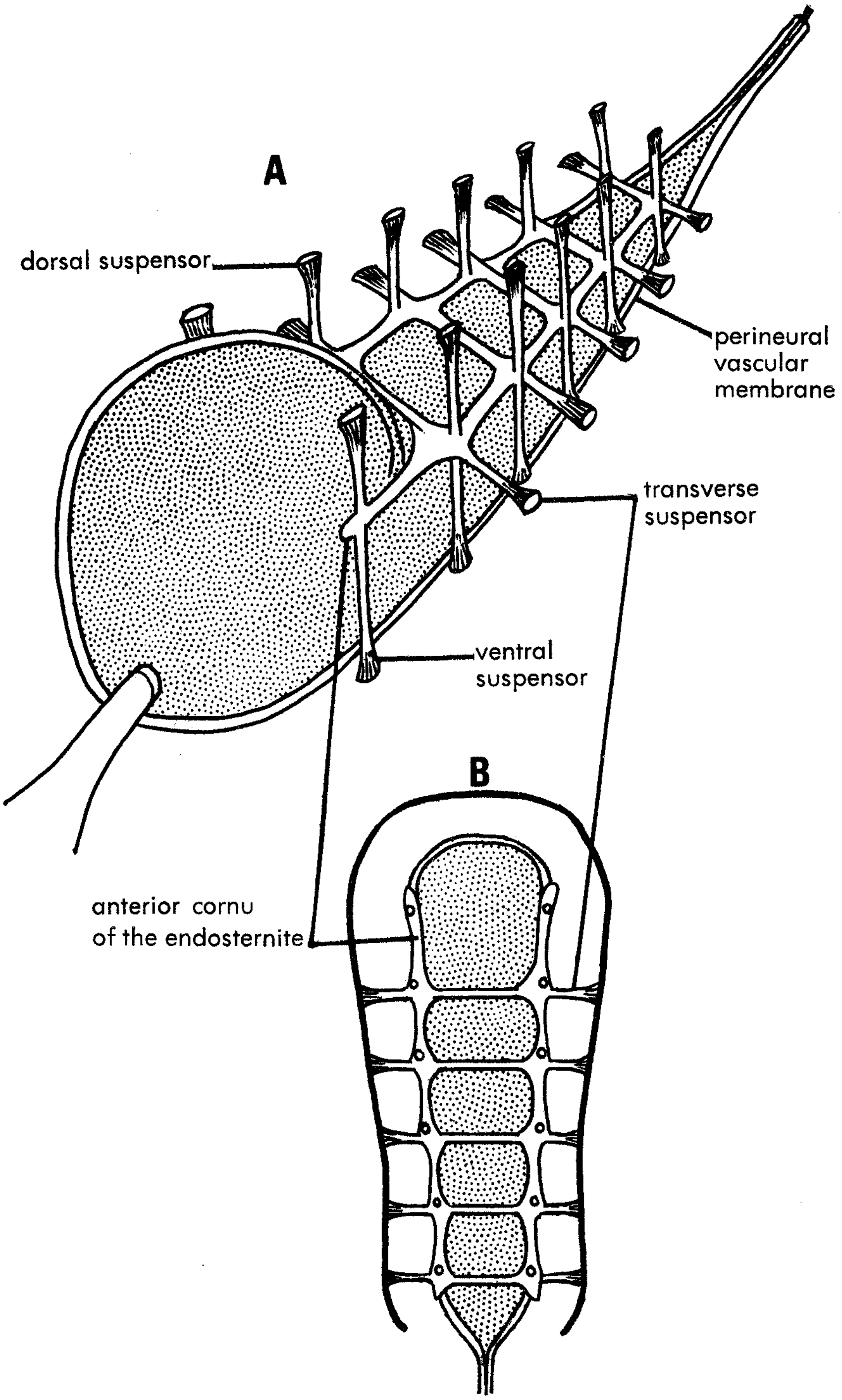


Fig. 33.–A: hypothetical model of the primitive chelicerate endosternite, as formed by fusion of the perineural vascular membrane with the connective tissue of dorsoventral and transverse muscles. The view is anterodorsolateral. B: dorsal view of same. The circles represent the positions of dorsoventral muscles.

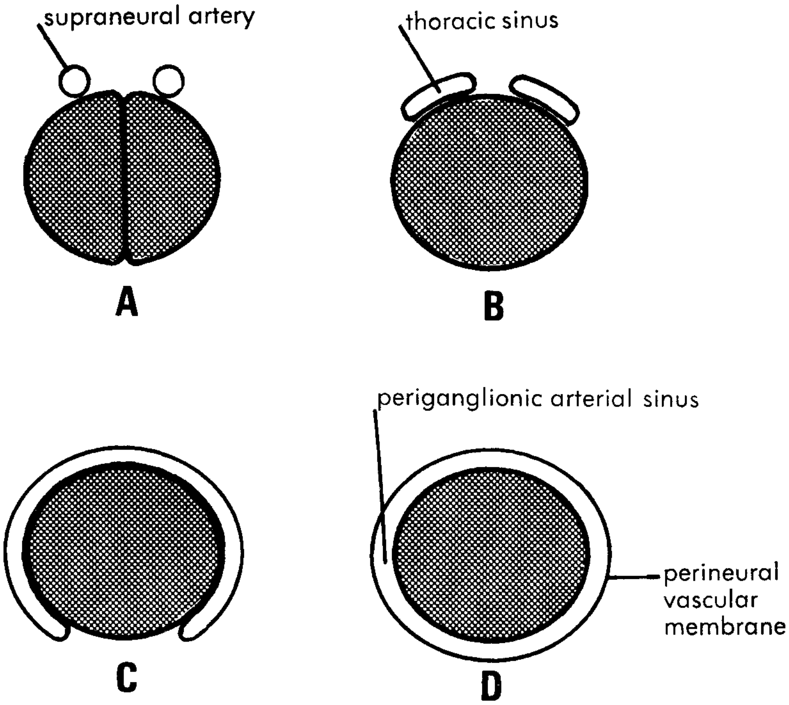


Fig. 34.–Hypothetical origin of the perineural vascular membrane. All diagrams represent transverse sections through the subesophageal ganglionic mass, shown with dark shading. A: prechelicerate condition, with paired supraneural artery. See Fig. 29. B: paired thoracic sinus, found in all adult pulmonates, and in the larval *Limulus*. See Fig. 30. C: intermediate stage. See Fig. 31. D: periganglionic arterial sinus, found in all apulmonate chelicerates. See Fig. 32.

