The Structural Morphology of Walking Mechanisms in Eumalacostracan Crustaceans

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THE STRUCTURAL MORPHOLOGY OF WALKING MECHANISMS IN EUMALACOSTRACAN CRUSTACEANS

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CONTENTS

Nearly all eumalacostracan orders possess members that are capable of walking by means of their pereopods. This study analyses the skeletomuscular mechanics that make walking possible. It includes at least one member of each order, except for the Stomatopoda: Isopoda (four suborders), Tanaidacea (two suborders), Cumacea, Spelaeogriphacea, Amphipoda (two suborders), Mysidacea (two suborders), Theromosbaenacea, Decapoda and Syncarida. In each case an attempt was made to find primitive or generalized forms. The movement of living animals was observed wherever possible. Because the condition of the endopodal podomeres tends to be relatively stereotyped, primary attention was focused on the base of the limb, that is, body, coxa and basis.

All taxa have some features in common. Most importantly, the orientation of the podomeres is such that the entire limb lies in a plane (the 'limb plane'), whose integrity is preserved in normal locomotion. However, the limb plane can bend to compensate for bottom irregularities, and for the benefit of grooming, feeding, swimming or burrowing. In walking, 'extensible strut' motions (Gray 1944) result from extension and flexion within the limb plane, and 'rowing' motions are accomplished at the limb base.

Rowing motions are complex, involving tilting and rotation of the limb plane and require special adaptations. Two major patterns exist. In eucarids and syncarids, the coxa forms a gimbal, where the dicondylic body–coxa articulation allows promotion/remotion, and the dicondylic coxa–basis articulation allows abduction/adduction. In most peracarids, body–coxa articulation is either immobilized or capable of limited abduction/adduction, and coxa–basis articulation is monocondylic and can perform a complete suite of motions. Exceptions of varying degrees exist within tanaids and amphipods, and the mysidaceans show an intermediate morphology.

I suggest that the percaridan condition is apomorphic and that the evolution of the midventral thoracic marsupium was the driving force for change. Because the oostegites are coxal outgrowths, coxal promotion/remotion as a part of normal walking would disrupt the marsupium. As a result, the coxa lost this function, and coxa–basis articulation evolved to a morphology that would allow promotion/remotion as well as abduction/adduction.

INTRODUCTION

This study considers the evolution of walking mechanisms in malacostracan crustaceans, one of the dominant arthropodan taxa of marine communities. It began with a far more limited and seemingly unrelated intention, that of learning how swimming mechanisms evolved in deep-sea janiroidean isopods. The most primitive janiroideans, the Janiridae, are ambulatory and best represented in shallow water (Hessler *et al.* 1979). Because of the convenience of working with shallow-water forms, and because such a study must include an analysis of the ambulatory system from which swimming evolved, in the summer of 1975 I began an investigation of walking in *Janiralata* spp. (figure 1).

That study revealed a pereopodal skeletomuscular system that was fundamentally different from that of the more commonly studied decapod crustaceans (Young 1959; Snodgrass 1965; Macmillan 1975). Curiosity about the taxonomic distribution of the two systems prompted a survey of key members of the Eumalocostraca. This showed that some form of the system seen in *Janiralata* occurs throughout the Peracarida, but is absent elsewhere. It appears, then, that the evolution of this great division involved additional anatomical changes to those previously recognized (lacinia mobilis, oostegites, maxilliped).

This paper documents the various pereopodal skeletomusculatures, paying special attention to the coxa and basis, where the pattern of differences bears a special relationship to a fundamental adaptive feature of peracaridan evolution, the marsupium. *Janiralata* may not be the ideal focus for subsequent comparisons, but it is used both because it received my greatest attention and because it will be the basis for a study of the evolution of swimming in the Janiroidea. The discussion includes a consideration of the requirements imposed on a malacostracan walking limb and an analysis of how malacostracans satisfied these requirements, the evolutionary sequence that might have given rise to the pattern we see today, and a hypothesis that could explain why evolution proceeded as it did.

The larger framework of locomotory mechanics is described in works of Gray (1968), Manton (1977), R. McN. Alexander (1968, 1971), Hughes & Mill (1974), Wainwright *et al.* (1976), which are excellent accounts and guides to the earlier literature.

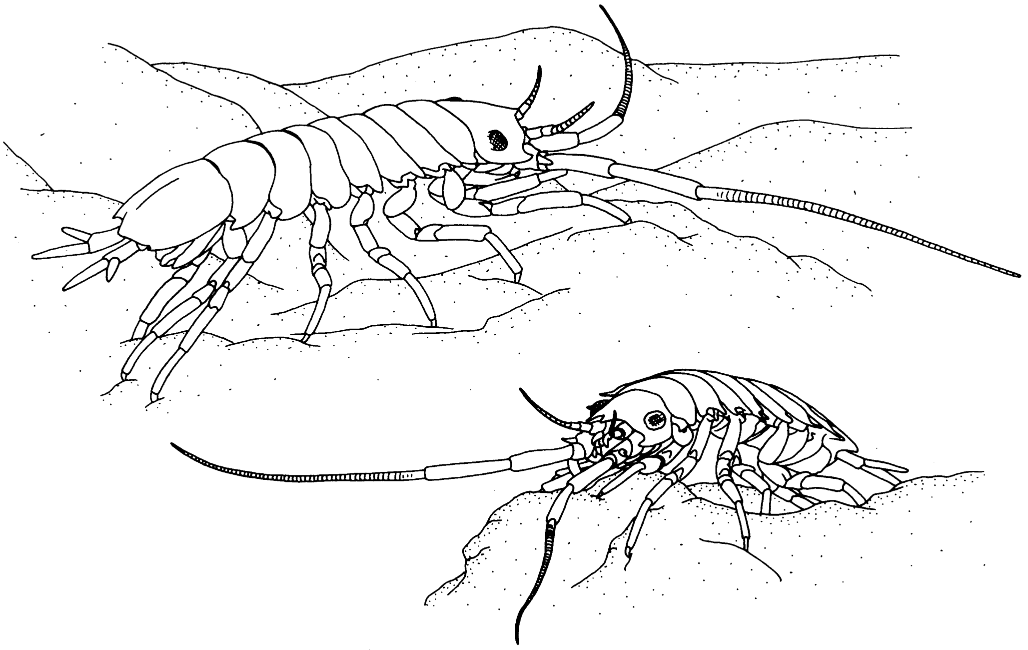

FIGURE 1. *Janiralata*. Two views showing typical stance.

METHODS

Nearly all the descriptions of musculature are the products of gross dissection, a technique whose utility for small animals is greatly underrated. Specimens stained with Mallory's phosphotungstic haematoxylin were studied in terpineol after dehydration. The most useful had not been fixed, but simply killed and preserved in ethanol. In these, only the muscle accepted the stain well.

Cuticular structures (body wall, hinge structures, ligaments, tendons) were easily studied after dissolving all other tissue with warm KOH and staining in the second half of Mallory's triple stain. The presence of $CaCO_3$ interferes with staining and was removed by pretreatment in acid alcohol. Terpineol was the preferred immersion medium.

Manipulation of preparations with a needle often revealed the potential range of movement of which a limb was capable, but whenever possible specimens were observed alive, for it is more critical to know what an organism is willing to do than what its carcass tells us it can do.

All drawings were made with the aid of Wild M5 or M20 drawing apparatus. The drawings of stationary *Janiralata* were made from specimens immobilized with clove oil. The technique, taught to me by Paul Illg, consists in putting a drop of clove oil in the water containing the animal. After several hours, the animal will stop moving without falling into a limp, unnatural position. At this point, concentrated formalin can be added, preserving the animal in a life-like posture.

DESCRIPTIONS

Isopoda

The Isopoda are currently divided into nine suborders: Flabellifera, Valvifera, Oniscoidea, Asellota, Anthuridea, Microcerberidea, Phreatoicoidea, Gnathiidea and Epicaridea. Instead of a systematic study of each group, a variety of conveniently available taxa was chosen, only the Epicaridea being deliberately avoided because their pelagic and epiparasitic existence might have resulted in modifications that would be difficult to compare to the morphology of ambulatory forms.

Janiralata (*J. occidentalis* and *J. solasteri*) was chosen because it exhibits the basic asellotan plan. Additional observations were made on the behaviour and external anatomy of the more primitive *Asellus aquaticus* from Lund, Sweden. *Ligia pallasii* and *Idotea wasnasenskii* were available in abundance at Friday Harbour. They are large, easy to dissect and are generalized representatives of their respective suborders, the Oniscoidea and Valvifera. Supplementary observations were made on the behaviour and external anatomy of the oniscid *Porcellio scaber* from Lund. I also studied *Crenoicus* sp. (Nicholls 1944) from Mt Kosciusko, Australia, because the fossil record of the Phreatoicoidea clearly indicates it is a taxon having a separate existence since the Carboniferous. These four isopodan suborders not only represent some of the most important taxa, but also encompass a breadth of morphological types and lineages that have been distinct for a considerable amount of time.

Janiralata, *Asellus*, *Porcellio*, *Ligia*, *Idotea* and *Crenoicus* are so similar to each other in pereopod morphology and walking mechanics that they can be considered together. All, except *Crenoicus*, were observed alive.

General structure

In none of the isopods considered here does the body show extreme specialization (figure 1). The head, seven pereonites and pleon are broadly joined to each other and freely articulated. The body is dorsoventrally flattened; the pereonites are similar in size and shape (figure 2) and are much wider than long. The appendages of the pereon serve primarily for locomotion, except for pereopod I, which often is used in feeding and is involved in reproduction and cleaning. In the brooding female, pereopods I–IV bear oostegites, forming a midventral marsupium. The pereopods are attached to the ventral surface of the body at the lateral margins (figure 3). They are similar in appearance although the first is often somewhat more heavily built for manipulative functions. The posterior pereopods are often more elongate.

Each pereopod is so constructed that a single plane (the 'limb plane') passes through the long axis of all podomers (figure 3). More graphically, a detached limb would lie flat on a plane surface. Anterior pereopods are directed forward, and posterior ones backward, although to varying degrees (figures 1, 2, 4). In asellotes and the oniscoideans, the most anterior pair angles more or less anteriorly, and going successively backwards, the angle of the limbs becomes more lateral and then gradually comes to occupy a posterior direction. The angle of the limb plane with vertical also shifts for successive limbs. For both anterior and posterior pereopods, the surface of the plane facing the midline is tilted upward. It is vertical only on the middle pereopod (figure 3: per. IV), and then only when it is directed laterally. In *Idotea*, anterior and posterior pereopods have a stronger lateral orientation, contributing to the animal's ability to walk on

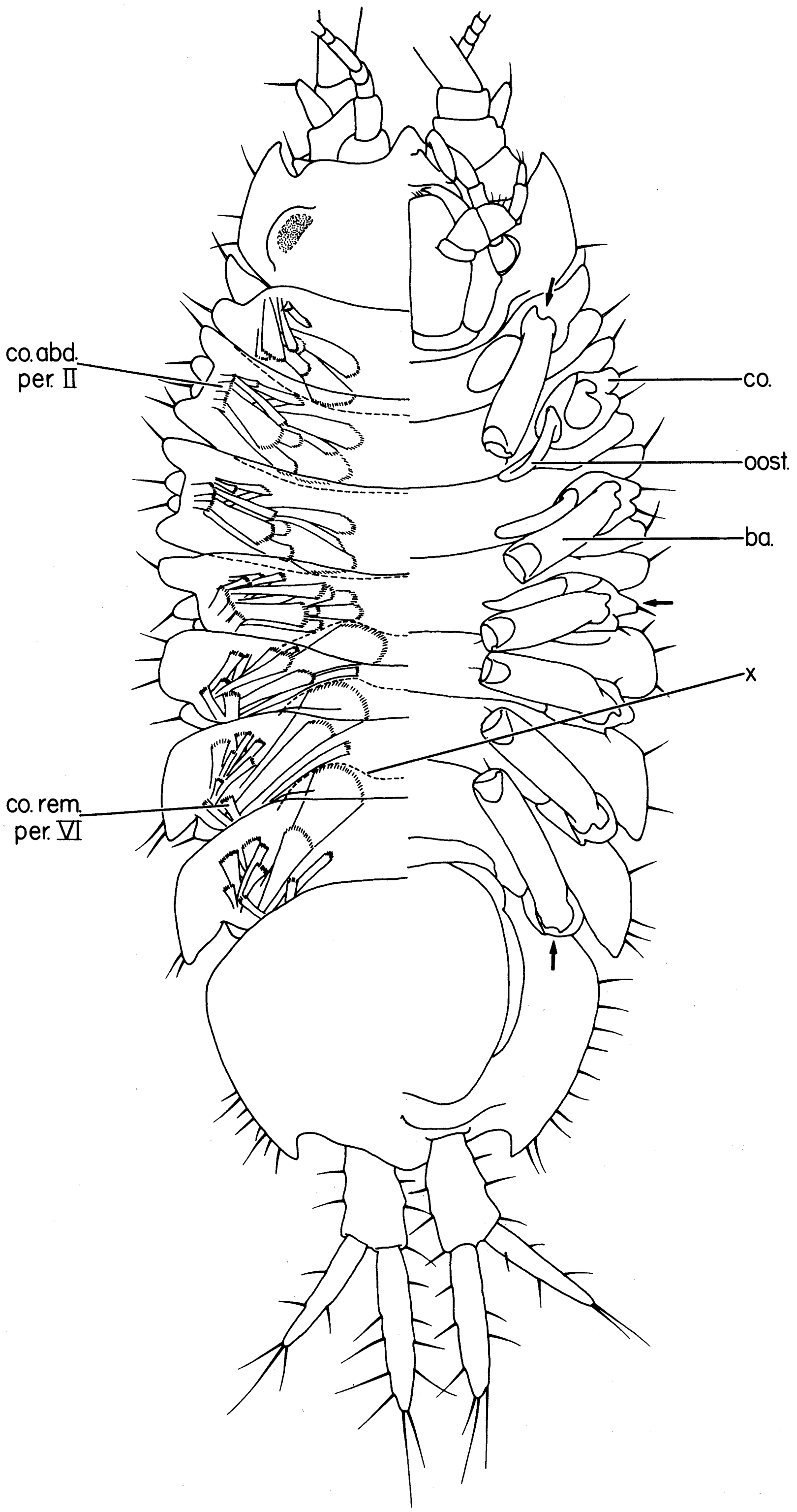

Figure 2. *Janiralata*, preparatory female. The right half is a ventral view showing the attachment and orientation of the pereopods. Pereopods I, III–VII are broken off beyond the basis, and per. II is missing beyond the coxa. Arrows at per. I, IV and VII point to the co.–ba. condyle (figure 8) and serve to illustrate the nearly 180° change in orientation of the limbs. The left half is a dorsal view showing the extrinsic pereopodal musculature. The coxal abductor/remotors (co.abd., co.rem.) also show the change in orientation. Symbol x, anterior edge of tergite of per. 7.

plant fronds. In *Crenoicus*, the pereopods do not display a serial gradation of orientation; pereopods I–IV are oriented forward, and pereopods V–VII backward.

Where it can be discerned, the coxa (co.) is very short (figures 3, 5). The other podomeres (basis (ba.), ischium (i.), merus (m.), carpus (c.), propodus (p.), and dactylus (d.)) are usually elongate, although the dactylus is often little more than a clawed process (figure 3). The basis is always especially elongate. The proportions of the other podomeres are similar among the various isopods (figures 6, 7) except in *Idotea*, where the carpus is reduced to a merus-like structure, and the propodus is enlarged to form the proximal member of a subchela (figure 7*a*). Again, this is an adaptation for grasping plant fronds. In the other taxa, carpus and propodus are similar in length and tend to be longer and more slender in posterior limbs, whose only function is ambulation.

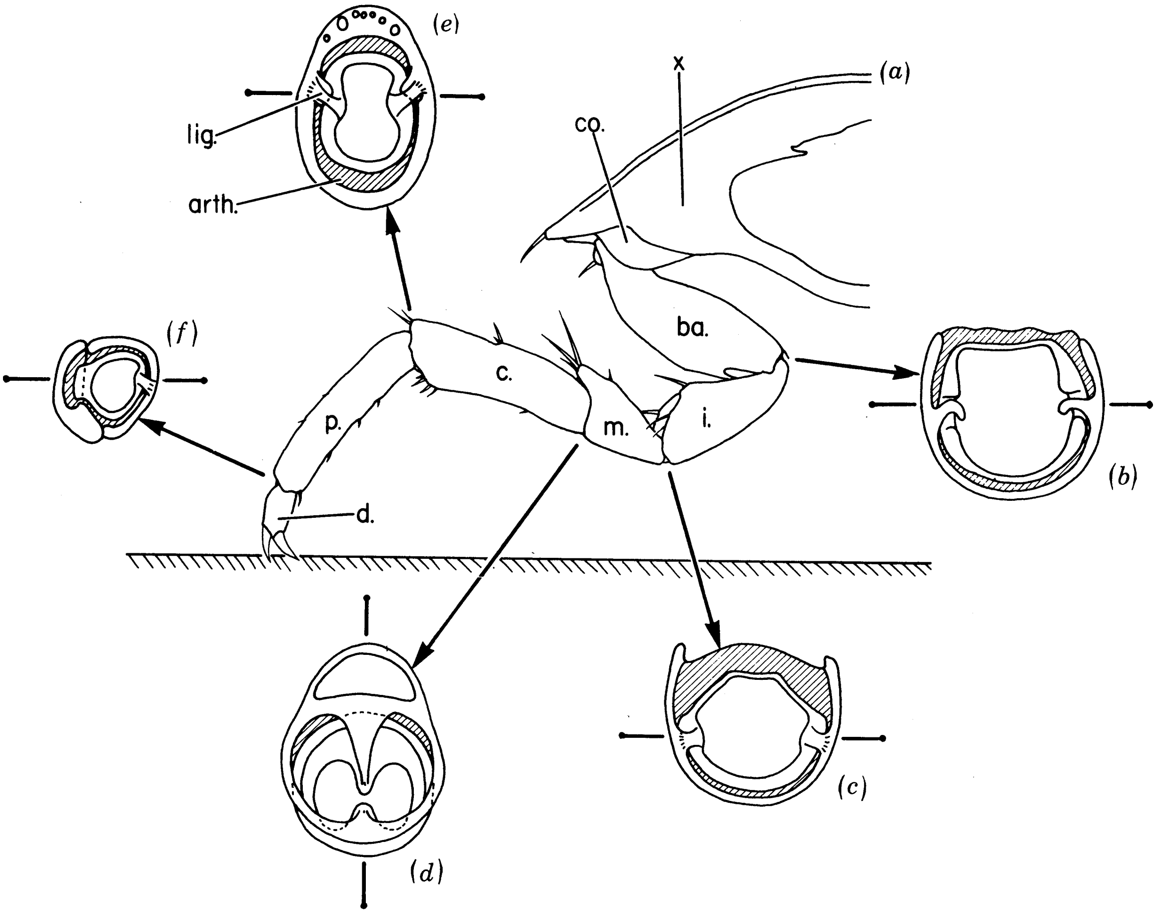

FIGURE 3. *Janiralata*, pereopod IV, right. (*a*) Anterior view showing stance. The entire limb lies in a plane (the 'limb plane'). (*b*–*f*) Articulations of ba.–i., i.–m., m.–c., c.–p. and p.–d., respectively. Each illustration is a plan view in the plane that passes through both condyles, approximately perpendicular to the axis of the podomeres. The outer structure is the more proximal podomere. The arthrodial membrane is indicated by diagonal shading. With ba.–i., unlike the other articulations, the condyles are not joined by ligaments, thus facilitating sacrificial dismemberment at this point. Symbol x, limb 'stalk' (p. 253).

In a resting position, there are three major flexures of the pereopod: between coxa and basis (co.–ba.), basis and ischium (ba.–i.), and carpus and propodus (c.–p.) (figure 3). The axis of the coxa points ventrolaterally. The basis bends inward, so that its long axis points

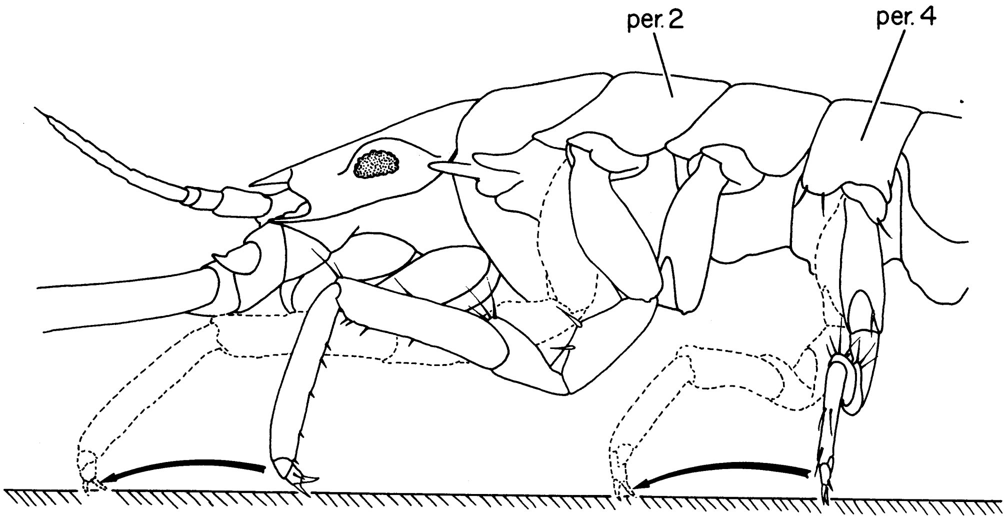

FIGURE 4. *Janiralata*, anterior half, showing promotor motion of pereopod II and IV. With per. II extension within the limb is the dominant action, whereas with per. IV it is rotation and promotion at co.–ba. and perhaps promotion at body–co.

