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A Study of Thoracic Skeletomusculature in Peracarida (Crustacea)

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A Study of Thoracic Skeletomusculature
in Peracarida (Crustacea)
(TITLE)

BY

Donna R. Gill

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

Master of Science in Education

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1972
YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
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12 May 1972
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The undersigned, appointed by the Head of the Department of Zoology, have examined a thesis,

A Study of Thoracic
Skeletomusculature in Peracarida
(Crustacea)

Presented by

Donna R. Gill

a candidate for the degree of Master of Science in Education and certify that it is acceptable to them.

ABSTRACT

Two species of peracarid malacostracans, a mysid, *Neomysis americana*, and an oniscid isopod, *Trachelipus* cf. *rathkei*, were used to study the skeletomusculature system. Serial sections, whole mounts, and gross dissections were made. Coxal promotors and remotors and basal adductors and abductors were the muscle groups examined.

The promotor and remotor muscles of *N. americana* were found to be numerous, well developed, taking origin primarily from the dorsal thoracic wall, and extending nearly ventrally to insert in the coxa; the adductor muscle and two abductor muscles are weakly developed. The coxa in *T.* cf. *rathkei* is incorporated completely into the pleura of the thorax and is not directly functional in locomotion. Coxal muscles were observed in the isopod, but could not be easily distinguished due to this incorporation. Many large muscle bands, originating from the dorsal and dorsolateral thoracic wall, were observed. Some of these muscles are coxal and some are strictly thoracic. The basis of *T.* cf. *rathkei* is quite large and held parallel to the body during locomotion. The adductor series is composed of several relatively small muscle bundles. The abductor series has fewer elements, but the muscle bundles are large.

These muscle patterns reflect functional adaptations that occurred during specialization from a primitive,

generalized form to an advanced, specialized form. These muscles were selected for modification and improvement in accordance with their functional possibilities during the peracarid adaptive radiation.

LITERATURE REVIEW

Calman (1909) established the modern system of classification of Crustacea by studying living forms and comparing external morphology. This was his basis for phylogenetic study of the malacostracous Crustacea. During the course of his studies, Calman devised a scheme of classification consisting of several characteristics that may approximate an ancestral type from which the more specialized members of the malacostraca have diverged. These characteristics or "caridoid facies" are as follows. The carapace envelopes the thorax region, the stalked eyes are movable, biramous antennules, a scale-like exopodite on the antenna, natatory exopodites on the thoracic limbs, two protopodal segments in the thoracic limbs, an elongated and ventrally flexed abdomen, and a "tail-fan" formed by the lamellar rami of the last pair of appendages spread out on either side of the telson.

Sidnie Manton (1928b) published a detailed description of the anatomy of lophogastrid mysidacean Crustacea. Her approach to phylogenetic study was similar to that of Calman in that it was observational and comparative. Manton studied internal anatomy as well as the external anatomy and habits of the lophogastrids. Manton (1928a, 1934) also used embryology of mysids and phyllocarids and related it to phylogeny in malacostracans. One aspect of the embryological study concerned "furcal rudiments" in *Hemimysis lamornae* and *Nebalia bipes*. She determined that the furcae are formed directly from the telson cuticle and at the first ecdysis they are shed with the old cuticle and are not reformed. The presence of furcae is considered a primitive character, but they are present in several malacostracans. In later years Manton turned to functional analysis as a basis for phylogenetic study of arthropods. A very important monograph employing this functional method deals with arthropod mandibular mechanisms (1964). The problem of dealing with hard and large food particles has been resolved in many ways in the Arthropoda. Two types of movements, the promotor-remotor swing and the adduction in a transverse plane, have been used in the evolution of jaw mechanisms. Manton studied the jaw musculature of species ranging from the Onychophora to primitive and advanced crustaceans. The Crustacea and Hexapoda are believed to have employed the promotor-remotor swing or rolling motion resulting in a squeezing or grinding mandibular action. This type of mechanism Manton believes was modified secondarily to give a strong holding and cutting in a transverse plane. The Myriopoda and Chelicerata have employed the adduction movement giving direct transverse biting. From her comparisons, Manton concluded that arthropod evolution is polyphyletic, with labiates, crustaceans, and chelicerates constituting distinct groups within the phylum.

Abdominal musculature of mysids, euphausians, and syncarids has been extensively described by R. J. Daniel

(1928, 1929, 1931). His analyses are extremely detailed, and have shown that there is a pattern which occurs in all the species studied. All of the species he studied possess many transverse abdominal muscles which are intersegmental and show a spiraling pattern. Since this pattern is very complex, it is therefore phyletically significant in that it is not independently derived in the separate groups. Daniel has also conducted investigations on the immature forms of shrimp and their bearing on phylogeny of this group of Crustacea.

Doris Cochran (1935) realized the lack of information regarding detailed internal structure of crustaceans, especially of the muscles. Her work involved the entire internal anatomy of the blue crab, Callenectes sapidus. The anatomy of the blue crab is quite different from that of shrimp and isopods in two respects. The appendages of the crab take origin from the lateral portion of the thorax while the appendages of shrimp and isopods take origin from the ventral thorax. The crab has a very large thorax and a reduced abdomen while the abdomen is very evident in shrimp and isopods. Because of these major differences, Cochran's paper is not of great interest in this present paper.

Howard L. Sanders (1963) described the external anatomy of the cephalocarid, Hutchinsoniella macracantha. His description also included functional morphology and larval development. The discovery and description of this recently discovered primitive species was the basis for the construction of the Class Cephalocarida.

R. R. Hessler (1964) described the skeletomusculature of *Hutchinsoniella macracantha*. He compared *H. macracantha* with Branchiopoda, Mystacocarida, Copepoda, Ostracoda, Cirripedia, and Malacostraca. The trunk musculature of these groups is similar and may be homologous, indicating a basic skeletomuscular plan within the Crustacea. Anita and R. R. Hessler (1970) investigated the reproduction system of *H. macracantha*. This species is hermaphroditic, which while not necessarily primitive is very unusual in arthropods.