Origin of the Chelicerate Endosternite

Primitively, according to my hypothesis, the endosternite formed as a result of the fusion of the perineural vascular membrane with the connective tissue of transverse muscles, serially arranged above the neuromeres of the central nervous system. At their points of contact with the membrane, these muscles became tendonified (non-contractile) cross-bars, and their lateral contractile extremities, which presisted as transverse suspensors, were the first muscles to insert on the endosternite. Originally, the transverse muscles may have been associated with a horizontal vascular septum lying in a plane beneath the gut and over the nervous system (Fig. 27D, E, F). Eventually, the cross-bars became involved with dorsoventral muscles through fusion of connective tissue. The upper and lower extremities of the dorsoventral muscles became became respecitvely the dorsal and ventral suspensors of the endosternite.

Originally, the dorsoventral muscles may have had a vascular function, for up and down movements of the endosternite may have had a role to play in maintaining arterial blood pressures. Mitchell (1957) pointed out that in the Hydryphantidae (Acarida) dorsoventral muscles are important in regulating local changes in blood pressure, and Parry and Brown (1959a and b) have shown that in some arachnids leg extension depends upon the maintenance of a cephalothoracic blood pressure higher than that of the abdomen. Hence, the original function of the endosternite may have been vascular rather than skeletal.

In my hypothesis, the primitive endosternite had the form of a lattice (Fig. 33), with transverse and dorsoventral muscles crossing perpendicularly above the subesophageal ganglionic mass, and with fenestrations filled in with perineural vascular membrane. The thickening of this membrane produced a nonfenestrated endosternite such as that which occurs in adult palpigrades. In a young palpigrade, such as that described by Börner (1904), rough handling can puncture the thin membrane and cause the endosternite to appear fenestrated (Börner illustrated it that way in this text figure 17). In the thelyphonid endosternite there are two persistent fenestrae, and in schizomids there is one persistent fenestra.

The "cephalothoracic" endosternites of thelyphonids and amblypygids extend into the abdomen through its first segment, so it is probable that the primitive endosternite did the same. Abdominal endosternites occur in *Limulus*, in scorpions, and in spiders, but these always exist independently in separate segments and are never fused into a centralized mass as they are in the cephalothorax. The abdominal endosternites of *Limulus* have been discussed; they are structurally similar to the cephalothoracic endosternite, but are probably not serially homologous to it because their transverse muscles insert upon movable appendages and lie beneath the nervous system. In scorpions, the circumneural ring appears to be the result of an overlapping of cephalothoracic and abdominal elements in one segment. The suprapectinal endosternite, which lies in the segment immediately posterior to the circumneural ring, is serially homologous to the inferior portion of the circumneural ring.

In pulmonate arachnids, were arterial development stops short at the thoracic sinus stage, the genes responsible for the development of the endosternite are still operative, and accordingly the endosternite develops as though it were morphologically independent of the arterial membranes. However, in the lungless spiders, where arterial development proceeds to the periganglionic stage, the endosternite is continuous with the perineural vascular membrane, as it is in the apulmonates. From these facts, one may infer that the neotenous retardation of the arterial development is a pulmonate specialization, and that the endosternite already existed (in prepulmonate ancestors) before the specialization occurred.

The palpigrade has the most primitive endosternite of all apulmonates, and it could well serve as a model of the prototype from which the nonpalpigrade apulmonates have evolved through specialization. In nonpalpigrade apulmonates, there has been a tendency toward reduction in the size and extent of the endosternite. This has been correlated with a corresponding tendency toward a general increase in the development of an apodemal endoskeleton. This trend is perhaps a result of terrestrialization, in which a selective premium has been placed on a specialized musculature requiring elaborate apodemes.

Opilionids of the suborder Palpatores have the most fully developed cephalothoracic endostermite of all the nonpalpigrade apulmonates, although transverse suspensor muscles are lacking in the entire order. Laniatore opilionids have an endosternite somewhat more reduced, and accordingly the coxal apodemes are more strongly developed in this suborder. The cyphophthalmids, which I regard as specialized opilionids, and by no means primitive, have an extremely reduced endosternite which could have been derived from either of the other two opilionid suborders.

The tick endosternite, which has a single pair of persistent transverse suspensors and three pairs of dorsoventral suspensors, has a paradoxical primitiveness which strangely belies the otherwise specialized morphology of ticks. Among nonpalpigrade apulmonates, the Acarida are second only to opilionids in endosternite development. The tick and the opilionid are similar in that both have a conspicuously developed perineural vascular membrane, although the tick endosternite is more vestigial. In some of the Acarida, the arterial system and the endosternite are reduced to the point of absence, but this is due probably to their small size, and to the fact that apodemes for muscle attachment have functionally superseded the mesodermal endosternite.

The pseudoscorpion endosternite is even more reduced than that of the tick, and the perineural vascular membrane is so vestigial that its presence can be detected only because portions of it are still adherent to the endosternites. The ricinuleid endosternite is virtually absent, but the perineural vascular membrane is well enough developed that vestiges of the endosternite can be identified.