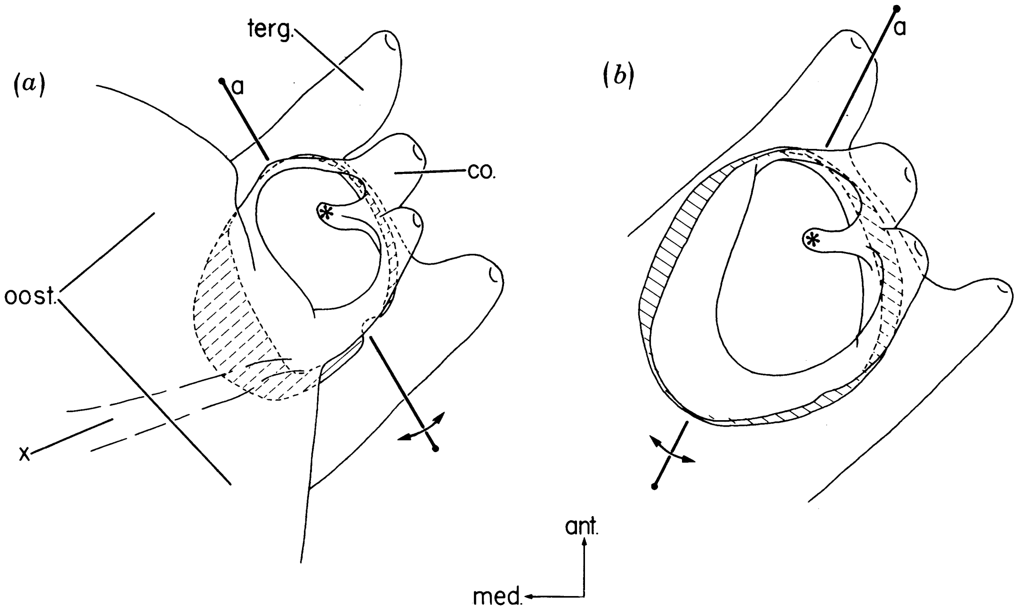

FIGURE 5. *Janiralata*, pereopod II, left. Ventral view with basis removed. (*a*) Brooding female with well developed oostegites. (*b*) Juvenile female lacking oostegites. Asterisk marks co.–ba. condyle. Note major shift in body-co. hinge line (a) when oostegite is present. Symbol x, reinforced shaft of oostegite.

ventromedially, except in *Crenoicus*, where it extends straight downward. The ba.–i. flexure is sufficiently great that the ischium angles laterally. The merus is bent very slightly dorsad, and the carpus is at best bent slightly ventrad. From this essentially laterad trend of merus and carpus, the propodus angles abruptly ventrolaterally, and the dactylus is bent at various angles to hook into the substrate. The overall effect is that the limb first extends ventromedially, then bends sharply to extend laterally and curve downward to the distal tip.

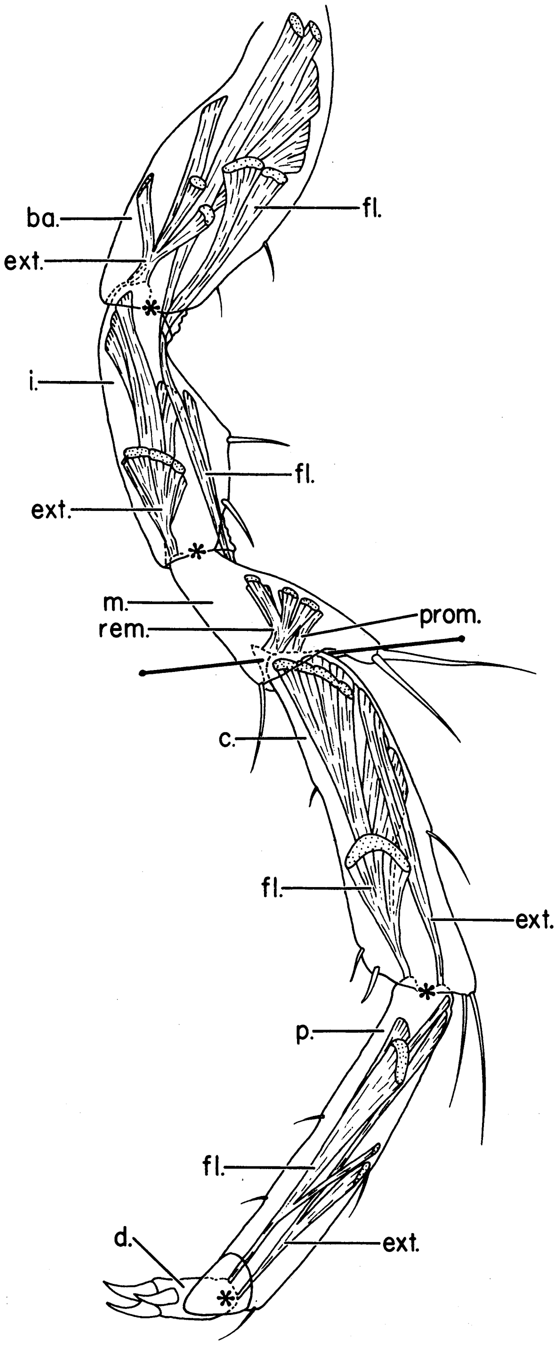

FIGURE 6. *Janiralata*, pereopod IV, right, coxa not included. Plan view showing intrinsic musculature. Asterisks represent posterior condyles. The anterior condyles are behind the posterior ones, defining hinge lines perpendicular to the limb plane. Only m.–c. has a hinge line parallel to the limb plane. The carpal promotor muscle is nearly equal to the remotor that lies almost exactly behind it.

Limb anatomy: articulations and musculature

As with general shape, the articulations and musculature of the limbs are much the same in the isopods studied and vary little throughout the limb series within an individual. The general plan in *Janiralata* will be described first, and then variations will be mentioned.

Each limb arises somewhat ventrally from the distal end of a broad stalk-like extension of the trunk segment, that is, the opening that connects the body cavity of adjacent trunk segments is only about half the actual width of the animal (figure 3). This 'stalk' (figure 3: x) angles anteriorly on anterior pereonites, laterally on pereonite 4 and posteriorly on posterior pereonites (figure 2), thus causing much of the serial variation in limb orientation. Because of this variation, the usual terms of orientation (lateral, posterior, etc.) do not apply uniformly to all the limbs. To circumvent this, all descriptions will be made as they would apply to pereopod IV. Appropriate transformations for other limbs should be made by using figures 1, 2 and 4 for reference.

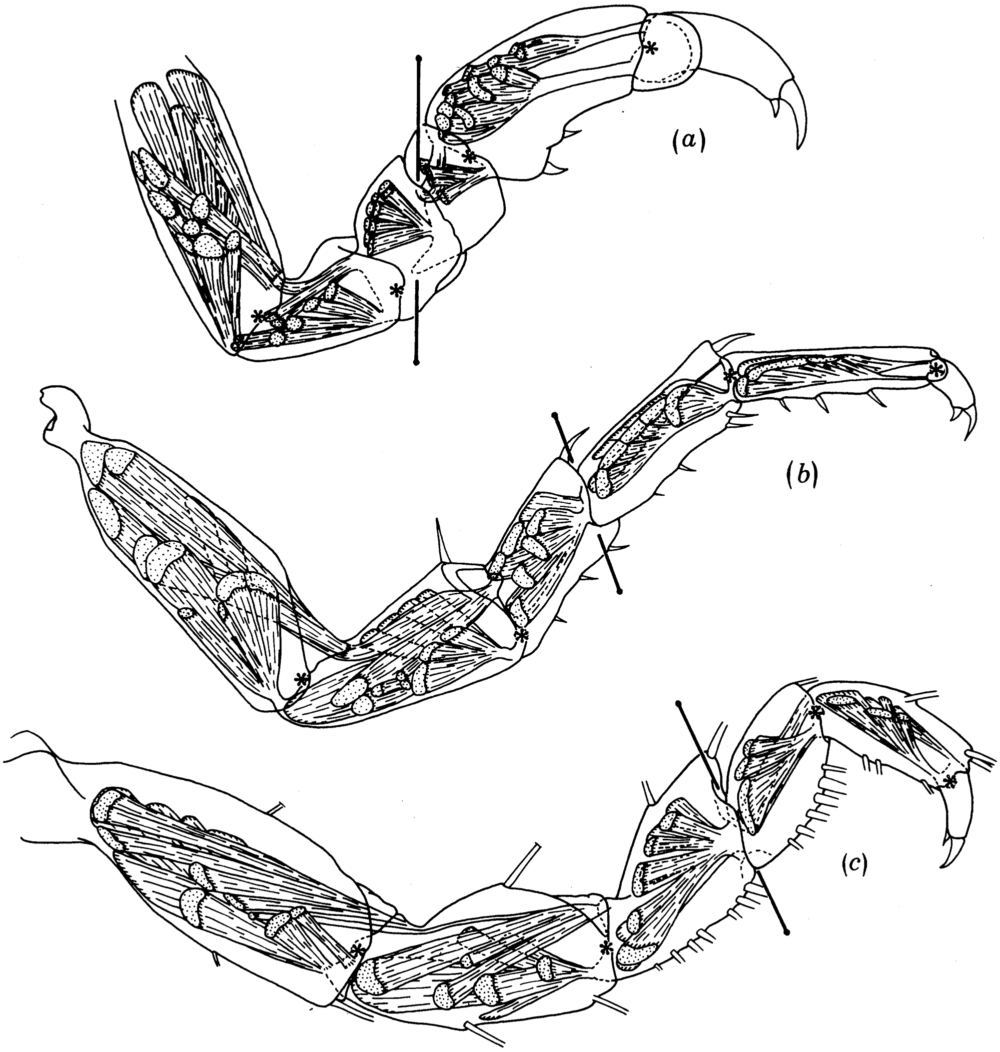

FIGURE 7. Isopodan pereopods, right, coxae not included. See figure 6 for further explanation. (*a*) *Idotea*, pereopod III. (*b*) *Ligia*, pereopod VI. (*c*) *Crenoicus*, pereopod III.

The coxa is united to the body (body–co.) by a narrow encircling arthrodial membrane (figures 5*b*, 8*a*, *b*: diagonal shading). This membrane is broadest anteriorly and posteriorly. Posteromedially, there is a poorly developed hinge point. Anterolaterally, there is none, although the arthrodial membrane is so narrow that it might act as one, thus defining an anterolateral–posteromedial hinge line. Two muscle groups cause coxal motion. Thin sheetlike bundles of very short fibres (figure 8*b*: co.rem.) extend from the tergum to the

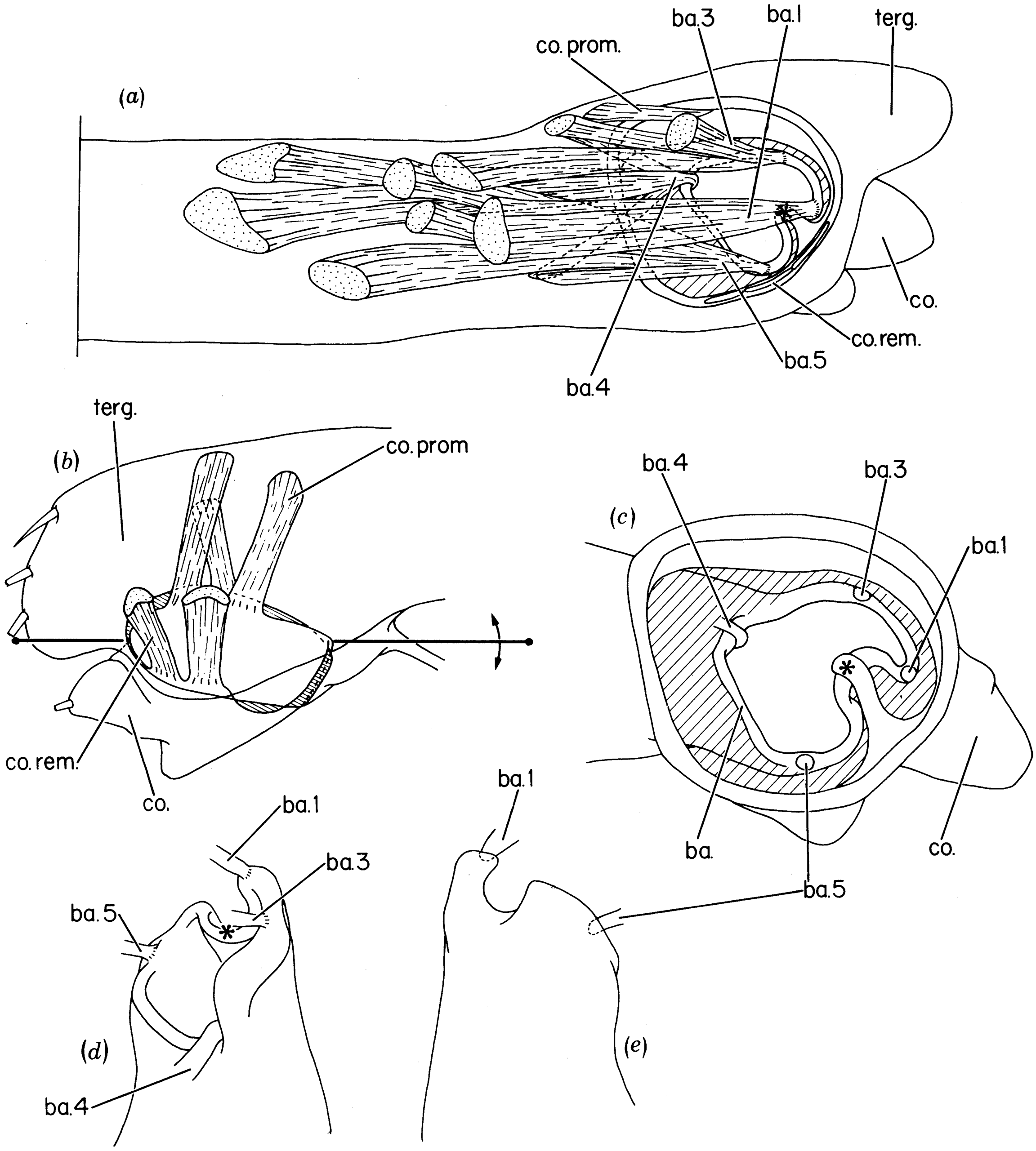

FIGURE 8. *Janiralata*, skeletomusculature of coxa and basis. (*a*) Pereopod IV, right, mature male. Dorsal view through tergite at attachment of muscles of basis, which are all extrinsic. The many muscle bundles converge to only four insertions, designated ba. 1, 3–5. The coxal promotor is drawn fully, but only the insertion area of the remotors is shown. (*b*) Pereopod V, left, mature male. Dorsal view through tergite of attachment of coxa and coxal extrinsic musculature. (*c*) Pereopod IV, right. View through coxa at co.–ba. articulation. (*d*, *e*) Pereopod IV, left. Proximal end of basis in anteromedial and posterolateral views, respectively.

posterolateral margin of the coxa. Opposing this are from one to three somewhat larger bundles (co.prom.) that originate on the anterior face of the segment and run ventrolaterally to insert on the medial edge of the proximal margin. Compared to other articulations of the limb, the coxal musculature is feeble, and the narrow arthrodial membrane limits the arc of motion. However, some promotion and remotion is possible.

The articulation of the basis with the coxa (co.–ba.) (figure 8*c–e*) and its musculature (figure 8*a*) are the most complicated in the limb. Nearly the entire perimeter of this articulation is supplied with a wide, flexible arthrodial membrane (figure 8*c*: diagonal shading). A rigid finger-like invagination of the coxal cuticle extends inwardly from the posterolateral margin and attaches tightly to the proximal margin of the basis by means of a heavy, but flexible ligament. At the point of attachment, the margin of the basis is folded inward so that the fulcrum is near the longitudinal axis (figure 8*d*, *e*).

The broad arthrodial membrane combined with the single, centrally located fulcrum allows considerable movement in all directions, including some rotation about the long axis. Because of infolding of the fulcral portion it is possible for opposing pairs of muscles inserted on other portions of the margin to power movement in any direction (figure 8: ba. 1, 3–5). Were the fulcrum not folded in toward the axis, abduction would not be possible unless some special lever had been provided, such as with the mandible of *Ligia* (Snodgrass 1950; Manton 1964).

In *Janiralata*, the muscles that move the basis insert on the proximal margin in four primary groups (figure 8*a*, *c–e*). The insertions are roughly 90° apart and form two opposing pairs. One pair includes a lateral abductor (ba. 1) and medial adductor (ba. 4), and the other contains an anterior promotor (ba. 3) and posterior remotor (ba. 5). The insertion tendons attach to several long muscle bundles, most of which radiate dorsomedially to origins on the tergite. One or two small bundles of muscles 4 and 5 originate on the sternum, and a bundle from muscle 3 originates on the anterior body wall.

The geometry of this, in combination with the cuticular arrangement, would cause a flexible array of movements of the basis, depending on the combination and degree of contraction of the various muscles. There is one main limitation. The arrangement is not well suited for promotion/remotion because proximally the basis is bent in such a way that most bundles of muscles 3 and 5 (and 1 and 4) are oriented at strong angles to the podomere's axis. Further, external transverse coxal ridges anterior and posterior to the articulation restrict promotion/remotion of the basis. This configuration results primarily in rotation of the basis when muscles 3 or 5 contract. Because the tip of the dactylus, which contacts the substrate, is far removed from the axis of the basis, even slight rotation of the basis gives the limb tip a considerable excursion. Also, contraction of those lateral bundles of muscle 3 or 5 that do angle steeply to more dorsolateral origins would have a promotor/remotor component.

All the more distal podomere articulations except that between merus and carpus (m.–c.) follow a common pattern. Two ligamentous condyles on opposite sides of the articulation form a hinge line that runs through the centre of the articulation, perpendicular to the limb plane (figure 3). There is an extensive, flexible arthrodial membrane, and where extreme flexion takes place the sclerotized portion of the podomere may even be emarginated, such as at the distolateral end of the basis. Tendons insert in two opposing positions on the distal podomere (figure 6). In only one case does a bundle extend beyond the proximal podomere; a flexor of the merus goes through the ischium to take origin on the proximal portion of the basis. All these articulations are well designed for flexion and extension in the limb plane.

The m.–c. articulation does not permit much movement because the arthrodial membrane is small and the base of the carpus is telescoped into the end of the merus (figures 3, 6). It has a dorsoventral hinge (i.e. in the limb plane) formed by heavy dorsal and ventral ligaments. Two opposing fans of short muscles (figure 6: rem., prom.) originate at the merus and insert in the proximal carpal margin, away from the hinge line. This allows limited bending of the distal half of the limb out of the limb plane, as was occasionally seen on the living animal. The limb plane can bend at c.–p. because of weak hinge ligaments; although limited disarticulation is possible the muscles are not arranged to power such movement.

The pattern varies little within the limb series. The origins of coxal muscles shift somewhat throughout the series. In pereopods I–III an additional muscle (ba. 2) is split off from muscle 1 and inserts without a well developed tendon on the margin of the basis just anterior to it. On pereopods V–VII a single, additional, small, short muscle (ba. 7, not illustrated) originates on the posterior portion of the proximal coxal margin and extends anteroventrally to insert on the medioposterior margin of the basis, between muscles 4 and 5.

There are also variations in the size of the muscle groups (figure 2). Of special interest are those of the coxa and basis, which are least bulky in pereopod IV and largest in pereopod V–VII, where muscle 4 of the basis and the anteromedial muscle of the coxa are particularly well developed. This is interesting in that the adduction by muscle 4 and the promotion by coxal muscles of pereopods V–VII would pull the limb anteriorly as in the recovery movement of forward progression or the power stroke in moving backward. Since such bulk is unnecessary for recovery movement, its enhancement probably reflects the need for backward retreat.

Janiralata exhibits one significant developmental difference. In brooding females with fully developed oostegites, the medial portion of the coxal ring of the oostegite-bearing limbs is much narrower, and the body–co. arthrodial membrane is correspondingly wider (figure 5*a*). As a result, the articulation point has shifted laterally so that the hinge line is essentially anteroposterior. This change is abrupt; the preceding female instar is as in males and younger females (figure 5*b*), even though they possess rudimentary oostegites.