M. Glaessner (1956), H. K. Brooks (1962, 1969), and F. R. Schram (1968, 1969a, 1969b) have studied the fossil record left by the eumalacostracans. Glaessner contends that classification of living organisms is not an adequate basis for study of genetic relations, and although comparative functional morphology and embryology are fairly valid, fossil corroboration is needed. He concludes that "living malacostracous Crustacea are heterogeneous results of successful evolutionary trends with strong adaptive radiation and dispersal, undifferentiated lines, or survival of living fossils". Glaessner states that the "inherited division of the body into externally unsegmented anterior and a more or less isometameric posterior portion with corresponding differentiation of appendages into two groups which must be coordinated" is the main development in the evolution of this group.

Brooks (1962) observed that some paleozoologists and students of crustacean evolution assumed that the original crustaceans had a precoxal segment making the number of protopodal segments three. Sanders' study of _H. macracantha_ and Brooks' study of the fossil group Eocarida (1969) supposedly revealed that both had only one protopodal segment and cast doubt on the theory that crustacean ancestors had three protopodal segments. Brooks' comparison of eocarids with the more primitive living eumalacostracans such as the euphausians, lophogastrid mysidaceans, and syncarids has emphasized the supposed significance of the single segment in the thoracic protopod. Brooks theorized that this was a primitive crustacean characteristic that has been lost or supressed in the living forms. Schram (personal communication) has restudied the eocarid material and found evidence of two protopodal segments. This would make Brooks' theory of supression obsolete and would be in agreement with Calman's theory that the hypothetical malacostracan ancestor possessed two protopodal segments. It is thought that the eocarids must be the ancestors of the modern eumalacostracans with the exception of the Hoplocarida.

Schram (1969a, 1969b), studying the Middle Pennsylvanian Hoplocarida, stated that this group probably arose independently of the other eumalacostracans. The Hoplocarida possess features, "hoploid facies", distinct from the "caridoid facies" recognized by Calman (1909). The "hoploid facies" are as follows. The carapace covers the entire thorax; the cephalon is divided by a kinesis into an anterior procephalon bearing the stalked compound eyes and a triflagellate first antennae, and a post cephalon; the rostrum is movably articulated; thoracopods primitively all alike with a three segmental protopod, a one segment outer branch, and a four segment inner branch; abdomen is very large containing the bulk of gonads, digestive caeca, heart, respiratory organs, and the abdominal muscles; telson styloid with caudal furcae and the uropods blade-like. The structural differences between the Hoplocarida and the rest of the eumalacostracans are probably derived independently within the two groups. One difference between the Hoplocarida and the Malacostraca which is of particular interest in this present paper is that the hoplocarids possess three protopodal segments as found in the fossil Paleosquilla brevicoxa and various Pennsylvanian forms as well as the recents, and that the caridoid groups possess two protopodal segments (Calman, 1909).

Functional anatomical studies of the Order Isopoda is rather scarce. Most sources such as Van Name's monograph (1936) are general descriptions of external anatomy and habits. Van Name has made some general comments on the isopod musculature. He theorizes that the light, roughened areas present on the tergites are points of thoracic muscle attachment. Snodgrass (1965) gives some special attention to the thoracic appendages and the number of protopodal segments. Gruner (1954) also discusses the protopodal segments and the degree of incorporation of the coxa into the pleura of the thorax.

INTRODUCTION

Study of the crustacean thoracic skeletomusculature has been largely neglected. External comparative morphology of living forms was the original basis for phylogenetic study of the malacostracous Crustacea (Calman, 1909). Later contributions were based on highly refined methods of functional analysis, e.g. comparison of locomotary and feeding mechanisms (Manton, 1964). Glaessner (1956) began to study fossil malacostracans in relation to the living forms in order to reveal aspects of phylogeny and evolutionary adaptations in this group of crustaceans. Fossil evidence is of value in the study of malacostracans because the exoskeleton shows many details of internal organization, and because the entire evolution of eumalacostracans takes place in post-Cambrian time. However, fossil material available for investigation and comparison is not abundant.

A comparative study of crustacean thoracic skeletomusculature will add to the anatomical information already known and hopefully create a better understanding of crustacean evolution.

This present work examines the thoracic skeletomusculature of two species of peracarid eumalacostracans, a mysid, *Neomysis americana*, and an oniscid isopod, *Trachelipus* cf. *rathkei*. These two species were used because of their availability and their extremes of phyletic relationship. *N. americana* represents the more primitive branch of peracarids while *T.* cf. *rathkei* is very advanced and represents the highest development of Peracarida.

Four groups of thoracic muscles were studied. These are the coxal promotors and remotors, responsible for directing the anterior and posterior movements of the coxa, and the basal adductors and abductors, for the medial and lateral movements of the basis. The coxa and basis were chosen because of the observations made by Calman (1909), Brooks (1962,1969), Sanders (1957), and Schram (1968, 1969a, 1969b) regarding the number of thoracic protopodal segments. The number of protopodal segments and the muscle structure and orientation has shed light on phylogeny and evolution among the malacostracans (Brooks, 1969). A comparison of the thoracic skeletomusculature of *N. americana* and *T.* cf. *rathkei* was therefore made to reveal their skeletomuscular anatomy and to investigate evolutionary aspects of the skeletomusculature system.

MATERIALS

This investigation principally involved two species of peracarid malacostracous Crustacea. *Neomysis americana* material, belonging to the Order Mysidacea, was collected from bottom samples in Buzzard's Bay, Massachusetts, by Dr. Frederick Schram on July 19, 1967. The isopod material, *Trachelipus* cf. *rathkei*, Order Isopoda, Suborder Oniscoidea, was collected from wood piles in Falmouth, Cape Cod, Massachusetts, by Dr. Schram during the summer of 1967. Supplemental material was also used to help interpret the above. *Archaeomysis* cf. *grebnitzkii* was collected on July 7, 1971, at Lost Creek Beach, Oregon. Specimens of a euphausian, *Stylocheiron* sp., were taken by trawl from the Atlantis II, research vessel of Woods Hole Oceanographic Institution, at 35° W. 2° S, in April of 1967.