In solpugids, the tendency toward reduction of the mesodermal endosternite has reached its most extreme degree, for in the entire order there is none at all (Millot and Vachon, 1949b), though the perineural vascular membrane is still present and functional. Solpugids have the most elaborately developed system of apodemes to be found in the entire Arachnida, and this fact misled Bernard (1896) to the conclusion that the endosternites of all arachnids are morphological apodemes, and hence, of ectodermal origin. Bernard was convinced that *Limulus* is a crustacean, based on its convergent similarity to the notostracan branchiopod, *Apus* (Bernard, 1892a, b). In reply to Lankester's (1881) *Limulus an Arachnid*, Bernard was intent upon proving that the endosternite of *Limulus* can in no way be homologous to that of arachnids, so he capitalized on the solpugid apodemal endoskeleton to force this point. Unfortunately, Comstock (1948) in writing his popular spider book, was influenced by Bernard's point of view, so that some American arachnologists have since been persuaded that the endosternite is an apodemal derivative in all arachnid orders. In his chapter on the internal anatomy of spiders, Comstock speaks disparagingly of the "... school of writers who believe that the endosternite is formed by the coalescence of the tendons of muscles." Apparently, these aspersions were directed toward Schimkewitsch (1893, 1894), and toward Pocock (1902), both of whom took the viewpont which this research confirms.

Lankester (1884), made a chemical analysis of the endosternite of *Limulus*, and he found that its constituents were "nearly equal quantities of chitin and of mucin." This fact posed a problem, for mesoderm is not thought of generally as giving rise to chitinous structures. In Lankester's address to this problem, he acknowledged that

> ... the presence of chitin in a tissue belonging to the skeletotrophic group, and derived from the mesoblast is a novelty. It appears to have been too readily assumed that the connective tissue of Invertebrata correspond in their chemical nature with those of the Vertebrata, and the notion that chitin is a product confined to the activity of the tissues of the epiblast has been hitherto adopted without sufficient basis in fact. The skeletal product of the protoplasmic cells which build up the endosternite of Limulus is chiefly chitin, and I am led, from the behaviour of the fibers and the trabeculae of the connective tissue in other regions of the body of Limulus, and in other Arthropoda, to suspect that this substance takes the place of collagen and chondrin in the skeletal tissues of the Arthropoda.

General Remarks Regarding the Phylogeny of the Arachnid Orders

The fossil record is very suggestive of the theory that scorpions arose either from a eurypterid ancestry (Beklemischev, 1958), or else from the immediate merostome ancestors of eurypterids (Stormer, 1944, 1969). The earliest scorpions may have been aquatic (Stormer, 1933), though there is an alternative possibility that the transition from water to land was made by the eurypterids themselves, so that scorpions may have arisen from terrestrial eurypterids (Barnes, 1967). There is an enigma which arises from the fact that