The other isopodan taxa are similar to *Janiralata*. The most important difference is the firm fusion of the coxa to the body in *Ligia* and *Idotea*, although the suture may still be distinct (figures 9*a*, 10*a*). *Crenoicus* shows an intermediate condition, with the coxa of pereopods I–IV fused and of V–VII articulated. This allows more limited movement than in *Janiralata*, but the movement is promotion–remotion as in corresponding limbs of *Janiralata*. Short, thin sheets of promotor muscles have the same attachments as in pereopods V–VII of *Janiralata*, but no remotors were seen. A puzzling observation in *Crenoicus* was that of feeble sheets of muscle from the lateral margins of the coxa of pereopods II–IV to the tergum shortly above. In view of the obvious immobility of this joint, there is no ready explanation. Except for *Asellus*, where it is as in *Janiralata*, the condition of the coxa in brooding females was not studied in other isopods.

The co.–ba. on all taxa is the same as in *Janiralata* except for small variations (figures 9–11). The basal margin anterior to the single condyle is produced in *Ligia* and *Idotea* to extend the lever arm of muscle 1 (figure 10*b*, *c*). *Crenoicus* lacks additional muscle groups, but muscles 2 and 7 are distinct on *Ligia* and *Idotea*. *Ligia* lacks the ventral bundle of muscle 5, but some of its limbs and those of *Idotea* possess a corresponding small bundle from muscle 3 (figure 9: ba. 6). *Ligia* and *Idotea* have dorsoventrally flattened bodies, as does *Janiralata*, and in all, the basis is curved so that its long axis is at a distinct angle to the average orientation of the muscles. In

Crenoicus, however, the body is approximately round in transverse section, and here the basis is not bent. Instead, the muscles arise on the sides of the body cavity (as opposed to the dorsal surface) and extend straight down to the limb, whose long axis is oriented in the same direction as the fibres. In *Idotea* (figure 9), some muscle bundles with common origin have such disparate orientations, that separate functions seem likely. The unique orientations of ba. 6 and ba. 7 are examples. If this is so, then it is also possible that even bundles that radiate in approximately the same direction have at least partial autonomy in innervation and specific function.

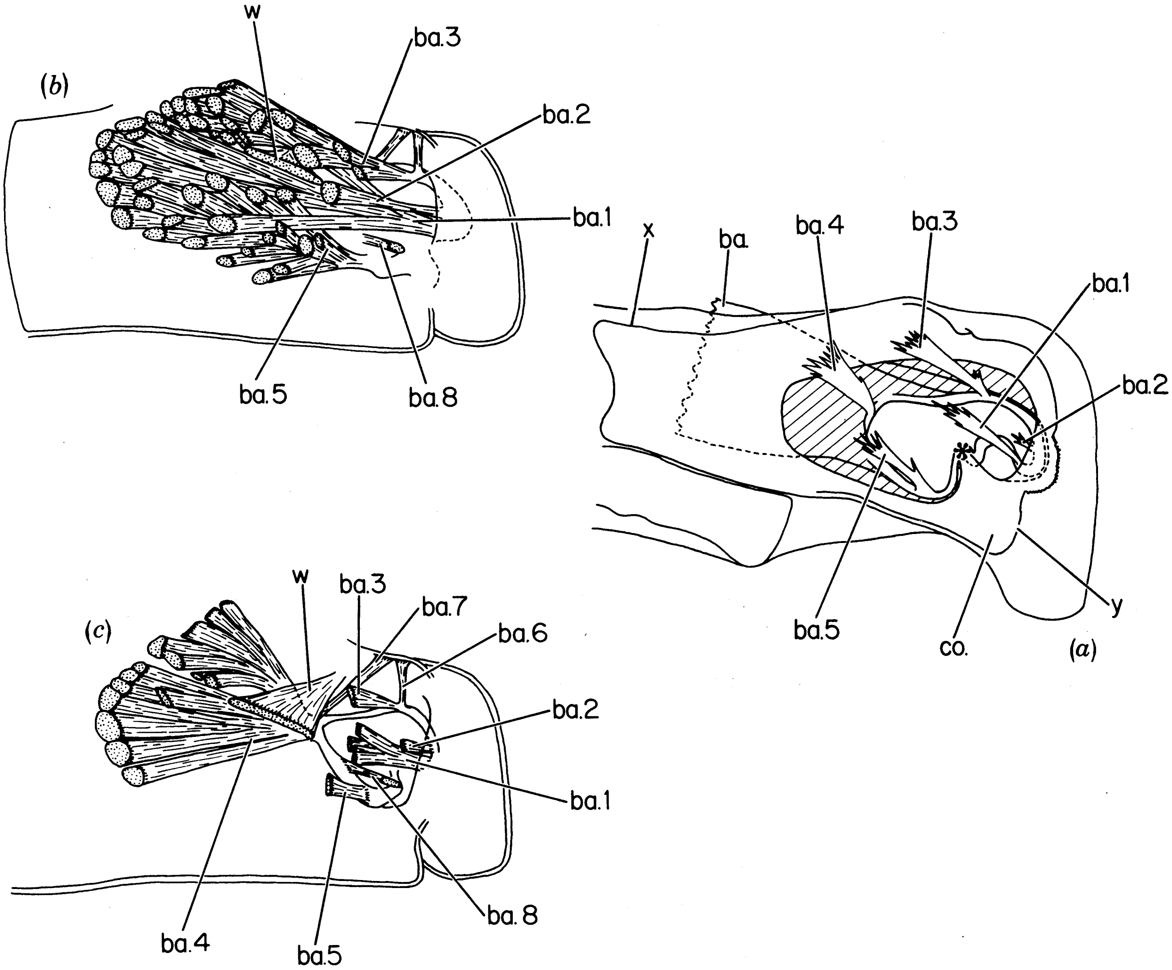

FIGURE 9. *Idotea*, pereopod V, right. (*a*) View through tergite at attachment of limb. The coxa is fused to the pereonite, forming the epimere and replacing much of the sternite. (*b*, *c*) View similar to (*a*), showing basal musculature. (*b*) Muscles shown completely, but origins not clearly indicated. (*c*) Main masses of ba. 1–3, 5 removed and insertions on proximal edge of basis more specifically illustrated. Symbols: w, a coxal tensor muscle; x, suture of coxa with sternite; y, suture of coxa with tergite (partially cut away to give view of attachment of basis).

All the more distal articulations and their musculature are essentially as in *Janiralata* (figure 6). This applies to the nature and orientation of the hinges and the extent of arthrodial membranes as well as to the position of muscle attachments. While there is considerable variation in the number and size of bundles composing an individual muscle, this does not affect the basic movement of the joint. Some similarities between the four suborders deserve emphasis. In all, the m.–c. articulation is the only one that does not have a hinge line perpendicular to the limb plane, and here it is parallel to the plane. Movement of the carpus is always powered by a pair of symmetrically positioned lateral muscle fans. The p.–d. articulation is usually buttressed on one side by a large, flat plate. In all, the only case where a muscle does not originate in the proximal podomere of an articulation is that of one bundle of the meral flexor which extends through the ischium into the basis, to originate in the proximal portion of the basis.

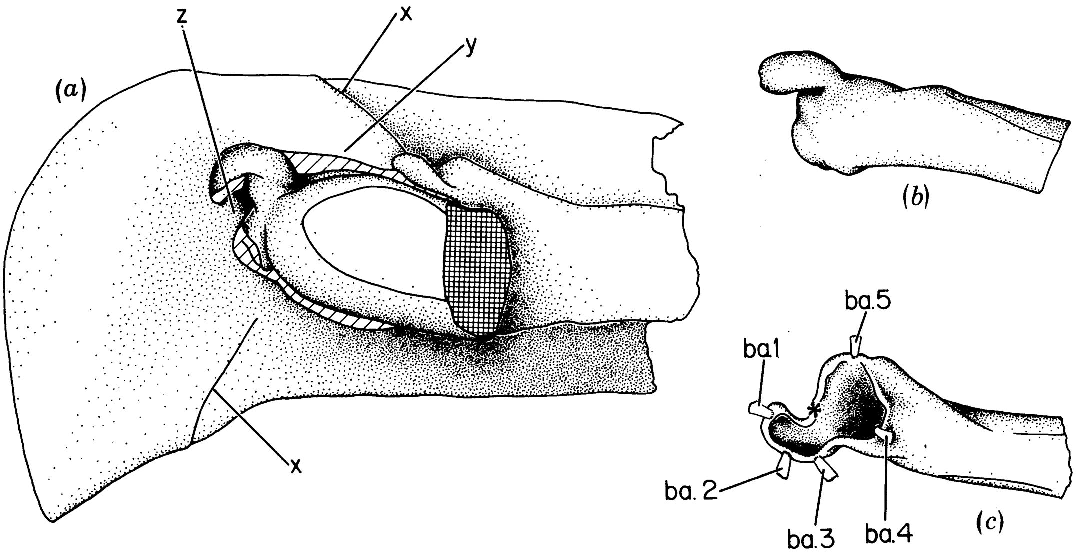

Figure 10. *Ligia*, articulation of coxa with basis. (*a*) Pereopod VI, right. Ventrolateral view of articulation externally. Crosshatching covers severed end of basis. (*b*, *c*) Pereopod IV, right. Proximal half of basis in lateral and medial views, respectively. Symbols: x, suture of coxa with sternite: y, anterior ridge, which limits promotion of basis; z, process bearing coxal portion of co.–ba. condyle.

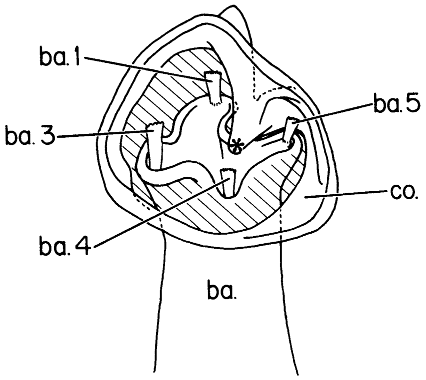

Figure 11. *Crenoicus*, male, pereopod VI, right. View through coxa of co.–ba. articulation (as in figure 8*c*).

Two further variations need mention. In *Crenoicus*, an additional single muscle bundle originates on the distal wall of the basis and inserts on the proximal margin of the ischium not far from the hinge. This does not signify a greater range of movement at this articulation because both condyles are strong. The muscle therefore acts as an accessory extensor, although its position is inefficient for this function. In all taxa but *Idotea*, the flexor bundles of the propodus insert via a single midventral tendon. In *Idotea* there are two symmetrical tendons, each servicing muscle bundles from its respective side. This perhaps relates to the extreme abbreviation of the carpus.

Walking

In *Janiralata*, with some exceptions detailed below, podomeres remain in essentially a single plane (the limb plane) in movements associated with walking (figures 3, 4, 12). The angle of the limb plane changes with respect to the principal axes of the body, as does the length of a straight line drawn between the base of the pereopod and its tip as the limb extends and flexes. In forward motion the limbs move in different ways because each has a different orientation. The spectrum of movements is best seen by comparing an anteroposteriorly oriented pereopod, such as pereopod II with the laterally directed middle pereopod, pereopod IV.

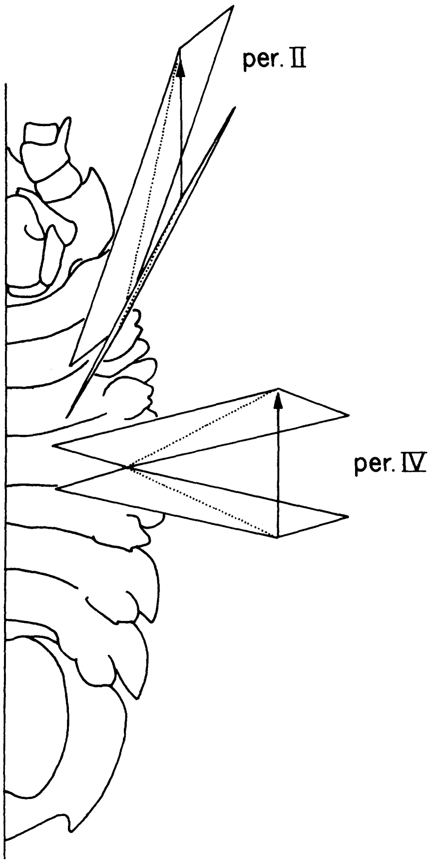

FIGURE 12. *Janiralata*, left, ventral. Pereopods II and IV are represented as limb planes during promotion (figure 4), to emphasize the components of movement. With pereopod IV, rotation and tilting of the limb plane dominate; extension plays little part, indicated by no change in the length of the dotted line running from the limb's origin to its contact with the substrate. On pereopod II, the lengthening of the dotted line emphasizes the importance of extension; here, where the limb plane is more nearly parallel to the direction of motion, rotation and tilting are present, but play a lesser role.

The dominant motions of pereopod II are extension and flexion (figures 4, 12). The limb tip is lifted from the substrate, stretched forward, primarily through extension at co.–ba., ba.–i. and c.–p., but also at i.–m. and p.–d., and set down again so that the tip of the dactylus again makes contact. The limb is then flexed, primarily at the same articulations, and this pulls the animal forward. Here flexion is the propulsive motion, and extension is used in recovery. With posteriorly directed appendages, such as pereopod VII, flexion and extension are also the dominant motions, but their roles are reversed.

In pereopod IV, flexion and extension play minor roles. The limb begins its power stroke with the tip of the dactylus at a level anterior to that of the limb base. The limb swings backward so that at the end of propulsion the dactylus is now posterior to the limb base. Simple geometric considerations show that the straight-line distance between limb tip and base is longer at the beginning and end of the power stroke than halfway through it, and it is for this that a small amount of flexion and extension must be employed. More important components in the movement of pereopod IV are tilting and rotation (figure 12). In the forward position, the anterior face of the limb plane is tilted upward and forms an acute anterior angle with the longitudinal axis of the body. In the backward position, a symmetrically opposite orientation obtains. While these motions are most obvious with a limb whose plane is transverse to the direction of motion, they are inescapable components in the motion of any appendage whose limb plane deviates from parallel to the direction of motion. Thus, all limbs display tilting and rotation to some extent, both being accomplished solely at the base of the limb, i.e. at co.–ba. and less universally at body–co. (see below).

Occasionally, slight bending of the limb plane was seen as the m.–c. or c.–p. articulations flexed to the side, but such motions are not a normal part of the walking cycle. Rather, they appear to be compensatory adjustments related to standing on irregular surfaces and to give play to the limb when its tip is accidentally dragged across the bottom or bumps into an obstruction. They may also have a more regular role in grooming movements.

The preceding analysis has been of an animal moving forward. However, the animal can obviously twist and turn, step sideways, and even walk rapidly backward when it encounters an obstacle or is menaced from the front. Under these circumstances, the components of limb movement alter to the extent that the direction of motion deviates from anteriad. That is, in moving sideways, pereopod IV operates primarily by means of flexion and extension, and pereopod II now requires rotation. Turning is facilitated by lateral bending of the trunk, but the amount that can be achieved is modest. While each limb has a dominant motion, all may be called upon to conduct the complete suite of motions, thus demonstrating a functional basis for the fact that all the limbs are essentially alike.

Janiralata spends a considerable amount of time grooming itself. Most of this effort is spent on the antennae, but it also cleans the pereopods. This is achieved by bending the head downward, and even flexing the body ventrally when a posterior limb is involved, and placing the limb between the maxillipeds. The limb is pulled back out in one clean stroke, presumably being brushed with the setae of the mouthparts. This function entails moving the limb into an unusual position, and is achieved primarily by means of bending at the co.–ba. articulation.

The animal at rest may employ more than one stance. When undisturbed, its ventral surface is at a distance from the ground; when disturbed, the animal crouches by means of limb flexion. By extending the intermediate pereopods and flexing the trunk dorsally, the more anterior pereopods are in a position to reach up for climbing onto higher surfaces.

In walking and most of the other movements, motion was undetectable between the coxa and the body, but this would be difficult to see in such a small, rapidly moving animal. That the coxa must move is shown by its articulation and musculature (figure 8*b*). The coxa of *Asellus aquaticus* is articulated to the body in the same way. Observation on these larger animals did reveal promotion/remotion at the body–co. articulation. When cuticular preparations of both *Janiralata* and *Asellus* were manipulated with a probe, body–co. proved to be the site where bending occurred during promotion/remotion of pereopod IV. Indeed, a coxal flange along the anterior edge of co.–ba. prevents more than a limited amount of promotion by the basis itself. Thus, the complex suite of motions made at the base of the limb stems from a stereotyped promotion/remotion at body–co. in combination with more complex movements at co.–ba.

This does not apply to the oostegite-bearing limbs of brooding females, where the body–co. hinge line is anteroposterially directed (figure 5*a*). Here coxal promotion/remotion is no longer possible and is replaced by an easily visible rhythmic abduction/adduction. This motion, reminiscent of breathing in terrestrial vertebrates, moves the oostegites in a way that causes oscillation in the volume of the brood chamber, and this ventilates its contents.

In spite of this important change, brooding females walk in the same way as other individuals, with the motions once conducted by body–co. now occurring at co.–ba. This is confirmed by the fact that the coxal flange that restricted basal motion in males and non-brooding females is essentially absent from the oostegite-bearing pereopods of brooding females.

The oniscids and valviferan move their pereopods in the same manner as asellotes, yet here the coxa is completely fused to the body (figures 9*a*, 10*a*). Extension and flexion within the limb plane is accomplished at articulations distal to the basis. Changes in the orientation of the limb plane occur only at the co.–ba.

Cooperation on the part of one large, slow individual of *Porcellio* gave the opportunity to study bending of the limb plane at m.–c. and c.–p. With the latter it is as in *Janiralata*, but with m.–c. I saw muscularly powered bending forward as pereopod IV was set down at the end of the recovery stroke. At the end of the power stroke, it bent backward. This lengthened the stride of the limb. It did not always occur, nor would it play this role in anteroposteriorly oriented limbs. It is possible that asellotes use this articulation in the same way.

Summary

The movements of the isopodan pereopod are dominantly extension and flexion within a limb plane. These motions are implemented by well-developed dicondylic hinges and a pair of opposing muscle masses for each articulation. The strong but flexible articulation between coxa and basis, with its attendant large array of possible muscle combinations provides flexibility for the necessary rotation and tilting motions of the limb plane that play such an important role in normal movement. The coxa is capable of some promotion/remotion in some taxa, but its role is taken over by co.–ba. in brooding females, or in all stages in other taxa. Where body-co. is fused, the coxa is no longer a podomere from a functional point of view, but an integral part of the trunk.

Tanaidacea

The pereopods of the tanaidaceans considered here, *Sphyrapus anomalus*, from the Norwegian Sea, *Apseudes spinosa*, from the Swedish west coast, and *Leptochelia savignyi*, from Puget Sound, are alike in most major features. Primary attention is given to *Sphyrapus* because it belongs to the more primitive suborder Monokonophora, and furthermore it was studied in detail before specimens of *Apseudes* became available. *Apseudes* and *Leptochelia* are burrow and tube dwellers, respectively. *Sphyrapus*, a deep-sea species, probably lives much like *Apseudes*.

Pereopod I is not discussed because it is highly modified in tanaidaceans and does not participate in locomotion. Unlike the isopods, pereopods II–VII in *Sphyrapus* are divided into two distinct groups. The limb plane (which may be gently curved) of pereopods II–IV is oriented anteromedially–posterolaterally. As with the isopods, the orientation is more transverse at the middle of the limb series. Beyond the basis, articulations are as in the isopods; all are dicondylic, with hinge lines perpendicular to the limb plane, except for m.–c., where it is in the plane. Thus, all except m.–c. limit movement to extension and flexion within the limb plane. C.–p. can be disarticulated to allow motion perpedicular to the limb plane, but this is passive.