METHODS

Serial sections were made to study the material. All specimens were fixed in a solution of super-saturated mercuric chloride and glacial acetic acid in a ratio of 9:1, treated with a super-saturated[1] odine tincture to remove the mercury, and preserved in 70% alcohol. A standard paraffin method was used for embedding *Neomysis americana*. After sectioning *N. americana* at ten microns, the mounted sections were post-fixed in super-saturated aqueous picric acid for a period of 10 to 24 hours. The picric acid was then washed out in several baths of 70% alcohol containing a small amount of lithium carbonate in order to remove all yellow color left by the post-fixative. The post-fixed slides were transferred to a mordant of 2% potassium dichromate and were allowed to remain in this solution for three hours. After washing thoroughly with several baths of water to remove excess mordant, the sections were stained with Mallory's triple stain. This post-fixative and mordant procedure was found necessary in order to obtain the proper degree of staining.

Due to the thickness of the chitinous exoskeleton in Isopoda, the standard alcohol-paraffin method of tissue preparation did not allow sufficient penetration of the paraffin into the specimens. The following method developed by J. R. Baker at Oxford University was substituted. Whole specimens were placed in ethyl cellosolve for eight hours. The ethyl cellosolve was then replaced with fresh ethyl cellosolve which was allowed to remain eight hours to overnight. After the ethyl cellosolve had been completely drained off, the specimen remained in methyl benzoate until it sank to the bottom of the container. The methyl benzoate was most effective when the isopod was left in the solution overnight. When the methyl benzoate had been drained off the specimen, two baths of benzene, one hour each were necessary to complete the clearing process. A bath of paraffin chips and benzene in a 1:1 ratio is prepared and placed in an oven until the paraffin just melts. The benzene will evaporate if this bath remains in the oven for a long period of time. The isopods were placed in the paraffin-benzene in the oven for one hour. The specimens were carefully removed from the paraffin-benzene mixture and placed in two successive paraffin baths, two hours each, before finally embedding. The isopod material was then sectioned and stained in the same manner as the *N. americana* material.

Numerous longitudinal, frontal, and cross sections were made of each species in an attempt to reveal the origins, insertions, and orientation of the muscle groups under study. The slides were studied under a binocular microscope. Final drawings were compended of the thoracic muscles.

In addition to the serial sections of *N. americana* and *T.* cf. *rathkei*, dissected specimens and whole mounts stained with acid fuchsin, of these species were also studied. Whole mounts and serial sections of the euphausian, *Stylocheiron* sp., and another mysid, Archeomysis cf. grebnitzkii, were used for comparative and supplementary purposes. This was necessary because the tissue of much of the N. americana material had undergone some lysis prior to fixing, making the specimens difficult to section, stain, and study.

DESCRIPTION OF THE ANATOMY

Neomysis americana

The coxal promotor series and the coxal remotor series of *Neomysis americana* are composed of several bundles of muscles which take origin from the lateral and dorsal thoracic wall. The thorax wall has a scalloped appearance in the frontal section which seems to accomodate the thoracic muscle masses. Names have been given by the author to the promotor, remotor, adductor, and abductor muscles involved in the study on the basis of their position and function. The terms anterior, posterior, lateralis, and medialis refer to the position of the muscles in the thoracomere. Promotor, remotor, adductor, and abductor refer to the function of the muscles. The terms major and minor designate the size of the muscles. The promotor series of muscles will be discussed first, starting with the most anterior.

The anterior promotor lateralis major (Figs. 1,2) originates about half way up the anterolateral thoracic wall. This group is composed of two small, thin and spindle shaped bundles of fibers. As the fibers extend ventrally, they become smaller and fuse. The distolateral anterior coxa is the point of insertion.

Slightly ventral from the above muscle group, the posterior promotor lateralis major (Fig. 2) muscles take origin from the anterolateral wall of the thorax. This posterior bundle is slightly smaller than the anterior promotor lateralis major, but spindle shaped. The two fibers of the posterior promotor lateralis major extend ventrally and fuse with each other as they approach the point of insertion. Insertion is on the distolateral anterior coxal wall, just posterior to the insertion of the anterior promotor lateralis major.

The anterior promotor medialis major (Figs. 1,2) takes origin from the upper fourth of the anterior thoracic wall. The point of origin is dorsal and slightly posterior to the origins of the two promotor lateralis muscle bundles. There appear to be several muscle fibers composing the two large bands of the anterior promotor medialis major muscles. The two large bands follow the curve of the thorax wall and extend ventrally to insert on the anterior half of the coxa. The anterior-most bundle, or the one just posterior to the posterior promotor lateralis major, appears to have three fibers that insert more ventrally. The insertion of the three anterior fibers is slightly ventral and posterior to the insertion of the posterior promotor lateralis major. The fibers of the anterior promotor medialis major that insert ventrally are decidedly ventral and posterior to the insertions of the posterior promotor lateralis major. The more posterior bundle of the anterior promotor medialis major group has three or more fibers that occupy positions slightly posterior to the insertions of the anterior and posterior lateralis major muscle groups.

The posterior promotor medialis major (Figs. 1,2) takes origin from the dorsal thoracic wall, posterior to the anterior promotor medialis major. This promotor group also is composed of two large bands of muscles. These bands extend ventrally following the thorax wall and insert on the distoanterior portion of the coxa in lateral and medial positions posterior to the insertion of the anterior promotor medialis major.

The anterior promotor minor (Fig. 1) muscle takes origin half way up the lateral thoracic wall, posterior to the four parts of the promotor series previously mentioned and anterior to the remotor series. The anterior promotor minor is composed of approximately four muscle bundles which extend diagonally from its origin anteroventrally to insert just below the dorsal rim of the coxa.

The last of the promotor series, the posterior promotor minor (Fig. 1) takes origin in the posterior half of the thoracomere on the ventrolateral thoracic wall. This promotor extends diagonally across the coxa to enter on the distoanterior rim of the coxa.

The remotor series seems to follow a generally similar pattern to that of the promotors. There are several bundles of muscles comprising the series. The remotors will be discussed from posterior to anterior positions to exemplify the similarity of pattern to that of the promotor series.