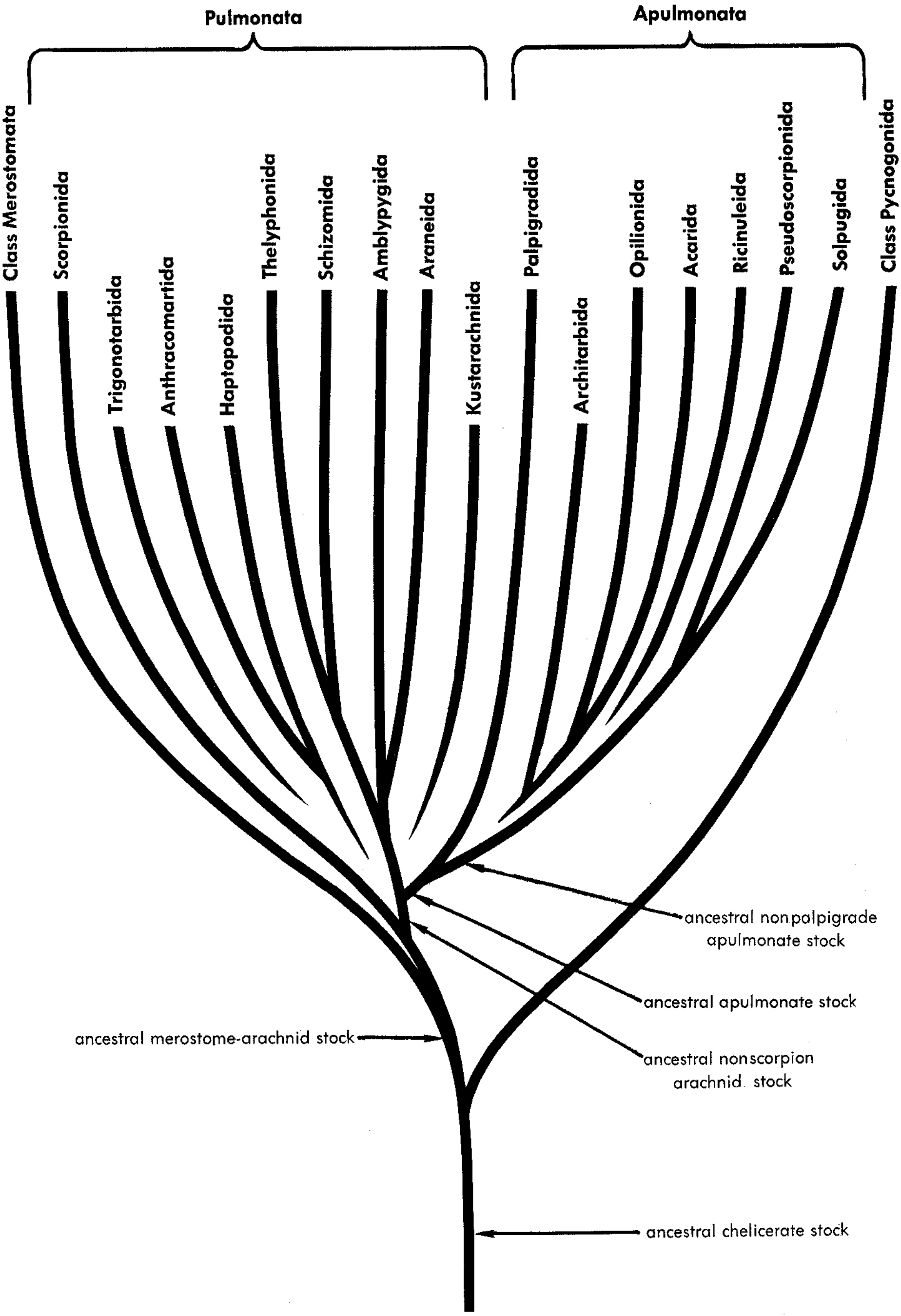


Fig. 35.—A proposed phyletic tree of the arachnid orders, based partly upon evidence presented in this paper. The five orders shown with shortened branches have been extinct since the Carboniferous Period.

neither modern scorpions nor their fossil forebears can be regarded as primitive arachnids, for scorpion morphology does not lend itself easily to a model of the hypothetical ancestral arachnid (Snodgrass, 1952). If the persuasion of the fossil evidence, that the first arachnids were scorpions, be accepted at face value, it becomes necessary either to derive all other arachnid orders from a scorpion ancestry, or else to contrive a diphyletic theory of arachnid origins. The latter possibility seems unnecessary to me in view of the similarities between scorpions and thelyphonids. Moreover, thelyphonids are so similar to schizomids that many authorities put these two together as a single order, the Uropygida, and there are no modern arachnologists who doubt the affinities of the Thelyphonida-Schizomida (Uropygida) to the Palpigradida. However, the enigma of which I speak lies precisely in the fact that, in certain respects, palpigrades are the most generalized of all known arachnids: (1) the cephalothoracic venter has five sternites, including a cheliceral sternite; (2) the endosternite has six pairs of ventral suspensor muscles (hypothetically, this is the primitive number); (3) the endosternite has five pairs of transverse suspensor muscles; (4) rudimentary respiratory organs (lung-sacs) are present, in some palpigrades in place of book lungs or tracheal spiracles. In these respects, palpigrades are more primitive chelicerates even than *Limulus.*

How is it possible to account for the primitiveness of palpigrades if a scorpion (or scorpion-like) stock was ancestral to the entire class Arachnida? Sharov (1966) offers a resolution to this problem by suggesting that the Arachnida is diphyletic: that scorpions and nonscorpion arachnids have each descended independently from a eurypterid ancestry. In order to do this, he invokes a great deal of parallel evolution in explaining the similarities of scorpions and nonscorpion arachnids, including independent emergence of these two terrestrial groups from marine ancestors. My own preference is for a monophyletic model of arachnid phylogeny, for this eliminates the improbabilities of convergent evolution which a diphyletic model requires.

I propose the hypothesis that arachnid evolution has involved neoteny and subsequent adaptive radiation from neotenous ancestors (Fig. 35). According to this view, the ancestral scorpion was a neotenous eurypterid (i.e., neotenous with respect to the development of the book lungs, the appendages, the lateral eyes, the endosternite, and the arterial system) which, through adaptive radiation, gave rise both to modern scorpions and the nonscorpion pulmonate arachnids. According to the same view, the original apulmonate arachnids were neotenous scorpions (i.e., neotenous with respect to the development of the cephalothoracic sternites and peltidia, the appendages, the respiratory organs, the endosternite, and the abdominal tagma) which gave rise both to modern palpigrades and the nonpalpigrade apulmonates. The foregoing part of this paragraph is intended here only as a suggestion; an intensive defense of this idea would exceed the scope of this study.

CONCLUSIONS

1. The chelicerate endosternite is embryonically of mesodermal origin.
2. The cephalothoracic endosternite has evolved from a vascular membrane which has incorporated the connective tissue of dorsoventral and transverse muscles.
3. The abdominal endosternites, when present, have evolved from the connective tissue of dorsoventral and transverse muscles, without the involvement of a vascular membrane.

4. In all chelicerates which lack book lungs there exists a perivisceral arterial sinus. This sinus persists in its most primitive state in pycnogonids. In *Limulus* and the apulmonate arachnids, it persists principally in the form of a periganglionic arterial sinus.
5. The thoracic sinus arterial system of pulmonate arachnids in an arrested stage of arterial development and is interpreted here as neoteny. This stage occurs in the larval *Limulus*, and presumably it occurs also during the embryogeny of other chelicerates.
6. In the apulmonate arachnids, the development of the mesodermal endosternite is inversely proportional to the development of the apodemal endoskeleton. Hence, the more highly developed the apodemal endoskeleton, the more vestigial is the endosternite.
7. The pycnogonid horizontal vascular septum is probably homologous to the ancestral progenitor of the endosternite in merostomes and arachnids.
8. The primitive function of the endosternite may have been vascular. Movements of the endosternite may have augmented cardiac contractions in effecting blood circulation through the perivisceral arterial sinus and into the appendicular arteries.
9. Probably, neoteny has been involved in the origin of arachnids from merostomes, and in the origin of apulmonate arachnids from pulmonates.
10. The Pulmonata is a natural monophyletic category. It includes the Scorpionida, Thelyphonida, Schizomida, Amblypygida and Araneida.
11. The Apulmonata is a natural monophyletic category. It includes the Palpigradida, Acarida, Opilionida, Ricinuleida, Pseudoscorpionida and Solpugida. The ancestral apulmonate stock diverged to give rise both to modern palpigrades and to the nonpalpigrade apulmonates.