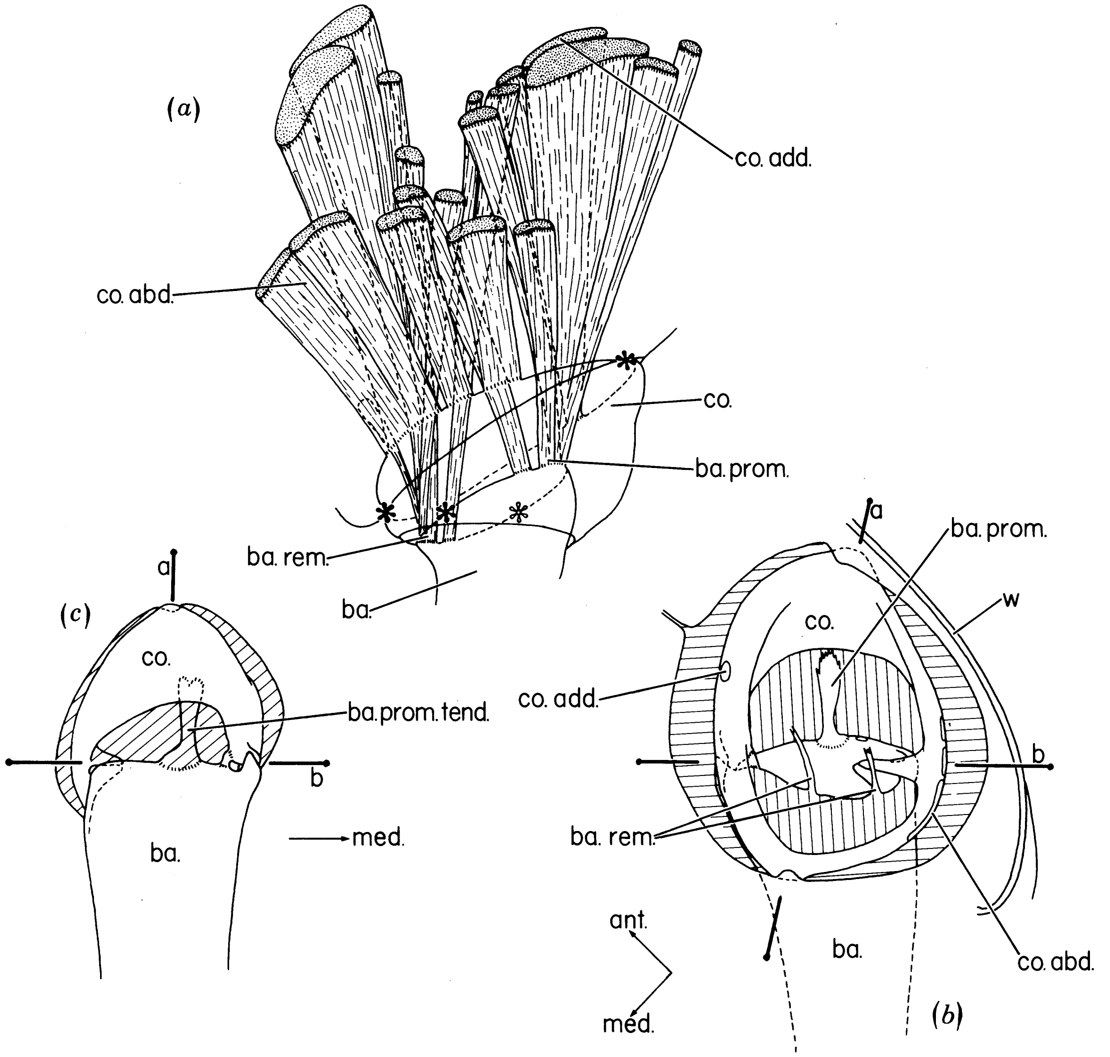

Figure 13. *Sphyrapus*. (*a*, *b*) Pereopod III, right. (*a*) Lateral view of body–co. and co.–ba. musculature. Skeletal structures diagrammatic. (*b*) View from within body of body–co. and co.–ba. articulations. (*c*) Pereopod II, right, proximal portion. Anterior view, in particular showing co.–ba. condyles. Symbol w, lateral body wall.

The coxa of pereopods II–VII articulates with the body. Its motion is always limited to one plane by a dicondylic hinge line. The hinge line on pereopod II is oriented almost antero-posteriorly (figure 13*c*). Going posteriorly, the anterior condyle shifts medially, so that on pereopod VII the hinge line is almost transverse. The change is most abrupt between pereopods IV and V, such that abduction/adduction is the basic motion of coxae anterior to this point, and promotion/remotion dominates posterior to it. The degree of mobility decreases posteriorly. Coxal musculature is like that of *Janiralata*. Band-like remotor/abductors (precise function depending on the limb) oppose longer, more cylindrical promotor/adductors (figure 13*a*).

They insert well away from the condyles, and originate on the dorsolateral body wall. The musculature is powerful on pereopod II, but decreases in size posteriorly and is feeble on pereopod VII (figure 14*a*).

The co.–ba. articulation is of two kinds. In pereopods V–VII it is essentially like that of the isopods (figure 14*b*). A strong, finger-like process projects inward posterolaterally from the distal end of the coxa. It articulates via a strong ligament with the infolded proximal rim of the basis at a point near that podomere's long axis. Elsewhere along co.–ba. there is ample arthrodial membrane. The result is a monocondylic articulation capable of bending in any direction.

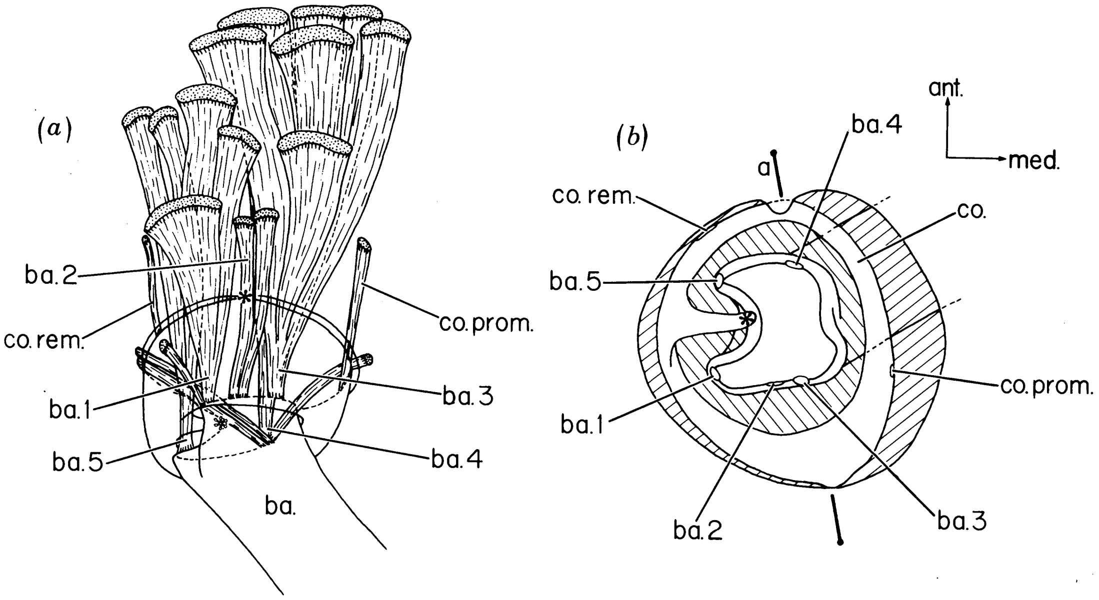

Figure 14. *Sphyrapus*. (*a*) Pereopod VII, right. Lateral view of body–co. and co.–ba. musculature. Medial body–co. condyle not shown. Muscles to the basis insert in five groups, as in some isopods (figures 9, 10). (*b*) Pereopod V, right. View from within body of body–co. and co.–ba. articulations. As with pereopod VII, basal muscles insert in five groups.

In pereopods II–IV, the co.–ba. is a dicondylic articulation (figure 13*b*, *c*). One of the condyles is similar to that of pereopods V–VII, although the coxal projection and basal infolding are less extreme. Opposite this, on the medial or anteromedial side, the second condyle is formed by a nob and adjacent notch on the coxal rim interlocking with a notch formed by a peripheral hook on the margin of the basis. A strong ligament prevents disarticulation. The resulting hinge line and the otherwise broad articulating membranes allow a wide arc of movement, but in a single plane. This plane is approximately perpendicular to that through the body–co. hinge line.

Almost all of the co.–ba. musculature originates on the lateral or dorsolateral body wall. On pereopods V–VII, as in *Janiralata*, the insertions are at five locations spread around the margin of the basis (figure 14*b*). For all but one (ba. 2, with use of the isopodan terminology), there are insertion tendons. One small bundle attaching muscle 1 originates at the coxa. The majority of bundles are nearly parallel to each other, but two small bundles inserting with muscle 4 angle strongly posteriorly and one anteriorly; all three originate from the ventromedial body wall. Their orientation makes them the only muscles that could cause rotation of the basis around its long axis.

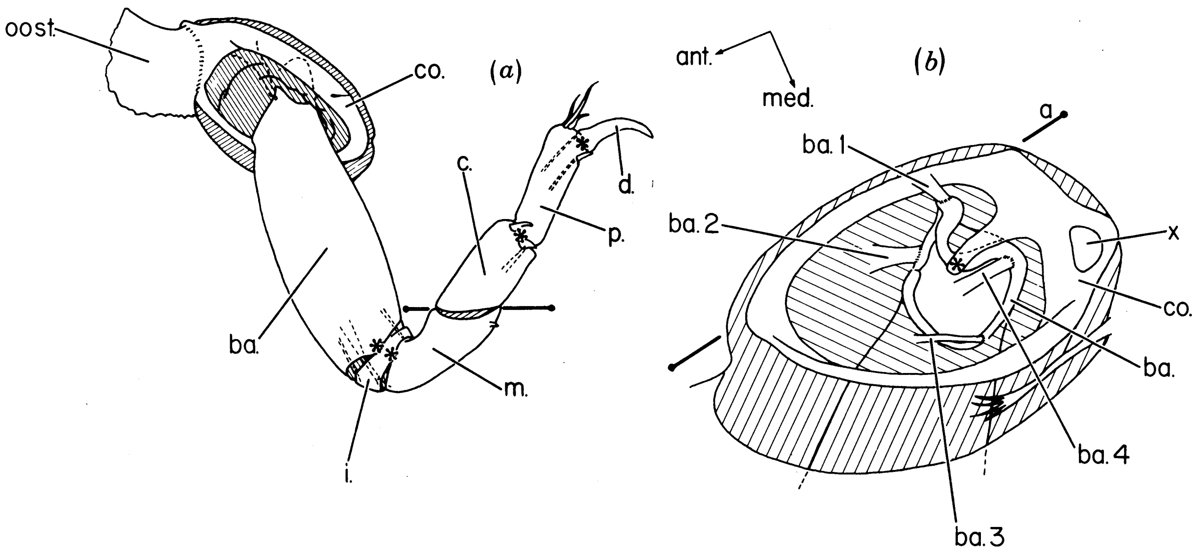

FIGURE 15. *Leptochelia*, brooding female, pereopod V, right. (*a*) Lateral view of whole limb, except that most of the oostegite is cut away. See legend of figure 6 for further explanation. (*b*) View as in figure 14*b*. The corresponding limb on *Sphyrapus* (figure 14*b*) is similar in all but the orientation of the body–co. hinge line. Four tendons insert on the basis. Symbol x, attachment opening of oostegite.

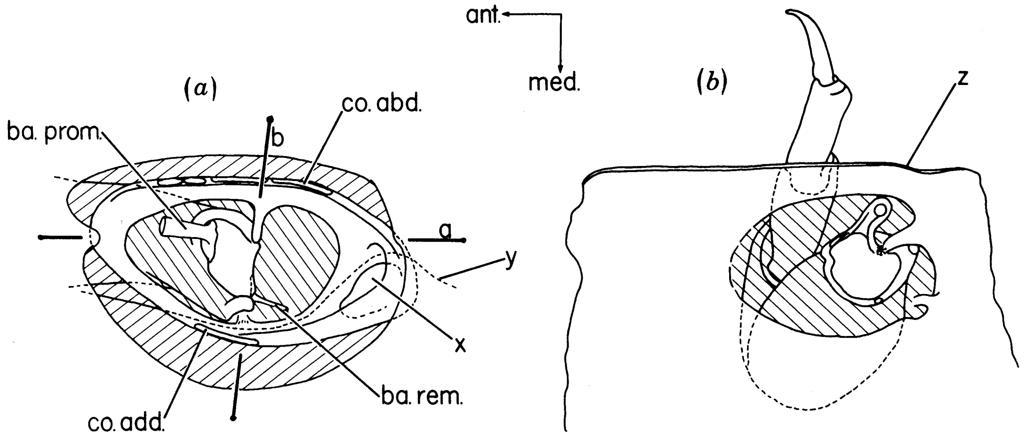

FIGURE 16. *Leptochelia*, brooding female. (*a*) Pereopod IV, right. View as in figure 14*b*. Figures 13*b*, *c* are of a similar limb. (*b*) Pereopod VI, right. View as in figure 14*b*. The coxa is completely fused with the body. Symbols: x, attachment opening of oostegite; y, margin of oostegite; z, lateral body wall.

On pereopods II–IV, there are four insertions, two by tendons from the margin of the basis posterior to the condyles, and two anterior to the condyles (figure 13*a*, *b*). Three of these insertions are by tendons. Unlike pereopods V–VII, the muscles of pereopods II–IV can only cause motion in the one plane.

The musculature of *Apseudes* was not studied; however, its skeletal structure, including insertion tendons are as above. *Leptochelia* hardly differs from *Sphyrapus* in significant ways (figures 15, 16); pereopods II–IV are all anteroposteriorly directed, whereas pereopods V–VII are all laterally directed. The coxa on pereopods VI–VII is immovable with respect to the body (figure 16*b*). On pereopods II–IV, the body–co. hinge line is oriented anteroposteriorly, allowing only abduction/adduction (figure 16*a*). The co.–ba. muscles of pereopods II–IV insert in two opposing positions, but in four positions on pereopods V–VII, all by tendons (figure 15*b*).

In all three tanaidaceans, pereopods II–V bear oostegites, which are cemented together to form an unbroken sac. In the monokonophorans, there is communication to the exterior between the limbs at the base of the oostegites.

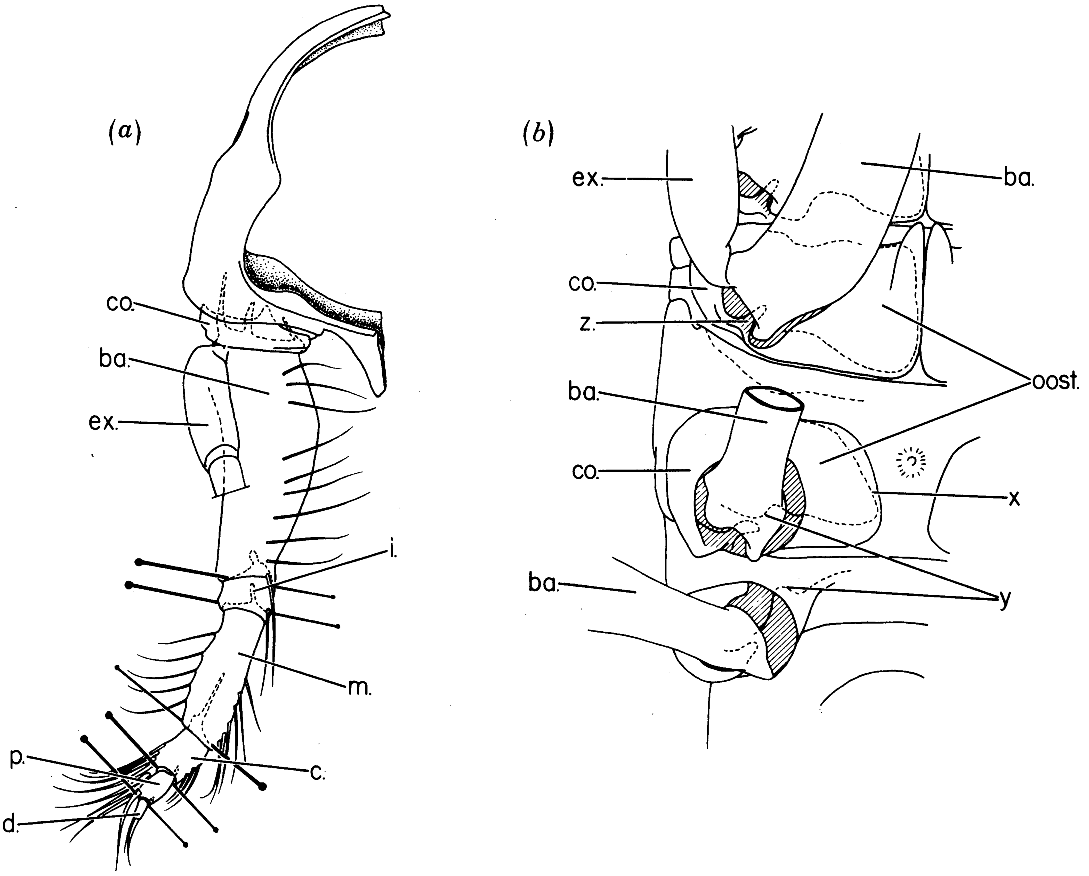

FIGURE 17. *Diastylis*. (*a*) Pereopod V, right, anterior. The hinge lines are oblique to the viewing plane; the lines representing them taper as they extend away from the viewer. (*b*) Ventral view of a preparatory female, showing proximal portion of right pereopods IV–VI. The coxa is fused to the body. Symbols: x, edge of attachment of oostegite, confluent with the edge of a posterior internal shelf (y) which overhangs the limb base and serves for muscle attachments; z, coxal portion of co.–ba. condyle.

Cumacea

Diastylis rathkei (from the Swedish west coast) is relatively unspecialized and lives on mud bottoms. As with cumaceans in general, it buries itself, using pereopods V–VII to dig in backward (Zimmer 1933); in moving from place to place, it swims by means of pereopodal exopods. Pereopods I–IV serve trophic functions and the lack of ambulatory function by their pereopodal endopods results in some special differences.

Even more than in tanaidaceans, there is a strong distinction between pereopods I–IV and V–VII. The former extend forward such that they are pressed up under the head, but with the exopods extending anterolaterally. Pereopods V–VI extend downward, bend posterolaterally at the ischium, and then curve ever more anteriorly at each successive articulation (figure 17*a*). As a result, the distal portion of pereopods V–VI is cup-shaped and anteriorly concave for burrowing. There is no simple limb plane. To a very slight degree this also applies to pereopod VII.

Because of the special functions and morphology of cumacean limbs, the skeletomusculature of the endopod was not considered. In the remaining description of coxa and basis, pereopod IV is given as an example of the anterior limb group, and pereopod VI of the posterior.

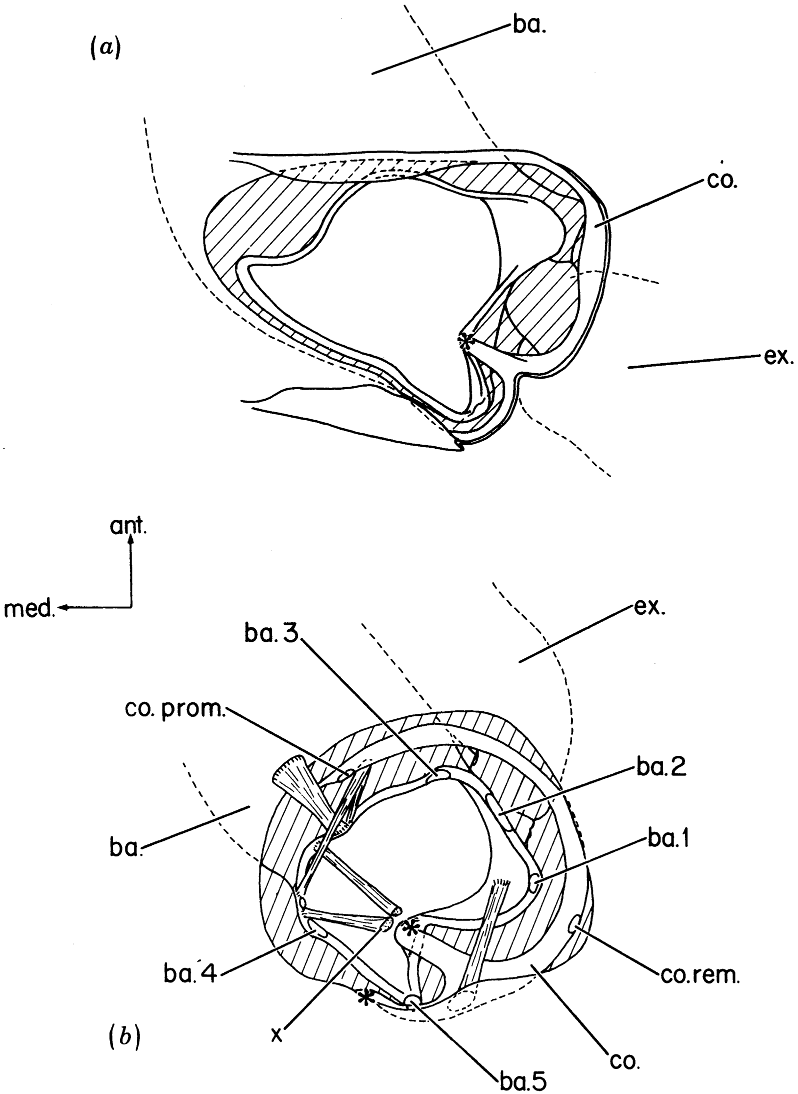

FIGURE 18. *Diastylis*. (*a*) Pereopod IV, right. View as in figure 14*b*. The coxa is fused to the body. The basal musculature (insertions not shown) is feeble. (*b*) Pereopod VI, right. View as in figure 14*b*. Only insertion areas are given for muscles with tergal origins. Basal muscles originating from the coxa or ventral body wall are shown entirely. Symbol x, origin on posterior shelf (not shown) of ventral body wall (figure 17*b*, y).