The posterior-most group or posterior remotor lateralis major (Fig. 1) takes origin from the ventrolateral thoracic wall slightly above the coxa. There appear to be two small and thin muscle bundles. These remotors extend ventrally and insert proximally on the posterior surface of the coxa.

The anterior remotor lateralis major (Figs. 1,2) takes origin from the thoracic wall anterior and dorsal from the posterior remotor lateralis major. The anterior remotor lateralis major is slightly larger in size than the posterior remotor lateralis major. The muscle is cone or spindle shaped, becoming somewhat curved as it extends ventrally. The point of insertion is the lateroposterior surface of the coxa anterior to the insertion of the posterior remotor lateralis major.

Anterior to the remotor lateralis major muscles, the posterior remotor (Figs. 1,2) takes origin from the upper fourth of the posterolateral wall of the thorax. This remotor follows the curve of the thoracic wall extending ventrally. This group appears to have two large bundles of muscles. The posterior-most appears to insert somewhat dorsally with some fibers inserting possibly on the medial surface of the coxa. The anterior-most remotor of this group extends ventrally to insert on the distal rim of the coxa. Both groups insert anterior to the two remotor groups previously mentioned.

The anterior remotor medialis (Figs. 1,2) takes origin from the dorsal thoracic wall. This muscle is located anterior to the posterior remotor medialis major and posterior to the anterior promotor minor. Two large bands of muscles appear to comprise the anterior remotor medialis major. Both bands of muscles extend ventrally following the curve of the thorax, and insert on the distolateral coxal wall anterior to the insertion of the anterior remotor medialis major.

The remotor minor (Figs. 1,2) takes origin from the lateral thoracic wall in the medial part of the thoracomere, posterior and ventral to the anterior promotor minor. There are two or three muscle bundles which extend posteroventrally to insert on the posteromedial coxal wall.

The basal adductor, (Fig. 1) originates from the medial rim of the coxa. From the point of origin, the adductor extends ventrally to insert on the posteromedial rim of the basis.

The abductor major (Fig. 1) originates from the distoanterior wall of the coxa. The muscle is spindle shaped. The abductor major curves ventrally and anteriorly toward its point of insertion, the anterior wall of the basis.

The abductor minor (Fig. 1) originates from the medial wall of the coxa. This muscle is also spindle or cone shaped. The muscle moves ventrally and slightly anteriorly to insert on the lateral wall of the basis posterior and ventral from the insertion of the abductor major.

KEY TO *NEOMYSIS AMERICANA*

(Figs. 1,2)

APLMa	Anterior Promotor Lateralis Major
PPLMa	Posterior Promotor Lateralis Major
APMMa	Anterior Promotor Medialis Major
PPMMa	Posterior Promotor Medialis Major
APMi	Anterior Promotor Minor
PPMi	Posterior Promotor Minor
PRLMa	Posterior Remotor Lateralis Major
ARLMa	Anterior Remotor Lateralis Major
PR	Posterior Remotor
ARMa	Anterior Remotor Major
RMi	Remotor Minor
Ad	Adductor
AbMa	Abductor Major
AbMi	Abductor Minor

Fig. 1	Longitudinal Section, Lateral Aspect
Fig. 2	Longitudinal Section, Medial Aspect

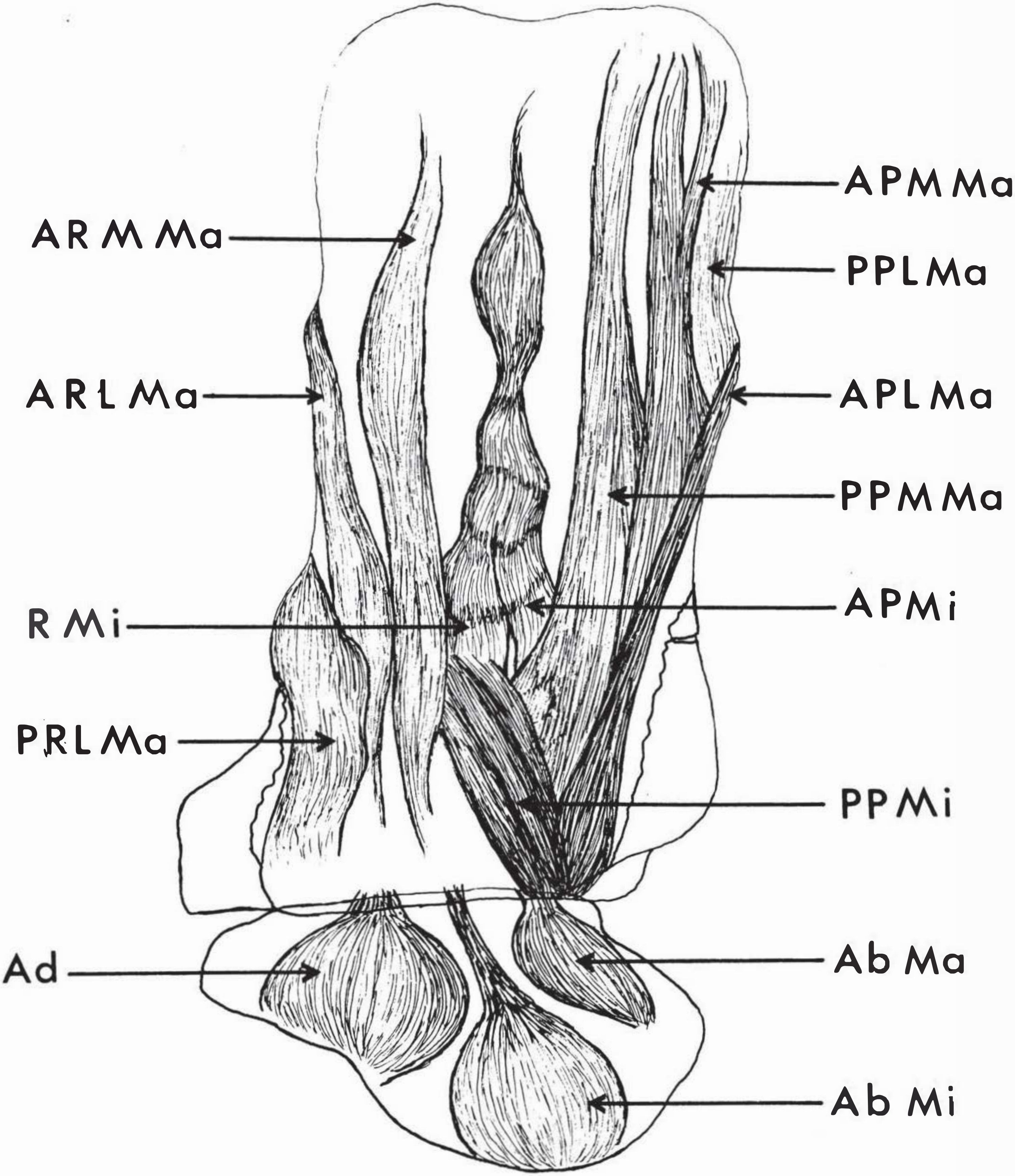
APMMa
ARMMa
PPLMa
ARLMa
APLMa
PPMMa
APMi
RMi
PRLMa
PPMi
Ad
AbMa
AbMi