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LITERATURE CITED

André, M. 1949. Order des Acariens, p. 794-892. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Appelt, V. 1900. Studie o nervové soustave Phalangiinu. Sitzungsberichte Königlich Bohmischen Ges. der Wiss. 38 p.

Baker, E. W. and G. W. Wharton. 1952. An introduction to acarology. Macmillan, New York. 465 p.

Barnes, R. D. 1968. Invertebrate zoology. 2nd ed. Saunders, Philadelphia. 743 p.

Beck, E. J. 1885. Description of the muscular and endoskeletal systems of *Scorpio.* Trans. Zool. Soc. London 11:339-360.

Beklemischev, V. N. 1958. Grundlagen der vergleichenden Anatomie der Wirbellosen, bd. 1-2. Deutscher Verlag Wiss. Berlin.

Benham, W. B. S. 1885. Description of the muscular and endoskeletal systems of *Limulus.* Trans. Zool. Soc. London 11:314-338.

Berland, L. 1949. Ordre des Opiliones, p. 761-793. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Bernard, H. M. 1892a. The Apodidae. Nature Series. Macmillan, London.

Bernard, H. M. 1892b. The apodemes of *Apus* and the endophragmal system of *Astacus.* Ann. Mag. Nat. Hist. 10:67-74.

Bernard, H. M. 1894a. Some observations on the relations of the Acaridae to the Arachnida. J. Linn. Soc. London (Zool.) 24:279-291.

Bernard, H. M. 1894b. Notes on the Chernetidae, with special reference to the vestigial stigmata and to a new form of trachea. J. Linn. Soc. London (Zool.) 24:410-430.

Bernard, H. M. 1894c. The endosternite of *Scorpio* compared with the homologous structures in other Arachnida. Ann. Mag. Nat. Hist. 13:18-26.

Bernard, H. M. 1896. The comparative morphology of the Galeodidae. Trans. Linn. Soc. (Zool.), Ser. 2, 6:305-417.

Blanchard, E. 1852-60. L'Organization du regne animal. Victor Masson, Paris.

Bonnet, A. 1907. Recherches sur l'anatomie comparée et le developpement des Ixodidés. Ann. Univ. Lyon, New Ser., 1:1-185.

Börner, C. 1901. Zur ausseren Morphologie von *Koenenia mirabilis* Grassi. Zool. Anz. 24:537-556.

Börner, C. 1904. Beiträge zur Morphologie der Arthropoden. I. Ein Beitrag zur Kenntnis der Pedipalpen. Zoologica 42:1-174.

Borradaile, L. A., F. A. Potts, L. E. S. Eastham, and J. T. Saunders. 1961. (4th ed., revised by G. A. Kerkut). The invertebrata. Cambridge Univ. Press, London. 820 p.

Buisson, M. du 1925. Recherches sur la circulation sanguine et la ventilation pulmonaire chez les scorpions. Bull. Acad. Roy. Belgique, Brussells 11(5):666-680.

Causard, M. 1892. Sur la circulation du sang chez les jeunes araignées. Compt. Rend., Acad. Sci., Paris 114:1035-1038.

Causard, M. 1893. Sur l'appareil circulatore de la *Mygale caementaria* Walk. Compt. Rend., Acad. Sci., Paris 116:828-830.

Causard, M. 1896. Recherches sur l'appareil circulatore des Aranéides. Bull. Sci. France et Belgique 29:1-109.

Cole, L. J. 1910. Peculiar habit of a pycnogonid new to North America with observations on the heart and circulation. Biol. Bull. 18:193-203.

Comstock, J. H. 1948(2nd. ed., revised by W. J. Gertsch). The spider book. Comstock, Ithaca, New York, 729 p.

Croneberg, A. 1888. Beitrag zur Kenntnis des Baues der Pseudoscorpione. Bull. Soc. Imper. Nat. Moscou, New Ser., 2:416-461.

Daday, E. von. 1880. Ueber den Circulationsapparat der Pseudoscorpione. Természetrajzi Füzetek 4:331-339.

Dohrn, A. 1870. Ueber Entwicklung und Bau der Pycnogoniden. Jenaische Z. Med. Naturwiss. 5:138-157.

Dohrn, A. 1871. Utersuchungen über Bau und Entwickelung der Arthropoden. 12–Zur Embryologie und Morphologie des *Limulus polyphemus.* Jenaishe Z. Med. Nat. 6:580-640.

Dohrn, A. 1879. Neue Utersuchungen über Pycnogoniden. Mittheil. Zool. Sta. Neapel 1:28-39.

Dohrn, A. 1881. Die Pantopoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. Fauna Flora Golfes Neapel 3:1-252.

Dufour, L. 1862. Anatomie, physiologie et histoire naturelle des Galéodes. Mem., Acad. Sci. Paris 17:338-446.

Evans, G. O., J. G. Sheals, and D. Macfarlane. 1961. The terrestrial Acari of the British Isles, vol 1. British Mus., London. 219 p.

Fage, L. 1949a. Classe des Mérostomacés, p. 219-262. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Fage, L. 1949b. Classe des Pycnogonides, p. 906-941. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Firstman, B. 1954. The central nervous system, musculature, and segmentation of the cephalothorax of a tarantula. Microentomol. Stanford Univ. 19:14-40.

Fox, R. M., and J. W. Fox. 1964. Introduction to comparative entomology. Reinhold, New York. 450 p.

Giltay, L. 1925. Note sur la morphologie du squelette cephalothoracique de *Galeodes caspius* Bir. Soc. Roy. Zool. Belgique 56:27-32.

Hansen, H. J., and W. Sorensen. 1897. The order Palpigradi Thorell (*Koenenia Mirabilis* Grassi) and its relationships to other Arachnida. Entomol. Tidskr. 18:223-240.