The coxa articulates with the body on pereopods V–VII. It is fused on the more anterior limbs, although a line of demarcation is present (figure 17*b*: x). The coxa does not form a complete ring because the medial third is not sclerotized except in the form of rudimentary oostegites in immature females. In pereopods V–VII, there is no discrete body–co. anterior condyle, but one is well developed posteromedially (figure 18*b*). The musculature was only studied on pereopod VI. As with the previous taxa, there is a short posterolateral remotor/abductor (figure 19: co.rem.) and a longer anterior promotor/adductor (co.prom.). These muscles are small compared to the musculature of the basis.

In all pereopods, there is a single articulating condyle in co.–ba.; the rest of the joint is formed by arthrodial membrane. In pereopods V–VII, the basic form of co.–ba. is the same as in isopods and pereopods V–VII in tanaidaceans (figure 18*b*). This morphology was even evident in pereopod IV, although in the anterior limbs the arthrodial membrane is more restrictive, particularly posteriorly (figure 18*a*).

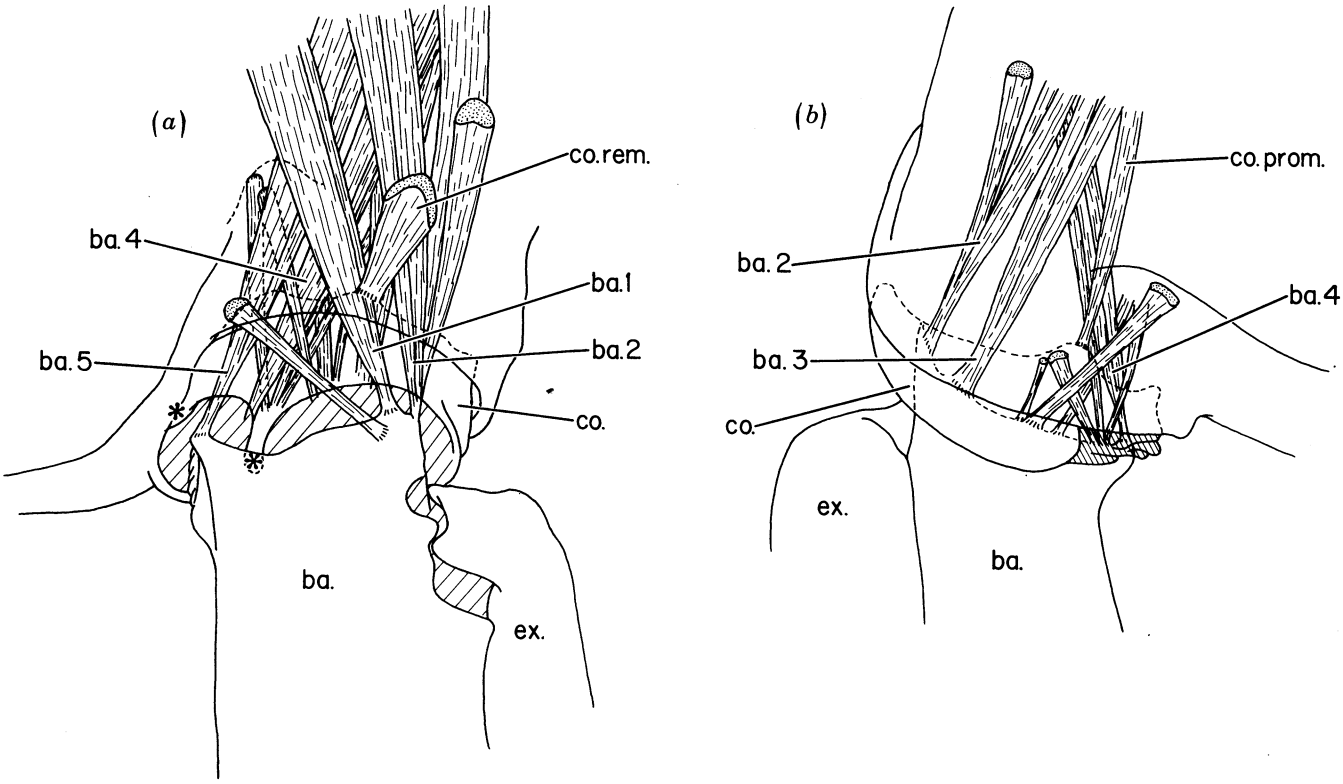

FIGURE 19. *Diastylis*, pereopod VI, right, showing musculature of coxa and basis. (*a*) Posterolateral view. Anterior insertions not completely drawn. (*b*) Anterior, but slightly lateral view. More posterior muscles not shown (see figure 18*b*).

The musculature of pereopod VI co.–ba. is similar to that of isopods, although more complicated. Most muscle bundles originate on the dorsolateral body wall and run parallel into the limb (figure 19), where they insert at five positions around the perimeter of the basis (figure 18*b*: ba. 1–5). Another insertion serves small oblique muscles that originate on the coxa or ventral body wall. Other small oblique muscles with similar origin insert with muscle 4, and one even inserts on the inner wall of the basis, distal to muscle 1 (figure 18*b*). As before, the small, oblique muscles seem adapted for rotation of the basis, while combinations of the larger muscles from the dorsolateral body wall move the limb in varying directions.

Oostegites stem from pereopods I–V; on preparatory females they have broad attachments on the ventral body surface, and on pereopods II–IV this attachment extends to the midline, completely replacing the sternal cuticle (figure 17*b*).

Spelaeogriphacea

The sole living representative of this order, *Spelaeogriphus lepidops*, is found in the groundwater system of Table Mountain, South Africa. The specimens used here were collected from a subterranean pond, where I found them walking on the sandstone bottom. The description below is based on the endopod of pereopod II and the proximal portions of pereopods IV–V. The precise limb is not important because they are all essentially alike, although the proportions of the distal three podomeres differ.

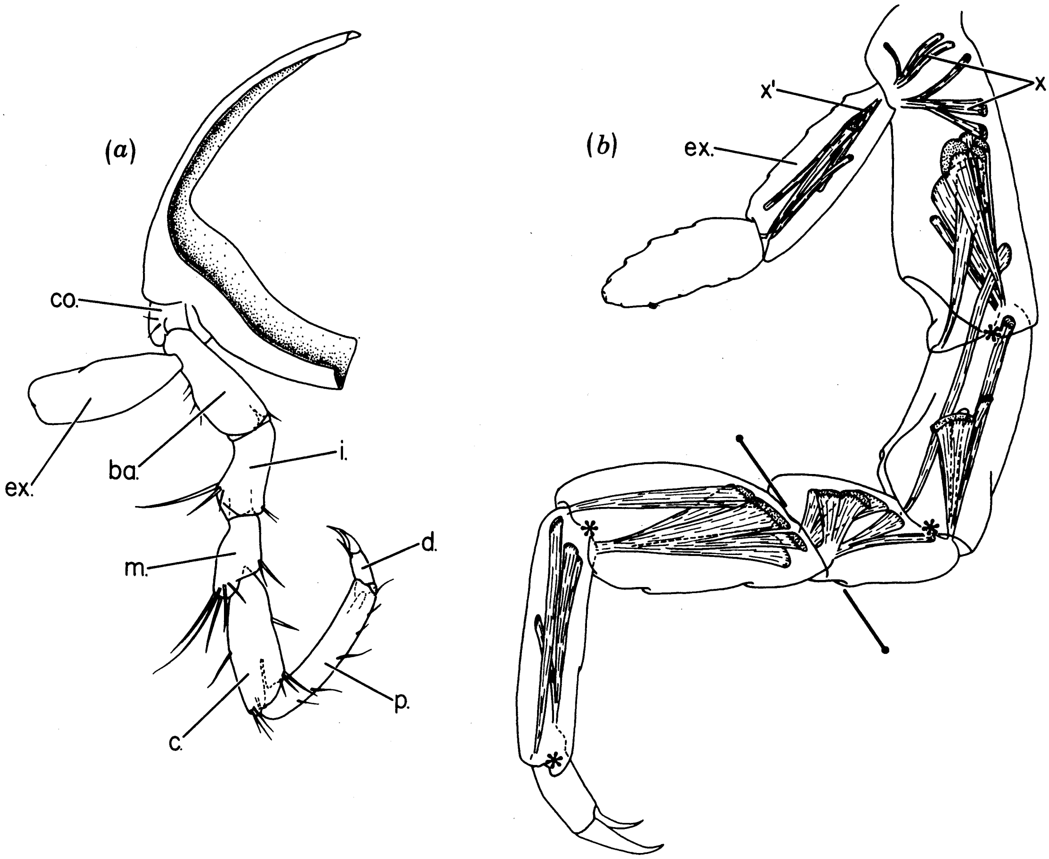

Figure 20. *Spelaeogriphus*. (*a*) Pereopod V, left, posterior. (*b*) Pereopod II, right, anterior, coxa not included. Intrinsic musculature. See figure 6 for explanation. Symbol x, exopodal muscles. Some bundles (x′) are of special interest because they are located within the podomere that they help move; this occurs in all peracarids with well developed exopods.

The pereopods have a well defined limb plane that includes basis and endopod (figure 20). All articulations from ba.–i. outward have dicondylic hinge lines that limit movement to extension and flexion in the limb plane. As in the isopods, the single exception is m.–c., whose dicondylic hinge line is in the limb plane. The limb plane of all the pereopods is oriented primarily transversely, with more anterior limbs having an anterolateral component and posterior ones having a posterolateral angle. As in isopods, the basis extends ventromedially. At ba.–i, the limb bends sharply outward, and the important downward flexure is at c.–p.

Endopodal musculature needs no description; it is very similar to that of the isopods (figure 20*b*); even the flexor of the merus that passes through the ischium to originate on the basis is present.

The coxa articulates with the body such that an anteroposterior hinge line runs laterally across the coxal margin (figure 21*a*: a). A single abductor bundle from the dorsolateral body wall attaches posterolaterally (figure 22*a*: co.abd.). The more powerful adductor consists of three bundles inserting anteromedially (figure 22*b*: co.add.), two arise directly from the dorsolateral body wall while the origin of the third is indirect, via a dorsal tendon.

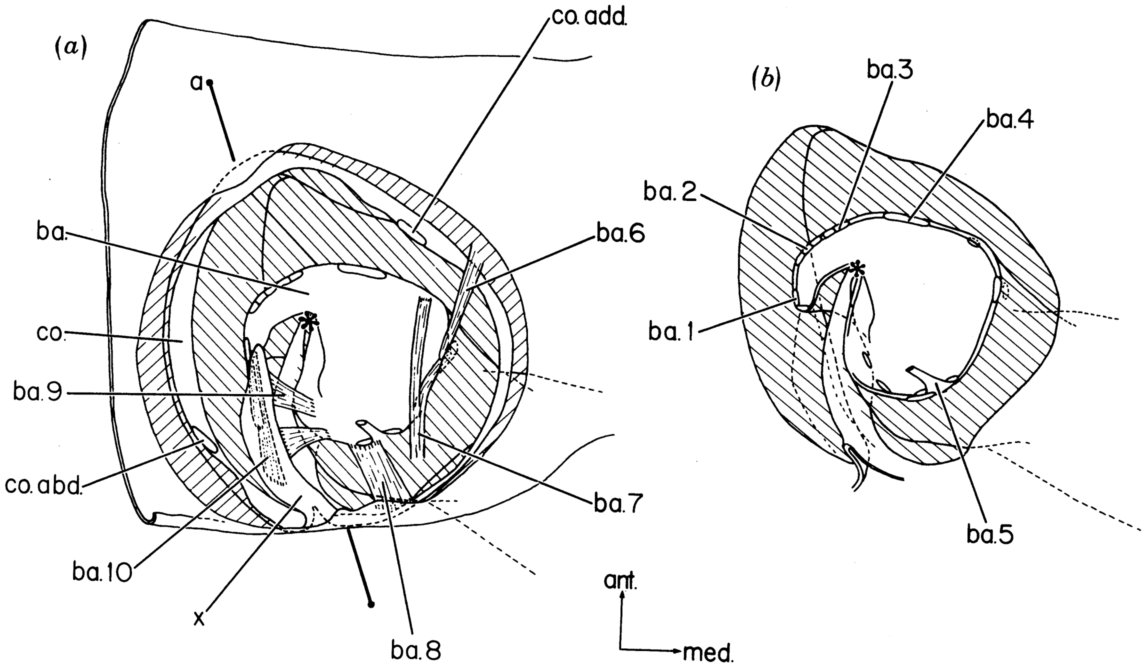

FIGURE 21. *Spelaeogriphus*, pereopod IV, left. Views as in figure 14*b*. (*a*) Body–co. and co.–ba. articulations. Musculature indicated as in figure 18*b* except that ventral body wall origins of the medial basal muscles (ba. 6, 7) are not shown. (*b*) Co.–ba. articulation. Only muscle insertions shown. Symbol x, vertical, blade-like apodemal invagination of coxa; the coxal projection whose apex bears the co.–ba. condyle lies below it.

The co.–ba. articulation is as in isopods (figure 21*b*). The invaginated coxal process is a vertical sheet whose ventral apex articulates with the basis. Externally, this invagination forms a posterolateral furrow that defines a small lateral epimere.

The musculature of co.–ba. is more complex in that there are more separate insertions and more small, usually obliquely oriented, muscles with ventral origins (figures 21, 22). The main muscle masses (ba. 1–5) originate on the dorsolateral body wall and run parallelly to the margin of the basis. Most insert directly onto the margin, rather than via a tendon. As in the previous taxa, the insertions are distributed in a way that allows the basis to be bent in any direction.

Four of the small oblique muscles (figure 21*a*: ba. 9 and 10, two muscles each) originate from a second long invagination (x) of the coxa, which is parallel to the first and just proximal to it. Three others (ba. 6–8) originate on the anterior or posterior ventral body wall. Several muscles insert on the wall of the basis rather than its proximal margin.

All pereopods except the last bear a small exopod laterally at the proximal end of the basis. Pereopods I–V bear oostegites (Gordon 1957).

Amphipoda

Only the Gammaridea will be considered in detail. Hyperiidea are totally pelagic and therefore not comparable to animals that spend all or part of their time on the bottom, and the Caprellidea are clearly derived from a gammaridean stock (Bousfield 1973). This analysis is based on *Gammarus pulex*, a freshwater species of a family whose morphology reflects the generalized gammaridean rather well (Barnard 1969). *Gammarus pulex* spends much of its time in leaf litter, crawling on its side rather than walking upright. To avoid placing undue weight on morphological features that might relate to specialized habits, attention also was given to two gammarideans with different habits and habitats. *Talitrus saltator* lives on sand beaches, where it burrows, scavenges in the flotsam, springs with its abdomen, and walks upright with its pereopods. *Neohela monstrosa* lives on mud bottoms, where it walks upright with its pereopods and swims with its pleopods. The caprellidean *Caprella linearis* was also briefly examined.

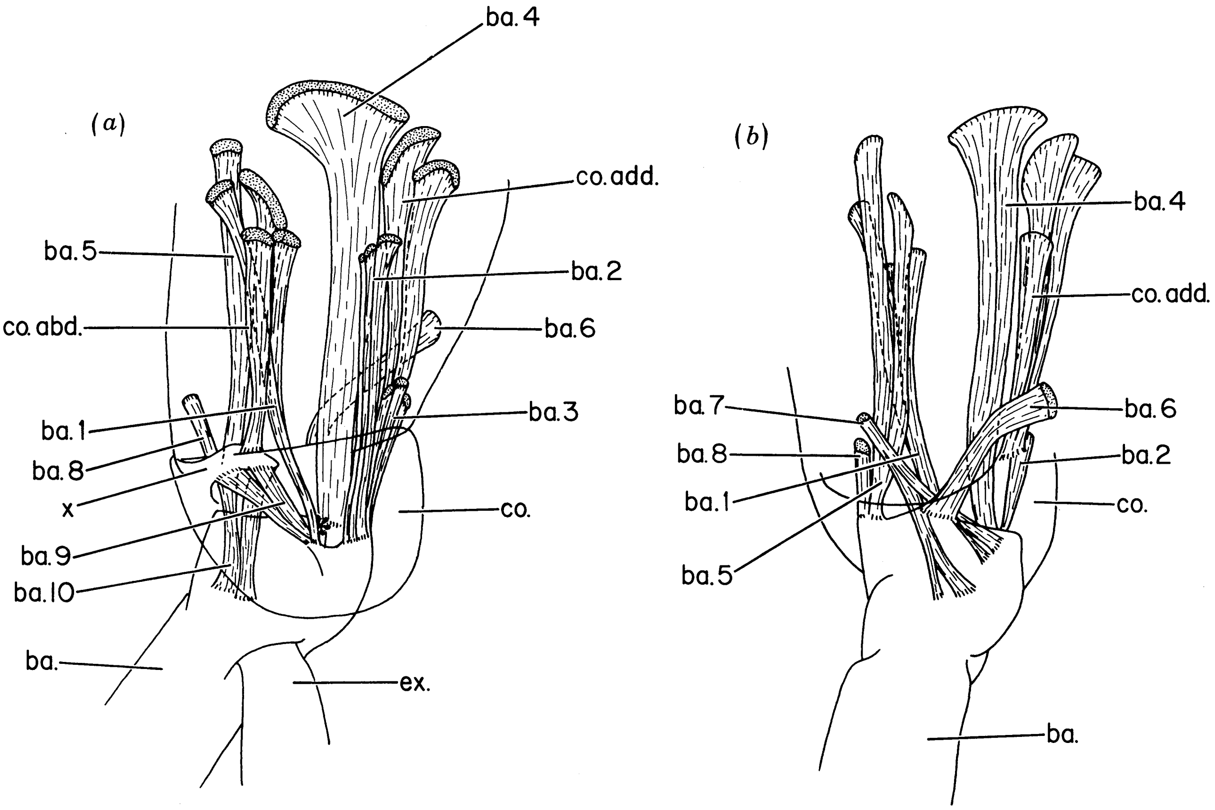

Figure 22. *Spelaeogriphus*, pereopod IV, showing musculature of coxa and basis. (*a*) Left limb, lateral view. Medial musculature not shown entirely. (*b*) Right limb, medial view. Lateral musculature not shown entirely. Symbol x, vertical, blade-like apodemal invagination of coxa (figure 21*a*).

The pereopods of gammarideans fall into three groups: pereopods I–II (the gnathopods), III–IV, and V–VII. In the present context, pereopods I–IV are so alike except for the limb plane that a description of pereopod III (figures 23–26) will cover them all. In pereopods III–IV, the basis and endopod lie in the limb plane. All articulations are dicondylic, and all hinge lines but m.–c. are perpendicular to the limb plane; the m.–c. hinge line is parallel to it. Thus, motion is primarily limited to extension and flexion in the limb plane, which is vertical and oriented anteroposteriorly. In the gnathopods the orientation of the hinge lines is successively twisted so that the distal chela can interact effectively with the mouth field. However, the proximal portion of the gnathopods is much like that of pereopod III.

The coxa of pereopod III is strongly expanded and flattened in a vertical, anteroposterior plane, and includes a large epimeral plate that hangs lateral to the basis (figure 23). The attachment of the coxa with the body is oval, and approximately 1.5 times longer than wide. Anterior and posterior condyles (figure 24*a*) delimit an anteroposterior hinge line. The arthrodial membranes are not wide. A strong medial tendon (figures 23*b*, 24*a*: co.add.) serves to attach several large bundles of coxal adductor muscles originating from the dorsolateral body wall and from a vertical facia that also serves for dorsal attachment of oblique trunk muscles. I could find no opposing coxal abductor muscles.