Fig. 1

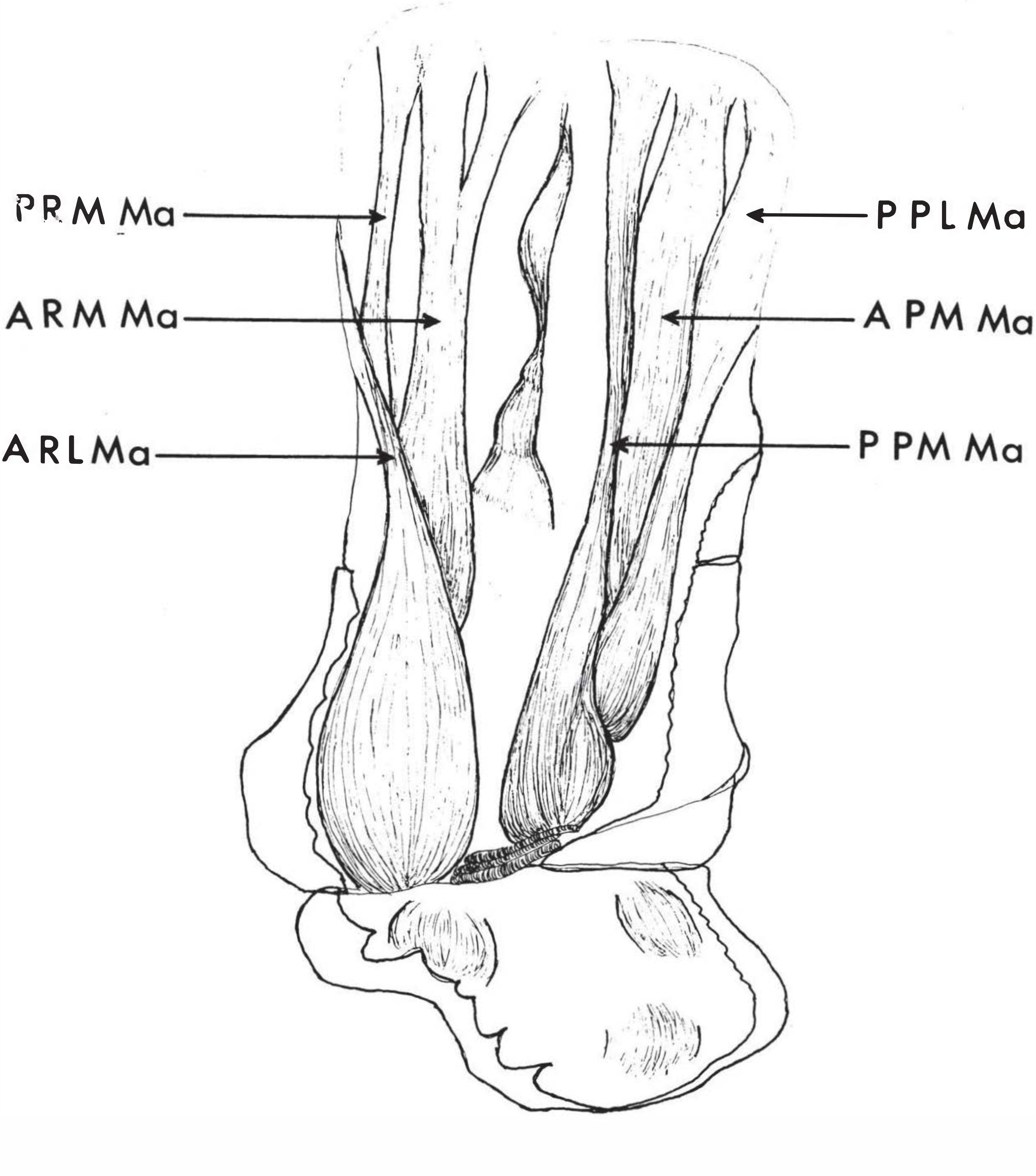

Fig. 2

Trachelipus cf. rathkei

Trachelipus cf. rathkei has a reduction in the number of functional protopodal segments. The coxa is incorporated into the pleura of the thorax and is not even defined by sutures. The coxa is therefore essentially immovable. The coxal muscles are evident in the pleura of isopods. These muscles are quite large and extend from the anterior and posterior dorsal thoracic walls to the ventral, lateral, and medial walls of the pleura. The tergites which range from gray and brown to blue possess intermittent light, rough areas. Some authors state that these areas are points of origin for the large muscle bundles that insert in the pleura and on the ventral thoracic wall. Although the coxal muscles are present and were observed in this study, it was not possible to distinguish these muscles on the basis of position and function.

The basal segment of the protopod is operated by the adductor and abductor muscles. These muscles are named by the author according to their location and apparent function. The adductor muscles will be discussed first beginning from the anterior position.