Hansen, H. J., and W. Sorensen. 1904. On two orders of Arachnida. Cambridge Univ. Press, London. 182 p.

Hoek, P. P. C. 1881. Nouvelles études sur les Pycnogonides. Arch. Zool. Expér. Gén. 9:445-542.

Houssay, F. 1886. Note sur le systeme artériel des scorpions. Compt. Rend., Acad. Sci., Paris 103:354-355.

Houssay, F. 1887. Sur la lacune sanguine périnerveuse chez les scorpions. Compt. Rend., Acad. Sci., Paris 104:520-522.

Hughes, T. E. 1959. Mites or the Acari. Athlone Press, Univ. London. 225 p.

Johnston, G. 1837. An attempt to ascertain the British Pycnogonida. Mag. Zool. Bot. 1:368-382.

Karandikar, K. R., and S. S. Thakur. 1946. Circulatory system of *Nereis cultrifera* Grube. Bombay (City) Univ. J. 14:33-36.

Kaestner, A. 1933. Verdauungs- und Atemorgane der Weberknechte *Opilio parietinus* de Geer und *Phalangium opilio* L. Z. Morphol. Okol. Tiere, Berlin 27(4):587-623.

Kaestner, A. 1968. Invertebrate zoology, vol. 2. Wiley and Sons, New York. 472 p.

Kingsley, J. S. 1884. The development of *Limulus*. Sci. Record 2:249-251.

Kingsley, J. S. 1885. Notes on the embryology of *Limulus*. Quart. J. Microscop. Sci. 25:521-576.

Kingsley, J. S. 1892. The embryology of *Limulus*. J. Morphol. 7:36-66.

Kingsley, J. S. 1893. The embryology of *Limulus*–Part II. J. Morphol. 8:195-268.

Kittary, M. 1848. Sur l'anatomie du *Galeodes aranoides*. Bull. Soc. Nac. Moscou 21:307-371.

Lameere, A. 1933. Precis de zoologie, tome 3. Publ. Inst. Zool. Torley-Rousseau. Univ. Libre Bruxelles.

Lankester, E. R. 1881a. *Limulus* an arachnid. Quart. J. Microscop. Sci. 21:504-548 and 609-649.

Lankester, E. R. 1881b. Reflections on the appendages and on the nervous system of *Apus cancriformis*. Quart. J. Microscop. Sci. 21:343-376.

Lankester, E. R. 1884. On the skeletotrophic tissues and coxal glands of *Limulus*, *Scorpio*, and *Mygale*. Quart. J. Microscop. Sci. 24:129-162.

Lankester, E. R. 1885. Comparisons of the muscular and endoskeletal systems of *Limulus* and *Scorpio*. Trans. Zool. Soc. London 11(10):311-313 and 361-371.

Levi, H. W. 1967. Adaptations of respiratory systems of spiders. Evolution 21:571-583.

Leydig, F. von. 1862. Ueber das Nervensystems der Afterspinne (*Phalangium*). Müller's Arch. Ant. Physiol. 1862:196-202.

Loman, J. C. C. 1917. Beiträge zur Anatomie und Biologie der Pantopoden. Tijdschr. Nederlandsche Dierkundige Vereeniging, Ser. 2, 16:53-102.

Menge, A. 1855. Ueber die Scheerendspinnen, Chernetidae. Nueste Schriften der Naturforschenden Ges. Danzig 5(2):1-42.

Millot, J. 1942a. L'Ordre des Pédipalpes doit-il subsister? Bull. Soc. Zool. France 67:141-145.

Millot, J. 1942b. Sur l'anatomie et l'histophysiologie de *Koenenia mirabilis* Grassi. Rev. Francaise Entomol. 9:33-51.

Millot, J. 1943. Notes complémentaires sur l'anatomie, l'histophysiologie et la répartition géographique en France de *Koenenia mirabilis* Grassi (Arachnida Palpigradi). Rev. Francaise Entomol. 9:127-135.

Millot, J. 1945a. Sur l'anatomie interne des Ricinulei. Ann. Sci. Nat. (Zool.), Ser. II, 7:1-29.

Millot, J. 1945b. Sur la constitution de l'abdomen des Ricinulei. Bull. Soc. Zool. France 50:72-74.

Millot, J. 1945c. Les Ricinuleids ne sont pas des Arachnides primitifs. Bull. Soc. Zool. France 70:106-108.

Millot, J. 1949a. Classe des Arachnides. I–Morphologie general et anatomie interne, p. 263-319. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Millot, J. 1949b. Ordre des Palpigrades, p. 520-532. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Millot, J. 1949c. Ordre des Uropyges, p. 533-562. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Millot, J. 1949d. Ordre des Amblypyges, p. 563-588. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Millot, J. 1949e. Ordre des Ricinuleids, p. 744-760. *In* P. P. Grassé [ed.], Traité de zoologie, de zoologie, tome 6. Masson et Cie, Paris.

Millot, J., and M. Vachon. 1949a. Ordre des Scorpions, p. 386-436. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Millot, J., and M. Vachon. 1949b. Ordre des Solifuges, p. 482-519. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Milne-Edwards, H. 1840. Histoire naturelle des crustaces. Paris.

Milne-Edwards, A. 1872. Recherches sur l'anatomie des Limules. Ann. Sci. Nat. Zool., Ser. 5, 17:1-67.

Mitchell, R. D. 1957. Locomotor adaptations of the family Hydryphantidae (Hydrachnellae, Acari). Naturwiss. Abhandl., Bremen 35:75-100.

Newport, G. 1843. On the structure, relations, and development of the nervous and circulatory systems, and on the existence of a complete circulation of the blood in vessels, in Myriapoda and macrourous Arachnida. Philosoph. Trans. Roy. Soc. London 133:243-302.