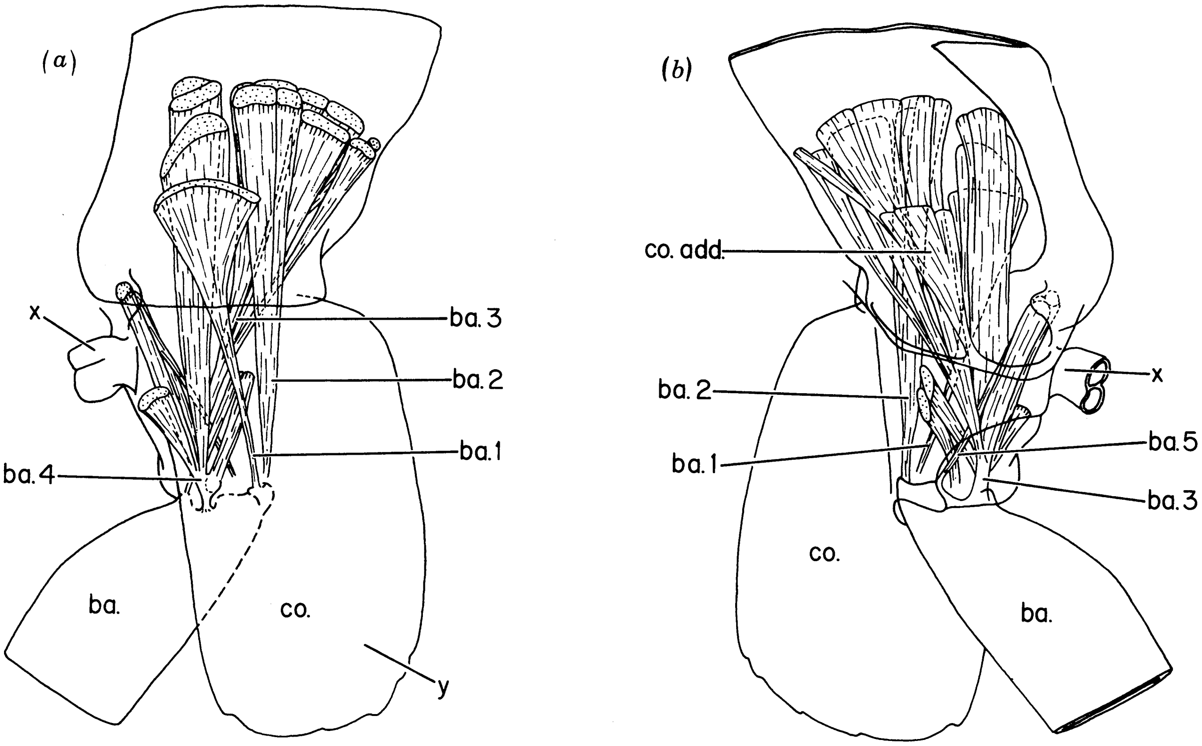

FIGURE 23. *Gammarus*, pereopod III, right. Coxal and basal musculature. (*a*) Lateral view. Insertions of medial muscles not shown. (*b*) Medial view. Insertions of lateral muscles not shown. Symbols: x, bases of branchia; y, coxal epimere.

The basis attaches to the medial face of the coxa by virtue of the large epimeral plate that hangs lateral to it. The co.–ba. is reminiscent of that on anterior pereopods of tanaidaceans in that it is dicondylic, with a nearly transverse hinge line (anterolateral–posteromedial) (figure 25). The lateral condyle is as seen in other peracarids; there is a strong ligamentous attachment from the tip of the coxal projection to the infolded rim of the basis. The medial condyle (figure 25*b*: y) is poorly developed, merely a place where the arthrodial membrane narrows. Elsewhere, the membrane is very wide, permitting a large arc of promotion/remotion. The medial condyle allows ample movement in other directions as well. Observation of living animals revealed promotion/remotion, abduction/adduction, and considerable rotation at the co.–ba. articulation.

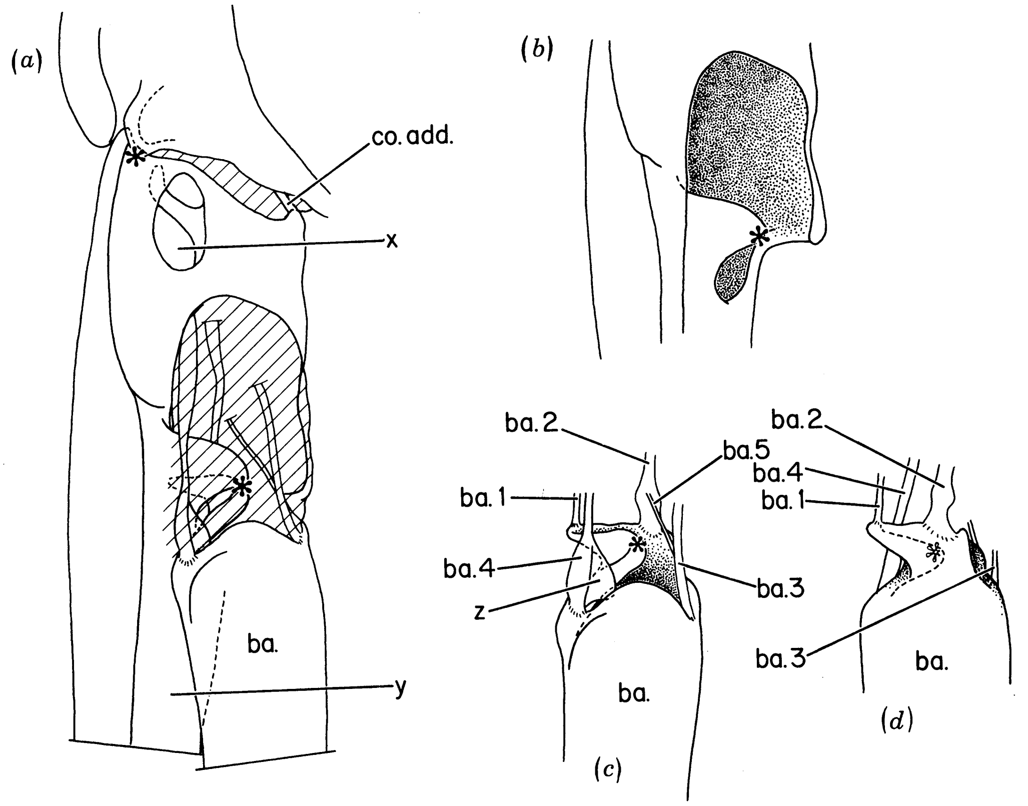

FIGURE 24. *Gammarus*, pereopod III. (*a*) Posterior view of left limb, showing body–co. and co.–ba. articulations. With body–co., only the posterior condyle is shown; the anterior condyle is behind it. (*b*) Central portion of disarticulated coxa; same view as in (*a*). (*c*) Proximal portion of disarticulated basis; same view as in (*a*). (*d*) Basis as in (*c*), but anterior view of right limb. Symbols: x, attachment opening of branchia; y, coxal epimere; z, shelf of ba. 4 tendon.

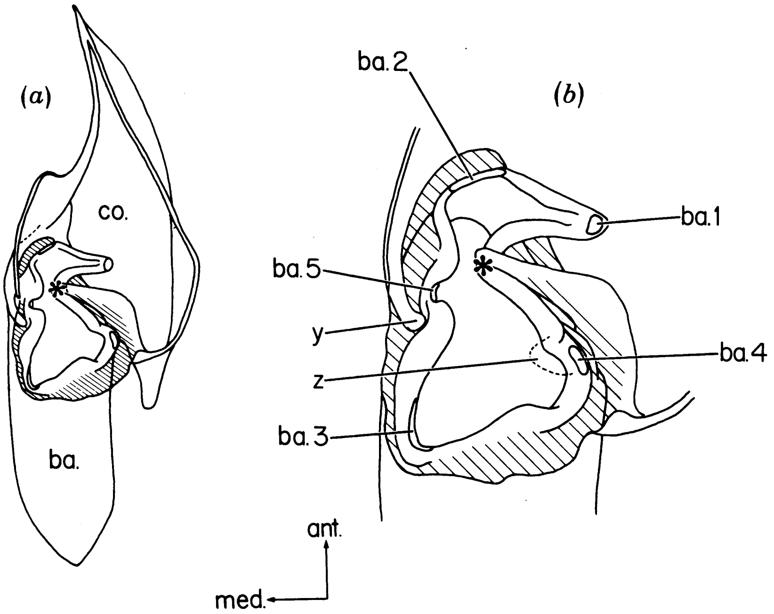

FIGURE 25. *Gammarus*, pereopod III, right. View of co.–ba., looking through coxa. (*a*) General view. (*b*) Close-up. Symbols: y, facultative medial condyle; z, shelf of ba. 4 tendon (see figures 24, 26).

Five groups of muscles insert by tendons at points evenly spread around the rim of the basis (figure 25*b*: ba. 1–5) as in the isopodan limb. One (ba. 5) inserts very close to the medial condyle; its action is probably facilitated by the loose articulation. Most of these muscles originate on the dorsolateral and lateral body walls (figure 23), but a few smaller, more obliquely oriented bundles originate on the coxa or the ventroposterior body wall.

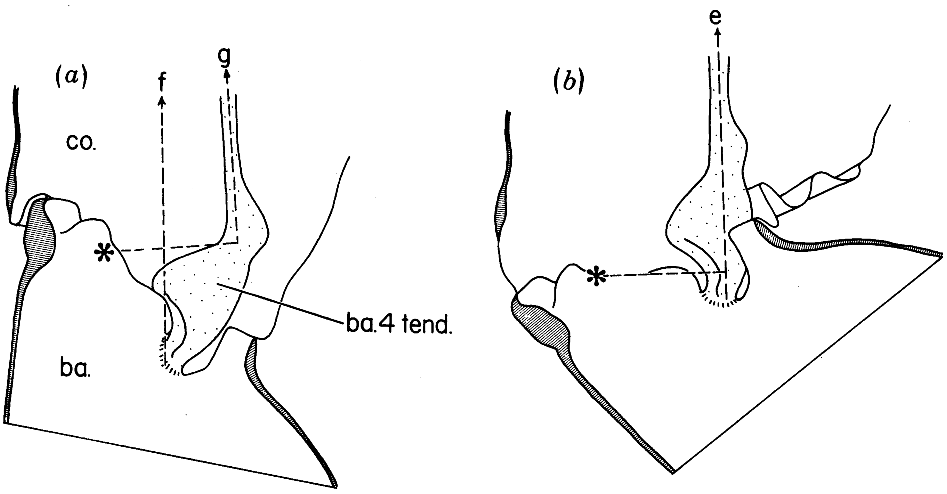

FIGURE 26. *Gammarus*, pereopod III, right. Detail of lateral half of co.–ba. seen in medial view to show action of ba. 4 tendon. (*a*) Basis promoted. (*b*) Basis remoted. When the limb is remoted, ba. 4 has a well developed moment arm (horizontal line from asterisk to axis of contraction, e). When promoted, the moment arm of ba. 4 (asterisk to f) would be short and ineffective if the rigid distal end of the insertion tendon did not butt against the rim of the basis, forcing the proximal portion of the tendon away from the condyle (asterisk to g). Symbols: e–g, arrows representing contraction of ba. 4.

The lateral muscle insertion posterior to the lateral condyle (figure 25*b*: ba. 4) deserves special attention. It makes a flexible union with the basis at the bottom of an emargination in the rim of the podomere (figure 26). Just proximal to this point, the tendon broadens into a sclerotized structure with an anterior shelf (figure 24*c*: z) that faces the anterior edge of the emargination. When the basis is strongly promoted (figure 26*a*), the shelf presses against the edge of the basis and forces the sclerotized portion of the tendon to rotate backward. If this did not happen, the insertion of the tendon would lie directly under the lateral condyle when the limb is strongly promoted and as a result would have no leverage to effect remotion. The sclerotized portion of the tendon thus acts as a secondary lever arm when the limb is in this position.

The limb planes of pereopods V–VII are oriented slightly obliquely from anteroposterior and extend posteriorly such that the distal portion of one limb is lateral to the proximal portion of the limb behind it. The ba.–i. and articulations within the endopod are as in pereopod III except that the condyles of c.–p. are rotated approximately 45° such that movement at c.–p. further increases the ability to bend the distal end of the limb plane laterally, beyond what is possible at m.–c. in other peracaridan limbs. The rotation at c.–p. causes the dactylus to be directed ventrolaterally and is related to the animal's need to crawl on its side. For gammarideans that walk vertically, it increases stability where lateral body flattening makes standing precarious.

In general, pereopods V–VII are the same. However, co.–ba. on pereopod VII differs in

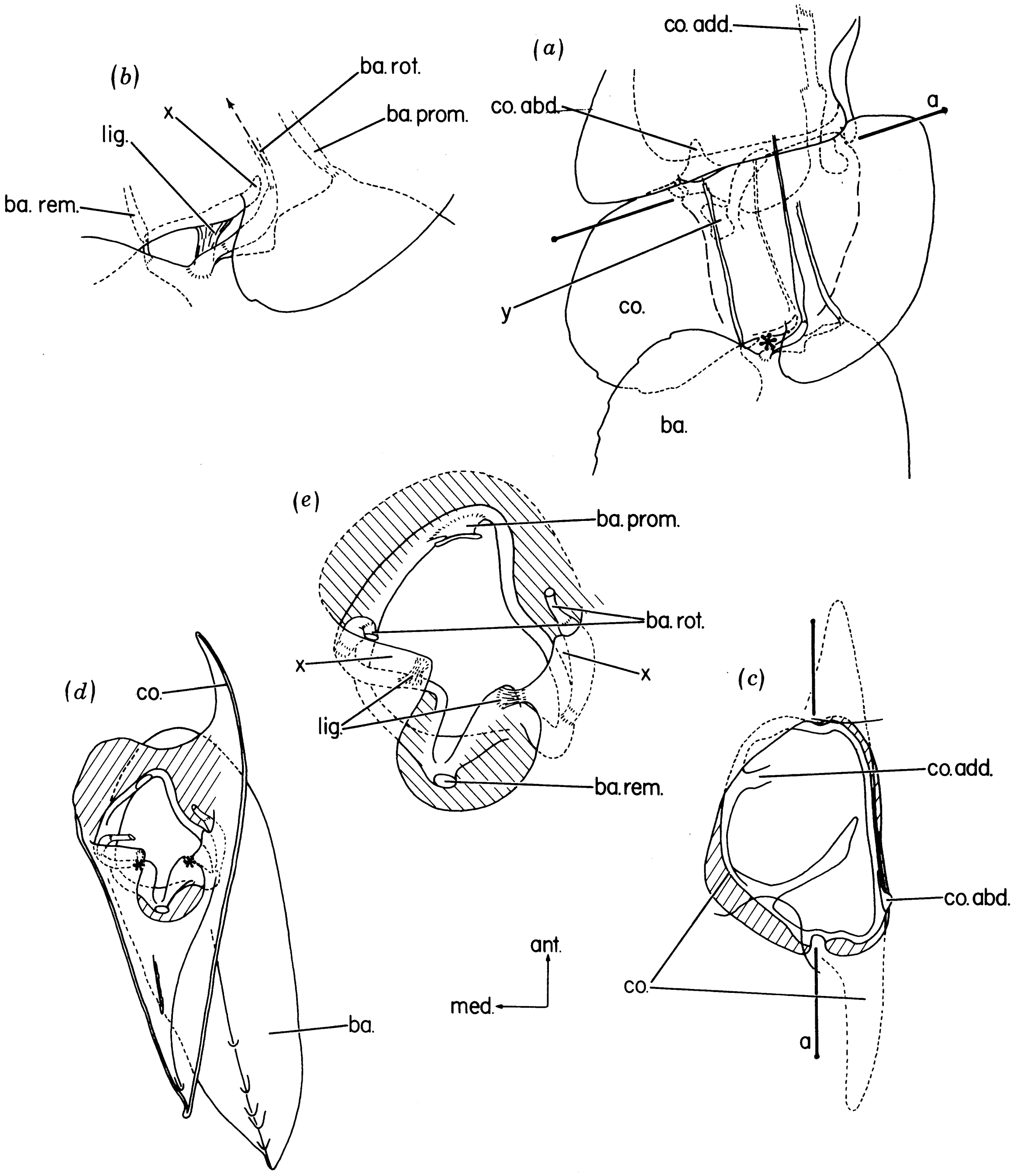

FIGURE 27. *Gammarus*, pereopod V, right. (*a*) Lateral view of body–co. and co.–ba. The medial co.–ba. condyle lies behind the lateral one, defining a hinge line perpendicular to the paper. (*b*) Detail of the lateral portion of co.–ba. Contraction (arrow) of the ba. rotator would bring its insertion tendon against the coxal shelf (x) and then pull forward, swinging the basis into an anteromedial/posterolateral orientation. The long condylar ligament facilitates this flexibility. Similar structures on the medial side of co.–ba. cause rotation in the opposite direction, but the overlap of coxa and basis (figure 27*a*) prevents the basis from attaining an anterolateral/posteromedial orientation. (*c*) View of body–co. from within the body. (*d*) View through the coxa co.–ba. (*e*) Close up of co.–ba. Symbols: x, coxal shelf; y, attachment opening of branchia (medial side).

fundamental details, which will be discussed separately. For the structure of the coxa and basis, pereopod V (figures 27, 28) was used to represent pereopods V–VI. As in pereopods I–IV, the coxa of pereopods V–VII is flattened, but does not have an epimere (figure 27*a*, *b*). Anterior and posterior condyles define an anteroposterior body–co. hinge line (figure 27*c*: a), and coxal adductors are arranged as on pereopod III. A small, flat abductor originating on the lateral body wall inserts directly on the posterolateral margin of the coxa on pereopods V–VI (figure 28*a*).

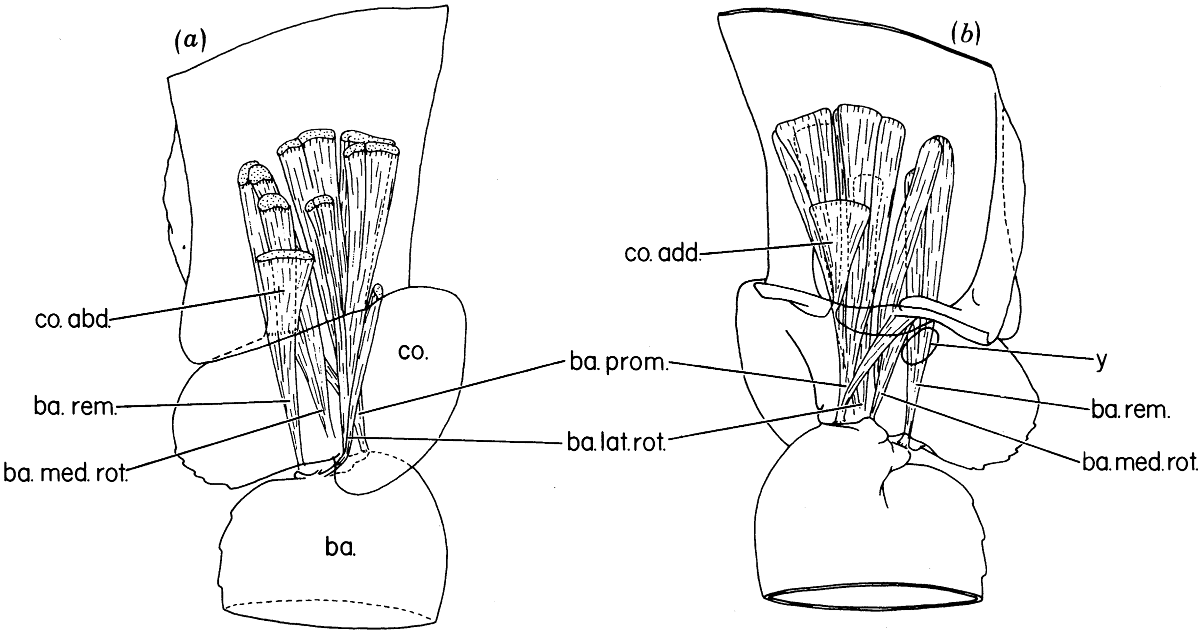

FIGURE 28. *Gammarus*, pereopod V, right. Coxal and basal musculature. (*a*) Lateral view; insertion of medial rotator not shown. (*b*) Medial view; insertion of lateral rotator not shown. Symbol y, attachment opening of branchia.

The co.–ba. on pereopod V is unlike anything described thus far. It is a dicondylic joint with a transverse hinge line (figure 27*a*, *b*, *d*, *e*). Both condyles are alike: a portion of the distal edge of the coxa bends inward, producing a broadly pointed apex which is joined by a ligament to the infolded posterolateral and posteromedial edge of the basis. This ligamentous attachment is relatively loose, and the arthrodial membrane of the rest of the articulation is wide. As a result, the basis not only promotes/remotes, but rotates; however, the flat distal edge of the coxa overlaps the basis anterolaterally and posteromedially (figure 27*a*), so that the limb plane can only rotate within the sector between anteroposterior and anteromedial/posterolateral. This was observed on living animals.

Muscles insert by tendon on the basis in four places: anterior, posterior, lateral and medial (figures 27*e*, 28). As usual, nearly all bundles originate on the dorsolateral or lateral body walls and run parallel to each other into the limb. The anterior and posterior muscles (ba.prom., ba.rem.) oppose each other in promotion/remotion.

The lateral and medial muscles (figures 27*b*, *e*, 28: ba.rot.) also oppose each other, but in an unusual way because of the complex course of their insertion tendons. Each tendon attaches peripherally and just slightly posterior to its corresponding condyle. It runs forward under the infolded distal edge of the coxa (figure 27*b*, *e*: x) and then extends dorsally past the anterior margin of the infolded edge. This distal portion of the tendon is thicker than the rest and is perhaps somewhat sclerotized. The tendon of the lateral muscle runs along a special groove in the coxal margin. When the lateral muscle contracts, the distal end of the tendon is pulled forward, and the limb rotates laterally. Action of the medial muscle returns the limb to an anteroposterior orientation.

The basis of pereopod V has small muscle bundles with ventral origins (figure 28), but in contrast to other taxa, their orientation is not markedly oblique, and thus not well suited for rotation.