The anterior adductor major (Fig. 3) takes origin from an apodeme in the ventral medial portion of the thorax. This muscle extends diagonally from the thorax to the proximolateral basal wall.

The anterior adductor minor (Fig. 3) takes origin from the same apodeme as the anterior adductor major. The anterior adductor minor also extends diagonally from the thorax to the proximolateral basal wall. The anterior adductor minor inserts distally and laterally from the anterior adductor major on the proximolateral basal wall.

The posterior adductor major (Fig. 3) takes origin from the dorsal thoracic wall, distally and laterally from the anterior adductor major and minor. The posterior adductor major curves medially then laterally aa it extends ventrally into the basis. The point of insertion is on the posterior wall of the basis in the proximal portion of this protopodal segment.

The posterior adductor minor (Fig. 3) takes origin from the dorsal thoracic wall, slightly medial from the posterior adductor major. The posterior adductor minor crossss the posterior adductor major posteriorly. The minor muscle bundle then curves laterally and medially to fuse with the posterior adductor major just before the posterior adductor major enters the basis.

The posterior adductor medialis (Figs. 3,4) takes origin from the dorsal thoracic wall slightly medial from the posterior adductor major and minor. The posterior medialis extends distally along the medial wall of the basis. The point of ineertion is the distal posteromedial basal wall.

The abductor muscle series is composed of fewer elements. However, these elements are somewhat larger in size. The abductor series will be discussed from the anterior to the posterior positions.

The anterior abductor (Figs. 3,4) is a spindle shaped muscle taking origin from the lateral wall in the ventral portion of the thorax, actually the coxal portion of the thorax. As the muscle extends ventrally into the basis, it curves medially and then laterally to insert on the proximolateral basal wall.

The posterior abductor (Figs. 3,4) is a very large muscle taking origin from the thoracic wall dorsally from the anterior abductor. The posterior abductor curves as it extends ventrally into the basis. This muscle occupies the center portion of the basis, extending the full length of the basis. The point of insertion is the distal rim of the basis. It is possible that some very small fibers insert on the lateral and medial walls of the basis, but this is not known for certain.

The figures of *T.* cf. *rathkei* (Figs. 3,4) show a number of muscles present in the basis which have not been presented thus far in the description. These muscles insert in the ischium and are not responsible for movement of the basal segment, and so are not relevant to the present study.

KEY TO *TRACHELIPUS* CF. *RATHKEI*

(Figs. 3,4)

AAdMa	Anterior Adductor Major
AAdMi	Anterior Adductor Minor
PAdMa	Posterior Adductor Major
PAdMi	Posterior Adductor Minor
PAdM	Posterior Adductor Medialis
AAb	Anterior Abductor
PAb	Posterior Abductor