Owen, R. 1873. On the anatomy of the American King-crab (*Limulus polyphemus*, Latr.). Trans. Linn. Soc. London 28:459-506.

Packard, A. S. 1871. The development of *Limulus polyphemus*. Mem. Boston Soc. Nat. Hist. 2:155-202.

Packard, A. S. 1880. The anatomy, histology and embryology of *Limulus polyphemus*. Anniv. Mem. Boston Soc. Nat. Hist. p. 3-45.

Pagenstecher, H. A. 1862. Zur Anatomie von *Argas reflexus*. Z. Wiss. Zool. 11:142-155.

Parry, D. A., and R. H. J. Brown. 1959a. Hydraulic mechanism of the spider leg. J. Exp. Biol. 36:423-433.

Parry, D. A., and R. H. J. Brown. 1959b. The jumping mechanism of salticid spiders. J. Exp. Biol. 36:654-664.

Patten, W. 1889. On the origin of vertebrates from arachnids. Quart. J. Microscop. Sci. New Ser. 31:317-378.

Patten, W., and W. Redenbaugh. 1899. Studies on *Limulus*. J. Morphol. 16:26, 91-200.

Petrunkevitch, A. 1922. The circulatory system and segmentation in Arachnida. J. Morphol. 36:157-185.

Petrunkevitch, A. 1955. Arachnida, p. 42-162. *In* R. C. Moore [ed.], Treatise on invertebrate paleontology, Part P, Arthropoda 2. Geol. Soc. Am. and Univ. Kansas Press, Lawrence, Kansas.

Pocock, R. I. 1902. Studies on the arachnid endosternite. Quart. J. Microscop. Sci. 46:225-262.

Quatrefages, A. de. 1845. Mémoire sur l'organisation des Pycnogonides. Ann. Sci. Nat., Ser. 3, 4:69-83.

Robinson, L. E., and J. Davidson. 1913. The anatomy of *Argas persicus* (Oken, 1818). Parasitol. 6:20-48.

Roewer, C. F. 1934. Solifugae, Palpigradi, p. 1-723. *In* H. G. Bronns Klassen und Ordnungen des Tierreichs, bd. 5, abt. 4, buch 4, lief. 1-5. Akademische Verlagsgesellschaft, Leipzig.

Rossler, R. 1882. Beiträge zur Anatomie der Phalangiden. Z. Wiss. Zool. 36:671-702.

Rucker, A. 1901. The Texan *Koenenia*. Am. Nat. 35:615-630.

Sanchez, S. 1959. Le développement des Pycnogonides et leurs affinités avec les Arachnides. Arch. Zool. Exp. Gén. 98(1):1-101.

Savory, T. H. 1964. Arachnida. Academic Press, London. 291 p.

Schaub, R. von. 1888. Ueber die Anatomie von *Hydrodroma* (C. L. Koch). Sitzungs. König. Akad. Wiss., Wein 97(1):98-151.

Schimkewitsch, W. 1884. Étude sur l'anatomie de l'Epeire. Ann. Sci. Nat. Zool. 17:1-94.

Schimkewitsch, W. 1885. Étude sur le développment des Araignees. Arch. Biol. 6:515-584.

Schimkewitsch, W. 1893. Sur la structure et sur la signification de l'endosternite des Arachnides. Zool. Anz. 16:300-308.

Schimkewitsch, W. 1894. Ueber Bau und Entwicklung des Endosternites der Arachniden. Zool. Jahrb., Abt. Anat. Ontog. Tiere 8:191-216.

Schneider, A. 1892. Sur le systeme artériel du scorpion. Tablettes Zoologiques 2:157-198.

Sharov, A. G. 1966. Basic arthropodan stock, with special reference to insects. Pergamon Press, New York. 271 p.

Snodgrass, R. E. 1935. Principles of insect morphology. McGraw Hill, New York. 667 p.

Snodgrass, R. E. 1952. A textbook of arthropod anatomy. Comstock, Ithaca, New York. 363 p.

Soresen, W. 1879. Om bygningen af gonyleptiderne, en type af arachnidernes classe. Naturhistorisk Tidsskr., Copenhagen 12:97-222.

Soresen, W. 1914. Recherches sur l'anatomie exterieure et interieure des solifuges. Oversigt over det Kongelige Danske Videnskabernes Selskabs. Forhandlinger. Bull Acad. Roy. Sci. Lettres Danemark 3:131-215.

Steding, E. 1923. Zur Anatomie und Histologie von *Halarachne otariae*, n. sp. Z. Wiss. Zool. 121(3):443-493.

Stormer, L. 1933. Are the trilobites related to the arachnids Am. J. Sci. 5th Ser., 226:147-157.

Stormer, L. 1944. On the relationships and phylogeny of fossil and Recent Arachnomorpha. Skr. Norske Videnskacad. 5:1-158.

Stormer, L. 1969. Oldest known terrestrial arachnids. Science 164:1276-1277.

Straus-Dürckheim, H. 1828. Considérations générales sur l'anatomie comparée des animaux articules. Ferussac, Bull. Sci. Nat. 14:370-380.

Straus-Dürckheim, H. 1829. On the comparative anatomy of the Arachnida (abstr.), p. 497-504. *In* J. F. Meckel, Traité général d'anatomie comparée, Paris.

Treviranus, G. R. 1816. Abhandlungen über den innern Bau der ungeflügelten Insekten, p. 1-86. *In* G. R. Treviranus, and L. C. Treviranus, Anatomischen und Physiologischen Inhalts. Göttingen.

Tulk, A. 1843. Upon the anatomy of *Phalangium opilio*. Ann. Mag. Nat. Hist. 12:163-165; 243-253; 318-331.