Pereopod VII differs from pereopods V–VI in that co.–ba. has only one condyle; the lateral one is absent (figure 29*a*); thus, the articulation is much like that in isopods. The posteromedial condyle has the same broad infoldings of basis and coxa, and the same loose ligament, and there are the same four muscle groups. However, the lateral and medial tendons do not run under shelves of the coxa, but extend vertically. For this reason, the limb has no obvious method of rotation; indeed, it may not do so, for the lateral ventral edge of the coxa slightly overlaps the basis over its entire length and would not permit the kind of rotation of pereopods V–VI. Pereopod VII also differs in apparently lacking a coxal abductor.

Only skeletal structures were investigated on the other amphipods. Except for pereopod VII, they are essentially as in *Gammarus*, even in the case of the caprellidean (figure 29*b*, *c*). Because *Caprella* lacks pereopods III–IV, pereopod II was studied instead. *Neohela* was of special interest because pereopods I–IV lack large coxal epimeres, yet its co.–ba. is the same as in those taxa that have them. Pereopod VII in *Talitrus* and *Neohela* is like pereopods V–VI in having a dicondylic co.–ba. *Talitrus* has a distal, lateral coxal flange that prevents rotation of the basis, and the rotational pulley system is not well developed; however, on *Neohela*, the flange is not developed, and the lateral pulley tendon is heavily built.

Mysidacea

The limbs of *Lophogaster typicus*, one of the primitive Lophogastridae from southwestern Norway, and *Archaeomysis grebnitzkii*, a species of the more advanced family Mysidae from the San Juan Islands, Washington, U.S.A., were studied in detail. Primary attention is given to *Lophogaster* because it is likely to display a more primitive configuration. As far as is known, neither mysidacean is actually ambulatory, although both spend time on the bottom. *Lophogaster* simply buries itself; locomotion is swimming implemented by the pleopods. When resting on the bottom, the basis angles forward, and the endopod extends laterally.

This analysis is based on pereopods IV–V, which typify most limbs. In a female *Lophogaster* with well developed oostegites, the coxa is a sclerotized ring, which is dominated medially by the base of the oostegite (figures 30*a*, 31*a*). Posterolaterally, the ring is nearly split. Medially, the body–co. arthrodial membrane is extensive. Laterally, there is no special membrane, but here the cuticle is very thin and flexible, being the base of the branchial zone (figure 31*a*: w). Anterior and posterior condyles are formed by well sclerotized, thickened body and coxal cuticle, each lightly connected by a ligament. They delimit an anteroposterior hinge line for abduction/adduction.

Strong muscles implement this movement. A fan-like sheet of adductors from the anteroventral body wall insert on an anteromedial coxal apodeme (figure 30*b*: co.add.). They are reinforced by a small bundle from the lateral body wall. Posteriorly, a thick abductor bundle from the posteroventral body wall inserts on the proximal edge of the coxa dorsolateral to the posterior condyle, and a longer, more slender bundle from the lateral body wall inserts just lateral to this (figure 31*b*: co.abd.).

The co.–ba. articulation (figure 32) is complicated. Posterolaterally, a vertical coxal invagination (z) forms an internal ridge that becomes deeper ventrally, where it is united by a ligament with the infolded posterolateral margin of the basis (figure 32*a*: v). This is the homologue of the single co.–ba. condyle of isopods, cumaceans and spelaeogriphaceans. As in amphipods and tanaidaceans, there is a second condyle (w), here on the anterior face of the limb. Elsewhere, co.–ba. has ample arthrodial membrane. These two condyles define a strong anteroposterior hinge line (b) for abduction/adduction.

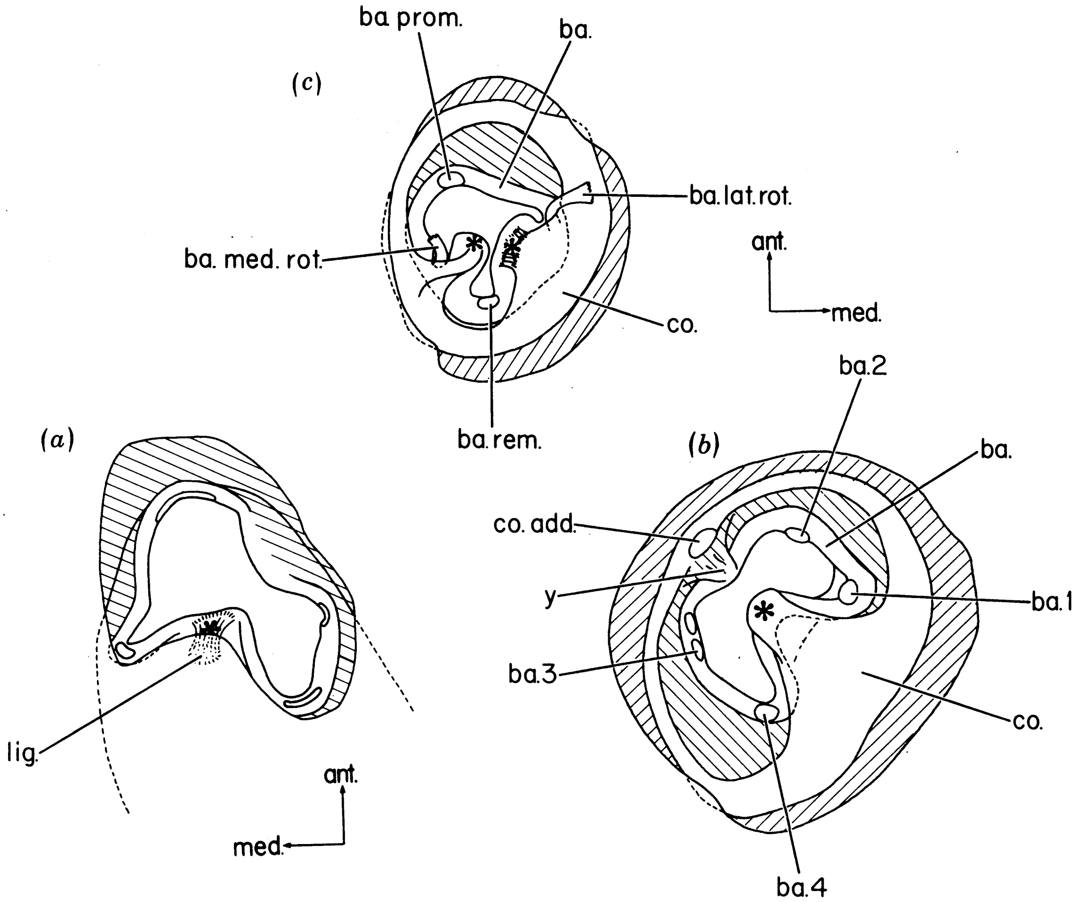

FIGURE 29. (*a*) *Gammarus*, pereopod VII, right. View through coxa at co.–ba. articulation. (*b*, *c*) *Caprella*, interior views of body–co. and co.–ba. articulations. (*b*) Pereopod II, right. (*c*) Pereopod V, right. These limb structures in this highly derived amphipod are essentially similar to those in a gammaridean (figures 25*b*, 27*e*, respectively). Symbol y, facultative medial condyle.

Unlike any limbs described so far, the basis of *Lophogaster* is subdivided by an additional articulation. Anteriorly, slightly distal to the blunt apex that forms the anterior co.–ba. condyle, a transverse horizontal line of thin, flexible cuticle isolates a broad, proximal triangle (figures 30*a*, 32*a*: x). The basis folds inwardly along this line.

The co.–ba. musculature is complex (figures 30*b*, 31*b*). All but one of the muscles (an abductor that runs laterally from the coxa deep into the basis) insert on or very near to the proximal margin of the basis. Three muscles (ba. 1–3) are long bundles from the lateral body wall, and the rest originate more ventrally from the coxa, and the lateral, ventroanterior, ventroposterior, or ventral body walls. More importantly, the insertions are positioned around the perimeter of the basis (figure 32*a*). One (ba. 5) inserts on a shelf extending inwardly from the middle of the distal margin of the anterior triangle.

While it would be impossible to predict the details of the action of so complicated a skeletomusculature, it is possible to discern its basic capabilities. The co.–ba. condyles make abduction/adduction possible, and there are ample opposing muscles to power this movement. The anterior, transverse, intrabasal hinge line also makes promotion/remotion possible (figure 32*b*, *c*). For this, the posterior co.–ba. condyle (v) acts as a fixed point. Infolding of the basis on the intrabasal hinge would in effect shorten the anterior face of the basis (that is, decrease the distance between the distal edges of the coxa and basis), and the limb would rotate forward, accomplishing promotion. Straightening of the basis along that hinge would cause backward rotation, that is, remotion. For promotion, the muscle (ba. 5) inserting on the middle of the distal edge of the triangle is critical in the initial stages, but after only a small amount of infolding all the other muscles on the anterior edge would enhance that action. All

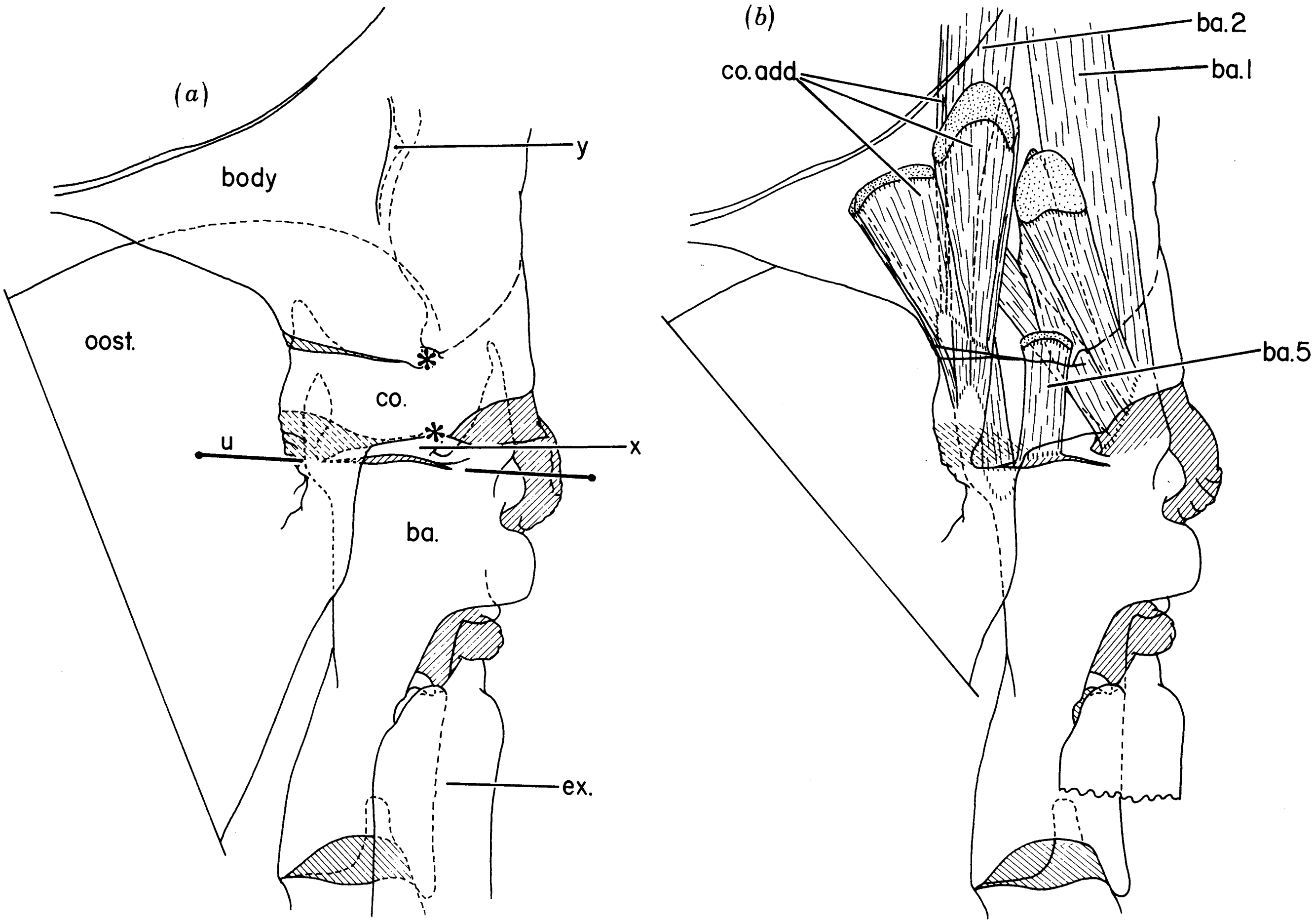

FIGURE 30. *Lophogaster*, brooding female. Pereopod IV, left, anterior view. (*a*) Cuticular structures. (*b*) Anterior coxal and basal musculature. Symbols: u, secondary intrabasal hinge line; x, secondarily articulated proximal triangle of basal cuticle (see figure 32); y, cuticular infolding for structural reinforcement.

the muscles posterior to the posterior co.–ba. condyle would act as remotors. Important here is the fact that promotion/remotion and abduction/adduction could be conducted simultaneously and in all combinations, that is, the co.–ba. hinge system is capable of movement in all directions.

Pereopods III–IV of a mature male *Archaeomysis* were analysed but as with *Lophogaster* all limbs are much alike. The basic construction of the proximal articulations is like that of *Lophogaster*. The body–co. and primary co.–ba. articulations are both dicondylic and have anteroposterior hinge lines (figures 33*a*, 34*a*). The coxa is not a complete ring (figure 34*c*), and is best developed posterolaterally. Posteriorly, the medial margin runs vertically between the body–co. and co.–ba. condyles; anteriorly, it becomes a wedge at a point just beyond the anterior co.–ba. condyle. There is the same intrabasal transverse articulation anteriorly, and the posterior co.–ba. condyle is invaginated, although not so strongly (figure 34*c*). A variety of

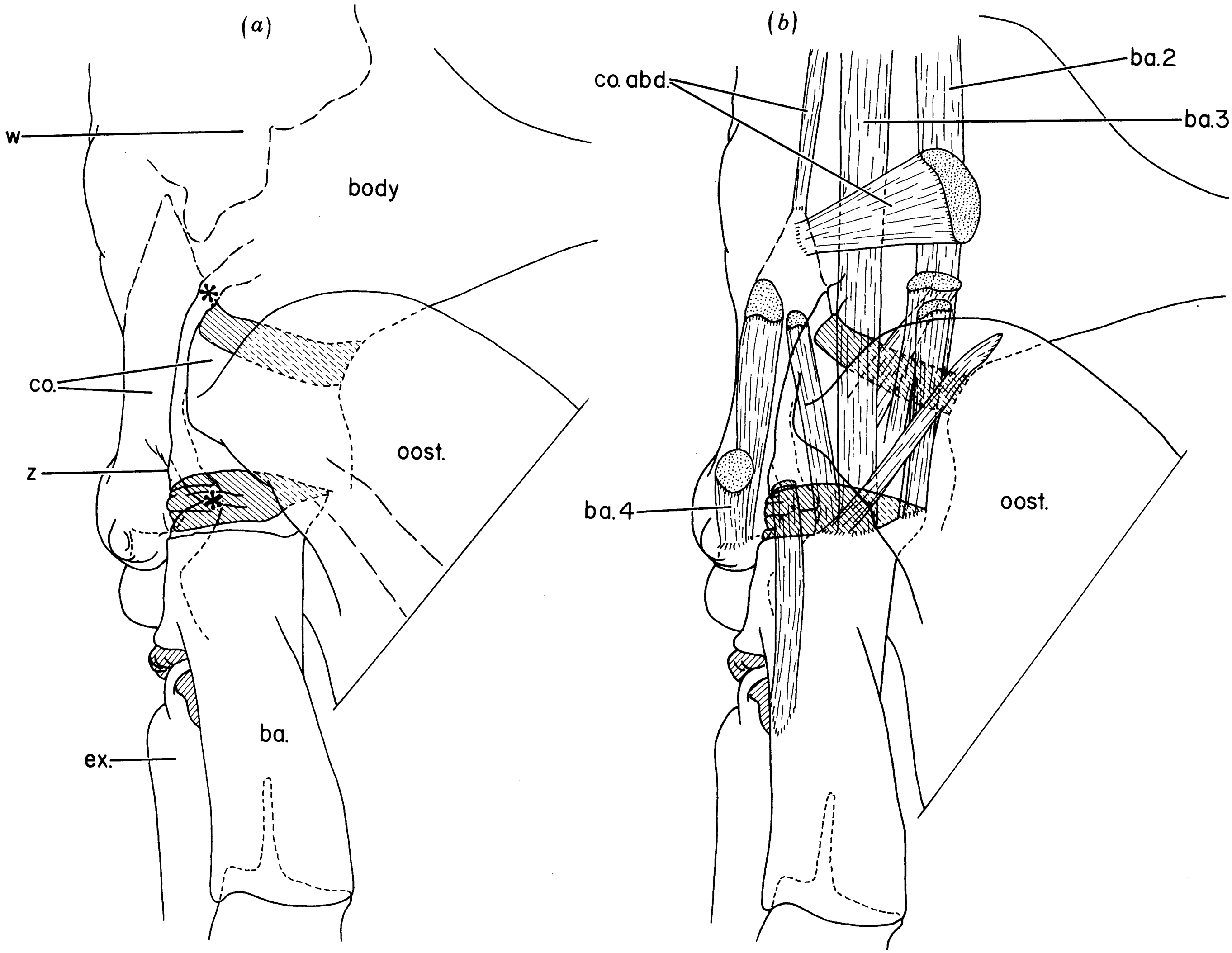

FIGURE 31. *Lophogaster*, brooding female. Pereopod IV, left, posteromedial view. (*a*) Cuticular structures. (*b*) Posterior coxal and basal musculature. Symbols: w, thin cuticle where branchiae arise; z, deep vertical invagination separating small lateral epimere and having at its inner apex the coxal portion of the posterior co.–ba. condyle.

muscles attach at several points around the basal margin. Not surprisingly, no coxal adductors could be found, and there is only one small abductor. Manipulation with a probe demonstrated limited flexibility at the body–co. articulation, but the co.–ba. shows general flexibility.

Thermosbaenacea

A superficial analysis was made of *Thermosbaena mirabilis* and *Monodella argentaria*. Small size and inadequate preservation precluded the possibility of studying the musculature, and the cuticle did not stain well, making it difficult to see the exact nature of many of the articulations. Fortunately, the present concern is primarily with the proximal articulations, and Siewing (1958) has dealt to some extent with the rest.

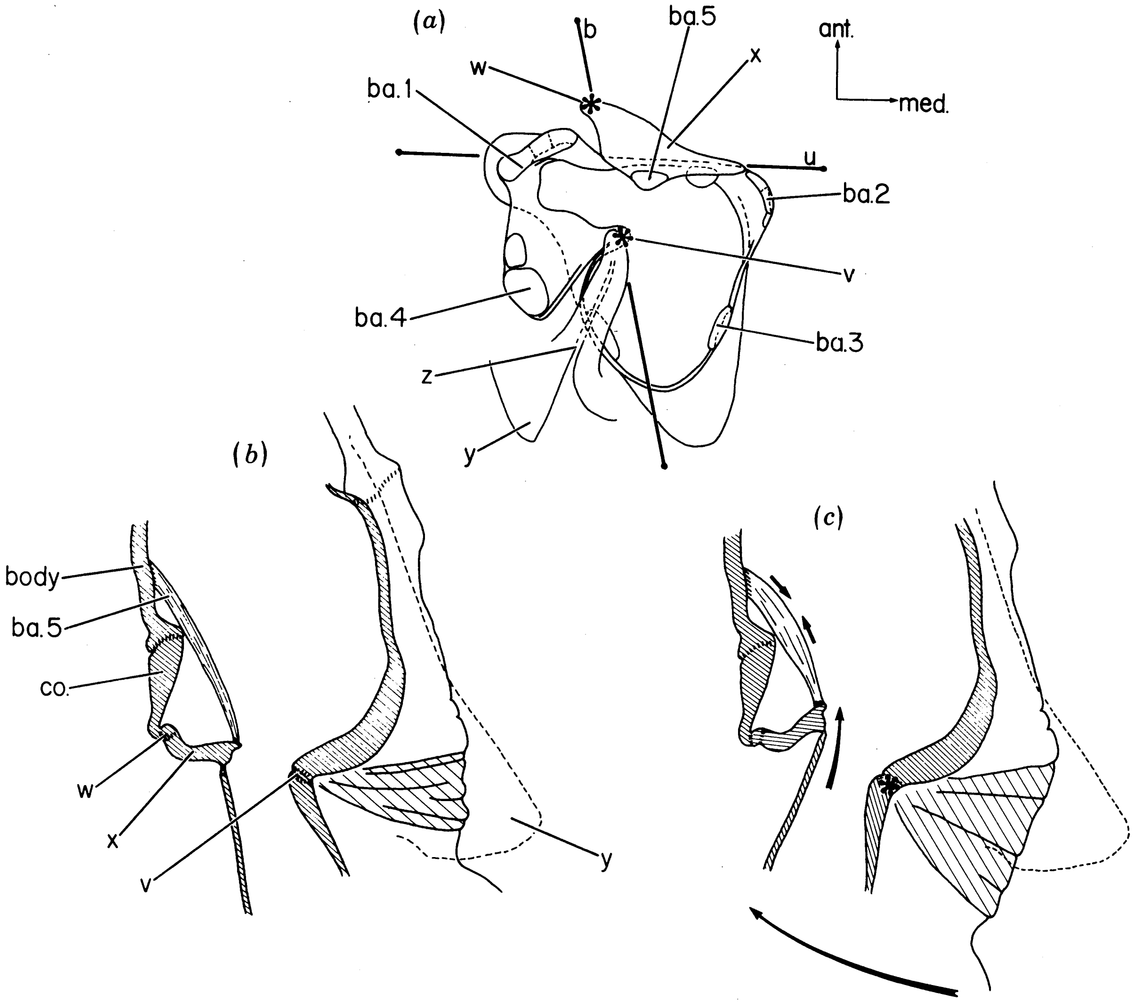

FIGURE 32. *Lophogaster*, brooding female. Pereopod IV, left. (*a*) View through coxa at co.–ba. articulation. Coxa not shown except at posterior co.–ba. condyle. The primary articulating hinge (b) formed by anterior and posterior co.–ba. condyles permits adduction/abduction. The secondary articulation (u) within the proximal anterior cuticle of the basis facilitates promotion/remotion, with the posterior co.–ba. condyle as fulcrum (see figure 32*b*, *c*). (*b*, *c*) Exsagittal cut through axis of limb to show promotion/remotion at co.–ba. (*b*) Basis in posterior position. (*c*) Basis during promotion. Lifting the distal edge of the proximal triangle of anterior cuticle (x) causes the basis to pivot anteriorly. Other symbols: u, secondary intrabasal hinge line; v, posterior co.–ba. condyle; w, anterior co.–ba. condyle; y, coxal epimere (above plane of paper in (*b*, *c*)); z, deep vertical invagination (see legend of figure 31).