Fig. 3	Cross Section, Anterior Aspect
Fig. 4	Cross Section, Posterior Aspect

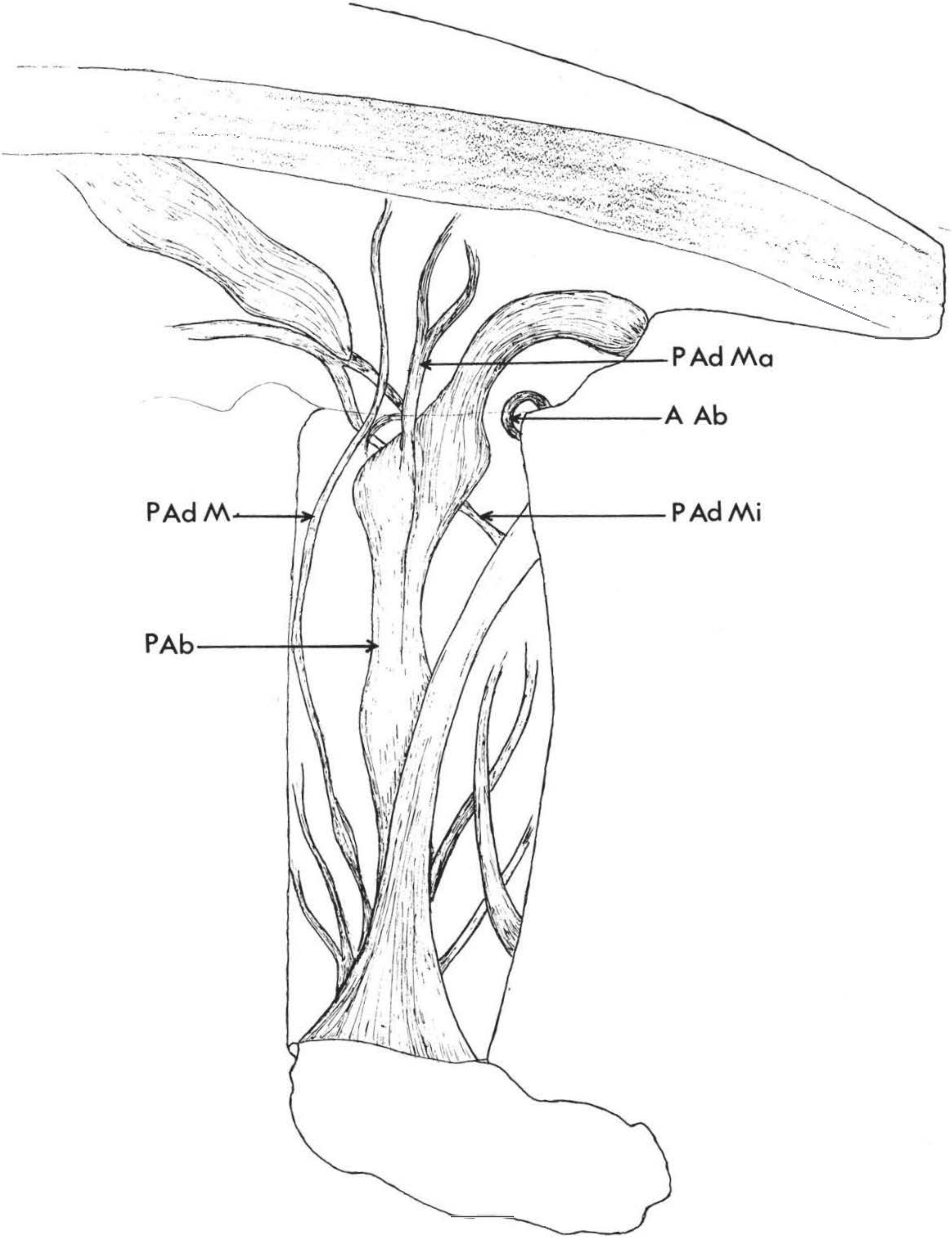

Fig. 3

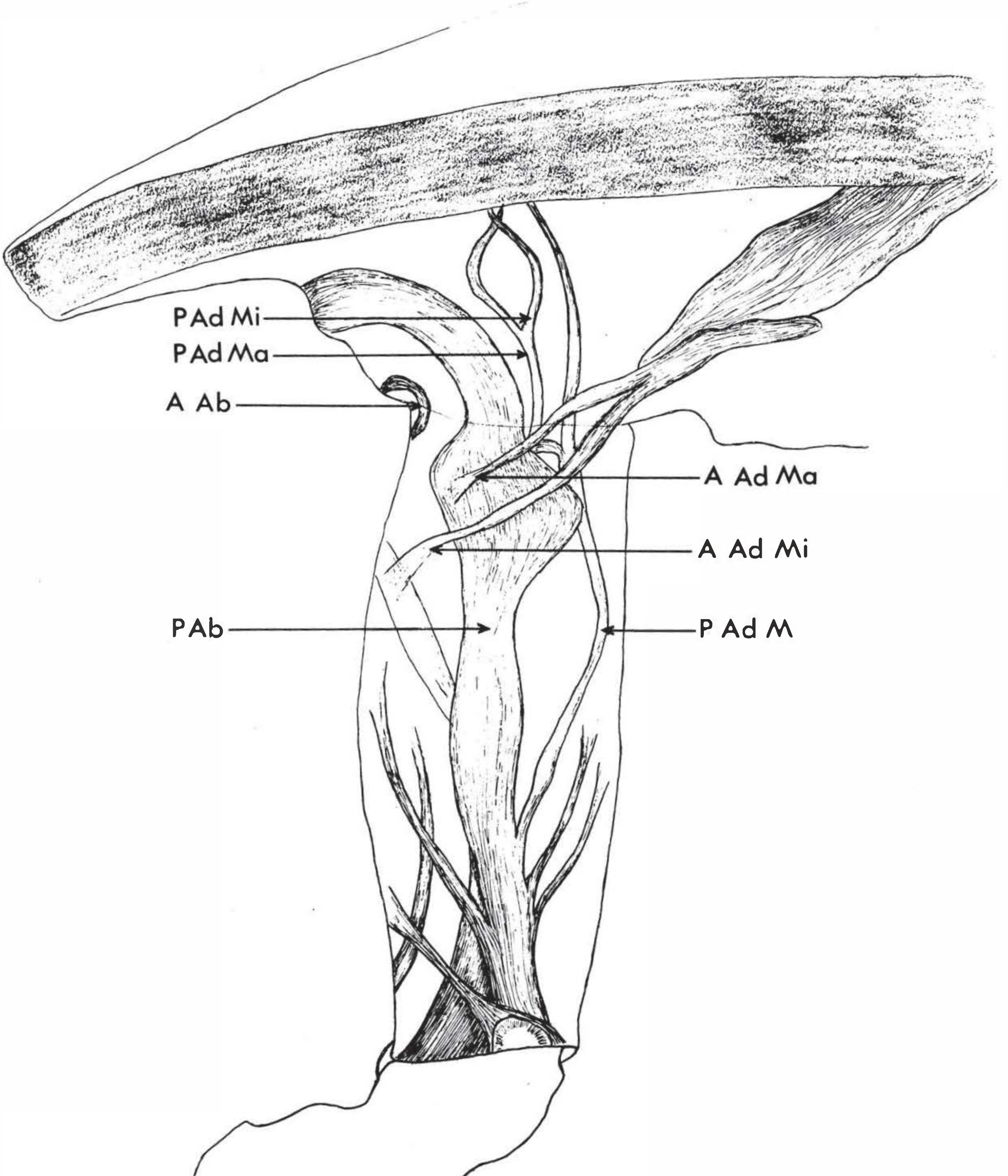

Fig. 4

DISCUSSION

A comparison of the preceding thoracic skeletomusculature descriptions of *Neomysis americana* and *Trachelipus* cf. *rathkei* reveals several major differences concerning the structure, orientation and function of the coxal promotors and remotors and the basal adductors and abductors. All of these differences are related to evolutionary changes in body structure. *Neomysis* is a strictly free swimming marine form and *Trachelipus* evolved into a raptant terrestrial species, although *Trachelipus* has gross external morphological characteristics almost identical to marine Isopoda.

The promotor series of *Neomysis* is composed of six elements, while the remotor series has five. All of these muscles insert in the coxa, are relatively large, and are well developed. In view of the number and size of the muscles, it appears that the two series may be almost equally antagonistic to each other. This would facilitate a strong forward and recovery stroke of the protopod which is necessary in swimming. Most of the promotors and remotors take origin high on the thoracic wall, extend ventrally and insert distally in the coxa. *Neomysis* is slightly flattened laterally for reduced resistance to water. The orientation of the coxal muscles is in compliance with this flattening or streamlining and swimming.

The basis in *Neomysis* is slightly smaller than the coxa. The number and size of the adductor and abductor muscles are much smaller in relation to the promotors and remotors. The coxa appears to produce most of the movement in the protopod, so the basal muscles probably function in support and in preventing tangling of the distal portions of the appendages. The predominate power stroke in swimming is remotion, using a dog-paddle-like stroke of the appendages.