Vachon, M. 1949. Ordre des Pseudoscorpiones, p. 437-481. *In* P. P. Grassé [ed.], Traité de zoologie, tome 6. Masson et Cie, Paris.

Van Beneden, P. J. 1846. Die Circulation in den niedrig organisirten Thieren. Neue Notizen aus dem Gebiete der Natur- und Heilkunde, no. 797. 37(5):65-74.

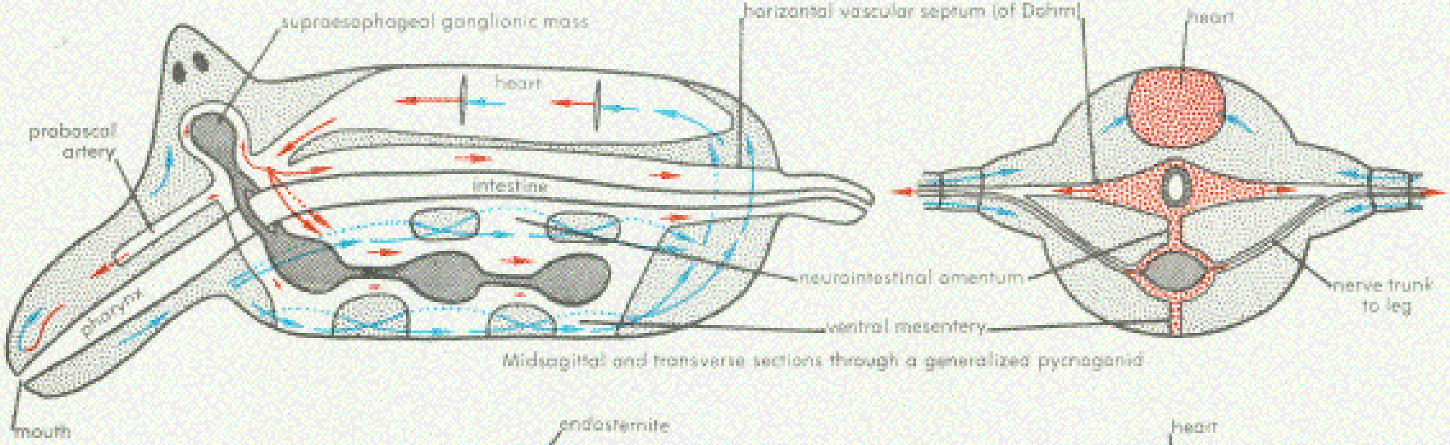
Vitzhum, H. G. 1940. Acarina, p. 1-1011. *In* H. G. Bronns Klassen und Ordnungen des Tierreichs, bd. 5, abt. 4, buch 5, lief. 1-7. Akademische Verlagsgesellschaft, Leipzig.

Weygoldt, P. 1969. The biology of pseudoscorpions. Harvard Univ. Press, Cambridge, Massachusetts. 145 p.

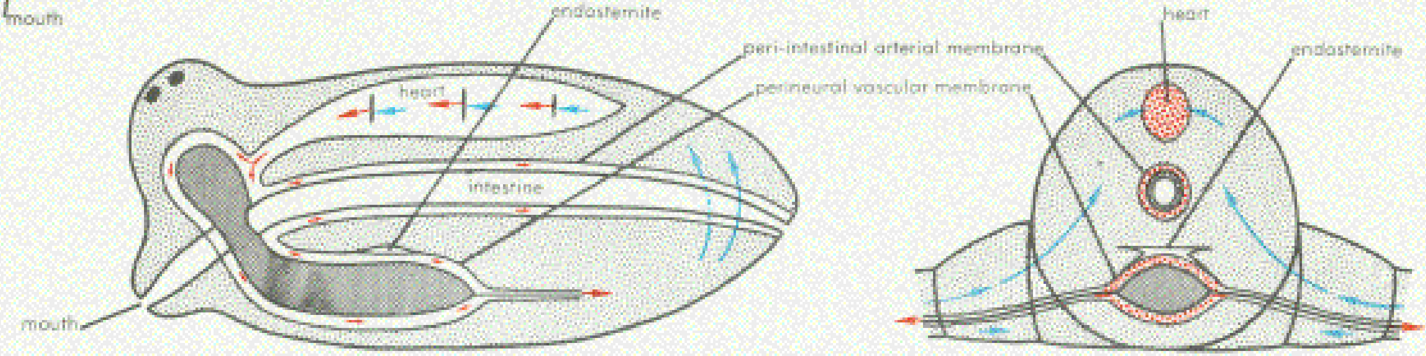
Winkler, W. 1888a. Das Herz der Acarinen nebst vergleichenden Bemerkungen über das Herz der Phalangiiden und Chernetiden. Arb. Zool. Inst. Wien 7:111-118.

Winkler, W. 1888b. Anatomie der Gamasiden. Arb. Zool. Inst. Wien 7:317-354.

Zenker, W. 1852. Untersuchungen über die Pycnogoniden. Müller's Archiv. Anat. Physiol. p. 379-391.



Midsagittal and transverse sections through a generalized pycnogonid



Midsagittal and transverse sections through a generalized merostome-arachnid

Fig. 25.—Blood flow diagrams comparing the basic circulation of a generalized pycnogonid with that a a generalized merostome-arachnid. The central nervous system is shown with dark shading. The venous hemocoel is shown with black stipples; the heart, arterial system and gut are unshaded. Red arrows represent the direction of arterial flow (the arterial system is restricted to the perivisceral arterial sinus), and blue arrows represent venous flow. Red stipples represent arterial flow which is perpendicular to the plane of the page. Oval windows above the pycnogonid nerve cord represent perforations in the neurointestinal omentum; ovate windows beneath the pycnogonid nerve cord