In *Trachelipus* the protopodal muscles are very different from *Neomysis* in structure, orientation, and function. The coxa in *Trachelipus* does not directly function in locomotion. The coxal muscles are present, but are difficult to distinguish because the coxa is completely fused into the thorax. The large bands of coxal muscles are easily confused with the large bands of dorsoventral thoracic muscles. Some muscles extend from the dorsomedial and dorsolateral thoracic wall diagonally and ventrally respectively into the pleura. Gross dissection of *Trachelipus* material seems to confirm Van Name's (1936) theory that the origins of these muscles may be seen on the external surface of the tergites. The origins appear to be the light, roughened areas that form a pattern which is repeated in each segment, as in trilobites (Eldredge, 1971).

The function of the coxal muscles is uncertain. *Trachelipus*, like all free-living Isopoda, is capable of forming a ball when disturbed. The coxal muscles, along with some of the thoracic muscles may aid in this defense mechanism by pulling the pleura toward the body. Observation of live specimens, not available at present, would help determine the accuracy of this theory. Trachelipus is dorsoventrally flattened. From personal observation, the author has noted that the sternites do not overlap as much as the tergites. The coxal muscles may aid in keeping the body parallel to the ground and dorsoventrally flattened by holding the pleura almost rigid.

The adductor series in Trachelipus is quite extensive. The extremely large basis is held parallel to the body during walking. The adductor muscles pull the basis toward the body, and would give support for holding the body off the ground.

In the Phylum Arthropoda, all muscle tissue appears to be striated and has fibrillae very similar to those found in vertebrates (Warren, 1959). The fibers are long, cylindrical structures with many nuclei which may be peripheral as in man (Windle, 1960), or central. Electron microscopy has helped relate structure to function in arthropod striated muscle. The anisotropic (A) band or dark band appears to have more solid material than the isotropic (I) band or light band during muscle relaxation. All of the bands increase in density during muscls contraction. However, the I band and the dark line or Z line within the I band becomes denser than the A band during marked contraction. It is thought that some sarcoplasmic material may move to the part of the myofibril around the

Z line during actual contraction. Therefore the formation of contraotion bands around the Z line are not at the expense of the A band (Warren, 1959).

Crustacean muscles depend on nerve conduction rather than muscle conduction (Prosser and Brown, 1961). Early histologic studies demonstrated that each muscle fiber receives branches from two or more axons. The leg muscles of many crustaceans may have triple, quadruple, or quintuple innervation. The nerve endings have been found to occur in great numbers on the surface of the muscle fiber. The whole muscle may be thought of as one motor unit. Some nerve fibers may function as motor stimulators while others are inhibitory. Innervation patterns vary greatly in different species of crustaceans (Prosser and Brown, 1961).

Striations on the fibrillae may be seen very distinctly in some crustaceans. This is particularly true of *Trachelipus*. The striations are quite evident in the stained serial sections as well as in stained dissected specimens. This is not true of *Neomysis*. Striations are known to be present (Prosser and Brown, 1961), but they do not clearly show up in the stained serial sections or stained whole mounts. *Neomysis* moves rapidly through the water and such rapid movement would necessitate many contractions per second. In order to facilitate these contractions, one would postulate many fibrillae per muscle packed closely together, and would be more distinct because of the close arrangement. Therefore they would be easy to distinguish. *Trachelipus* is a slow moving species and there probably would not be as many contractions per second as in *Neomysis*, the therefore would not be as many fibrillae per fiber. Thus, the striations would be less distinct because they would be larger and farther apart. The fact that the striations showed up very well in *Trachelipus* when they should not have, and that the striations were not evident in *Neomysis* when they should have been, may be due to the fact that it is very difficult to fix and preeerve striated muscle tissue. The muscle tiseue of *Neomysis*, which had undergone some lysis prior to fixing, underwent several extra processes (post-fixing and mordant stages) with harsh chemicals which could have destroyed or altered the fine aspects of the tissue.

One of the most important differences between *Neomysis* and *Trachelipus* is the number of protopodal segmente. *Neomysis* has two functional protopodal segments while *Trachelipus* has one. Thie aspect is particularly interesting from an evolutionary standpoint. All malacostraca are considered to be derived from a common ancestral form possessing morphological characters designated by Calman (1909) as the "caridoid facies". Many characteristics are encompased in the term "caridoid facies", but one of special interest involves the number of protopodal segments. Calman (1909) recognized two protopodal segments present in the ancestral as well as the more recent forms. Primitive malacoetracans such as *Neomysis* do have two functional protopodal segments. More advanced forms such as *Trachelipus* have only one functional protopodal segment, the basis. From Calman's point of view, this would probably be considered as advancement by functional adaptation. The reduction of protopodal segments occurs in all Isopoda except the most primitive, Ascellota.

Calman's theory of ancestral morphology has recently been questioned. Sander's discovery of *Hutchinsoniella macracantha* (1955) has been the basis for a new theory of appendage evolution. *H. macracantha* is a very primitive species possessing only one protopodal segment. However, the overall segmentation of the leg is weak. Hessler's account of the internal anatomy of *H. macracantha*, particularly the trunk muscles, suggests that the malacostracan trunk musculature may be derived from a cephalocarid type.

Brooks' (1969) study of Eocarida bore support of the theory, opposed to Calman's, that malacostracans such as *Neomysis* and *Trachelipus* may have evolved from a primitive type possessing one protopodal segment. Schram (personal communication) has restudied the Eocarida material of Brooks, and contends that there are two protopodal segments present in these forms. This discovery would place the pygocephalomorph eocarids even closer to the lophogastrid mysidaceans morphologically and evolutionarily.

The differences between the pygocephalomorph eocarids and the lophogastrid mysidaceans are well developed furcal lobes and median articulated spines on the telson. These primitive characteristics may be supressed or lost in modern forms. Some of these characteristics, such as the presence of a furca, which are retained in adult eocarids appear to be present to a lesser degree in euphausianss such as *Stylocheiron* sp. (Euphausians, through decapods are probably closely related to the mysids.) Thus the basis for the eocarids being ancestral to the caridoid eumalacostracans is that embryologically the caridoids have features that are present in the adult eocarids.

The isopods superficially appear to be an exception to the above concept. *Trachelipus* has two protopodal segments, however only the basis is functional. During the evolution of *Trachelipus* this characteristic probably appeared as an adaptation for benthic, littoral and finally terrestrial existence.

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