The body–co. and co.–ba. articulations do not differ between the two genera or apparently along the limb series. The junction between body and coxa is ovoid, with its long axis transversely oriented (figure 35). An indication of a lateral condyle suggests a transverse hinge line, and manipulation with a probe demonstrates promotion/remotion.

The co.–ba. is like that of the isopods in having a single invaginated condyle and arthrodial membrane around the perimeter. In all limbs the condyle folds in from the anterior margin, or somewhat anterolaterally in the more posterior pereopods. Manipulation shows an ability to promote/remote as well as to abduct/adduct.

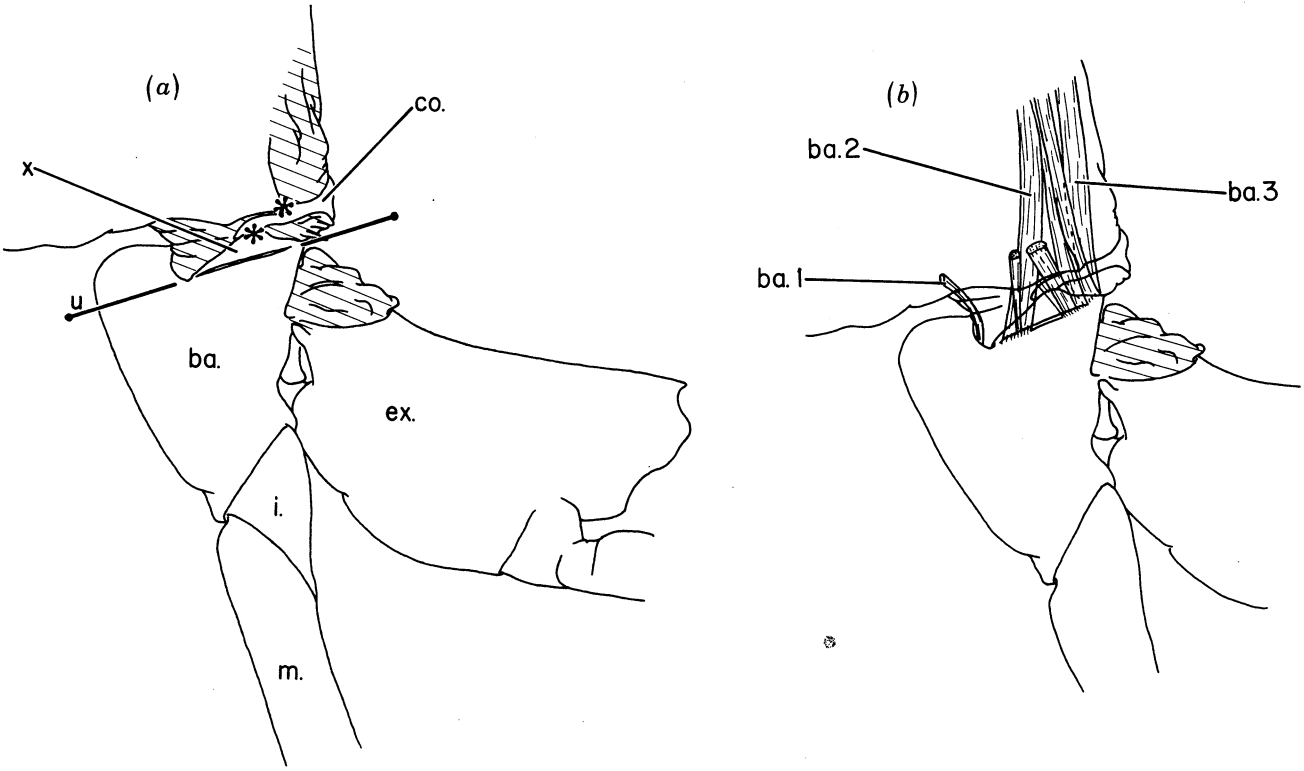

FIGURE 33. *Archaeomysis*, pereopod IV, left, anterior view. (*a*) Cuticular structures. (*b*) Anterior coxal and basal musculature. Symbols: u, secondary intrabasal hinge line; x, secondarily articulated proximal triangle of basal cuticle (see figures 30, 32).

The endopod lies in a limb plane that in the preserved animal tends to be transversely oriented.

Eucarida, Decapoda

The Decapoda is so large and varied an order that no species can represent them all. I chose a natantian, *Palaemon squilla* from Lyseskil, Sweden, because of its availability and because it possesses much of the generalized caridoid morphology of a primitive decapod. *Palaemon* is accomplished in both swimming and walking as is common among the Natantia. When swimming, it uses its pleopods; when walking, it relies upon its posterior thoracopods, pereopods II–V (following the standard decapodan nomenclature, wherein the first three thoracopods are called maxillipeds). The present analysis concentrates on pereopod III because it is a well developed, primarily ambulatory appendage. Pereopods I–II are modified for feeding and grooming, pereopod V is somewhat reduced, and pereopod IV is much like pereopod III.

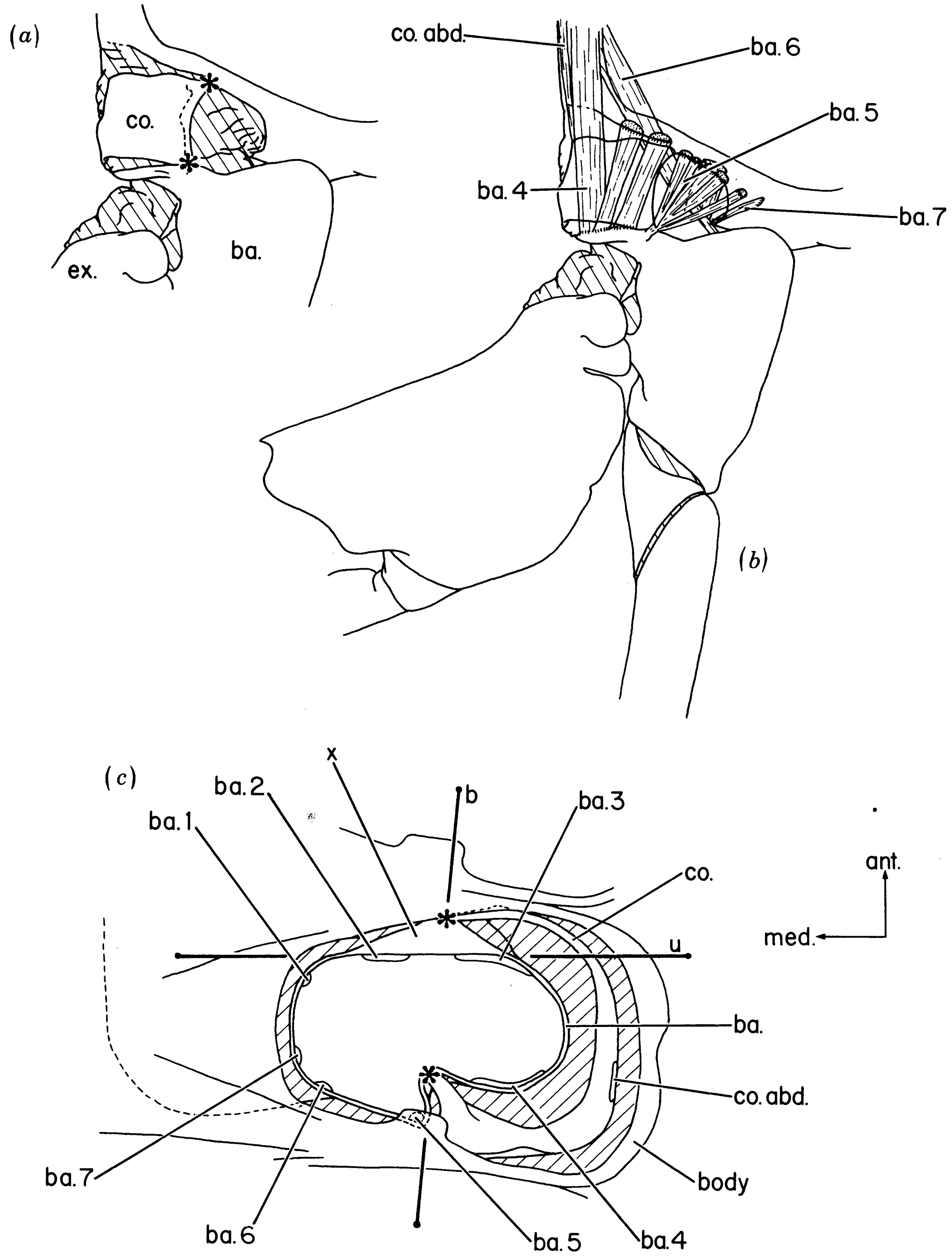

FIGURE 34. *Archaeomysis*, pereopod IV. (*a*, *b*) Left limb, posterior view. (*a*) Cuticular structures. (*b*) Posterior coxal and basal musculature. (*c*) Right limb. Interior view of body–co. and co.–ba. articulations. See figure 32 for further explanation.

Pereopod III is a generalized eumalocostracan thoracopod in that all of the malacostracan podomeres are present and freely articulating (figure 36*a*). The endophragmal system seen in higher decapods is barely developed here (figure 36*e*). The main specializations are the absence of an exopod and the transfer of the branchial epipods to the body wall.

Pereopod III, including the coxa, lies in a plane (figure 36*a*). The articulations, including body–co., are dicondylic, with well defined hinge lines. In co.–ba., i.–m., m.–c. and p.–d. the hinge lines are nearly parallel and permit flexion and extension within the limb plane. Ba.–i. and c.–p. are perpendicular to the others and permit bending of the limb plane, i.e. promotion/remotion. In normal walking, they do not play an active role; the limb remains in one plane. I have seen no major movement at ba.–i., and c.–p. seems mainly to compensate for irregularities of the bottom. For example, c.–p. bends backward when the tip of the limb bumps into something during promotion. C.–p. has only one tightly articulated condyle; the dorsal one is easily disarticulated without causing damage and is held in position by muscle tension. The endopodal musculature follows the common plan. Exceptions are c.–p., which has an additional small muscle inserting near the ventral condyle, and ba.–i. and i.–m. which lack the promotor and levator, respectively.

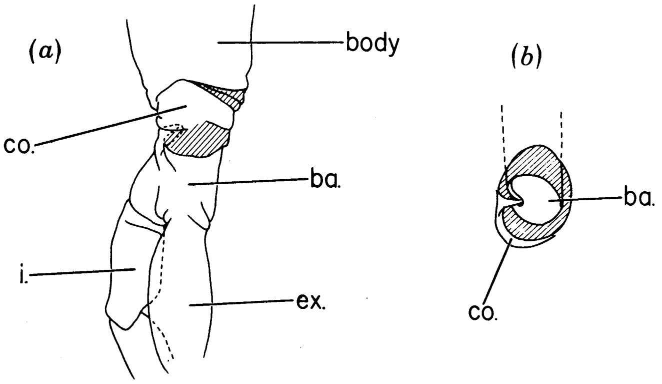

FIGURE 35. *Thermosbaena*, pereopod II, left. (*a*) Lateral view of proximal articulations. (*b*) Internal view of co.–ba. articulation.

The hinge line of body–co. is oriented dorsolaterally–ventromedially, with the dorsolateral condyle lying anterior to the other (figure 36*b*, *c*: a). Its motion is essentially promotion/remotion. A single pair of opposing muscle groups cause movement (figures 37, 38: co.prom., co.rem.). They insert on the coxal margin, a little closer to the dorsolateral hinge than to the ventromedial, and they originate on the lateral or dorsolateral body wall.

The co.–ba. hinge line is perpendicular to that of body–co. (figure 36*b*, *c*: b). Unlike all the dicondylic articulations encountered so far, where movement is by a simple pair of opposing muscle groups, the musculature of co.–ba. is extremely complicated (figures 36*d*, 37–39). There are 11 muscle bundles; most are large, originating from the lateral and posterior body walls (ba. 1–3), from a sclerotized invagination of the ventroposterior body wall that hangs over the limb base (ba. 4, 7), from an apodeme of the body–co. medial arthrodial membrane (ba. 8–10), and from the medial and posterior walls of the coxa (ba. 5–6, 11). These muscles extend at a variety of angles toward insertions along most of the proximal margin of the basis (figure 36*d*). Most muscles insert directly on the basis, but two groups of three muscles insert by tendons on the middle of the lateral or medial margins. In spite of this complexity, the muscles must be regarded as either levators (abductors) or depressors (adductors), because the dicondylic hinge will not permit any other motion.

In summary, the walking leg of *Palaemon* operates in much the same way as that of *Janiralata*. The distance between the tip and base of the limb is altered through extension and flexion of endopodal joints within a limb plane. This plane is rotated forward and backward (promotion/

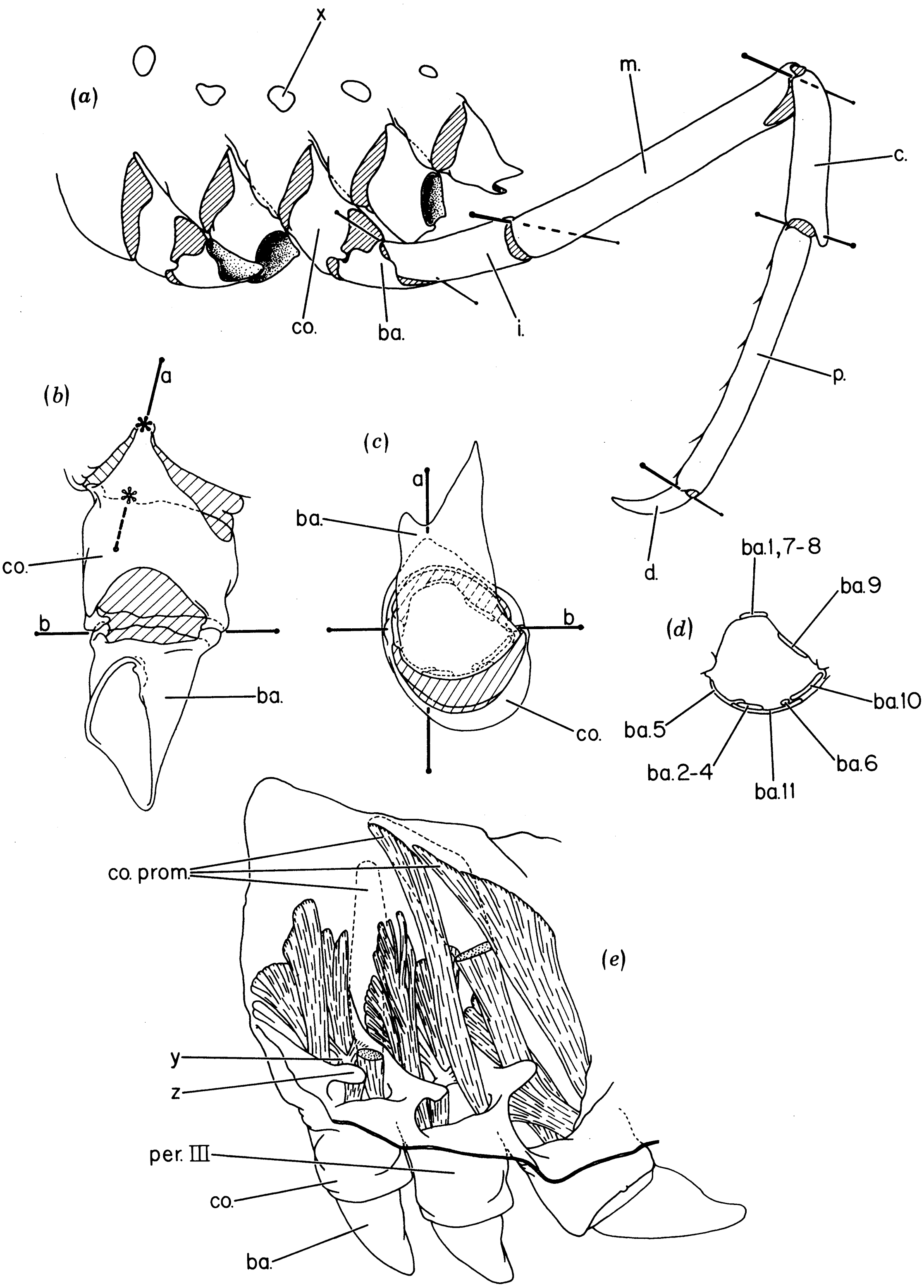

FIGURE 36. For description see opposite.

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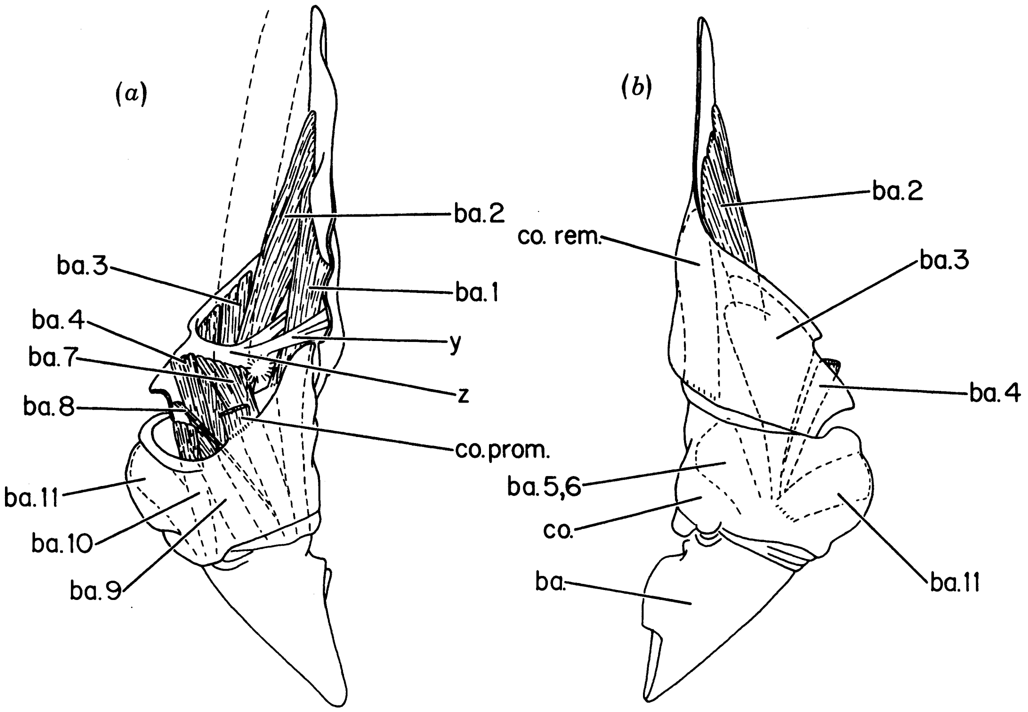

FIGURE 37. *Palaemon*, pereopod III, left. Coxal and basal musculature. (*a*) Anterior view. (*b*) Posterior view. The numbering does not imply homology with similarly numbered muscles in the Peracarida. Symbols: y, z, see legend of figure 36.

remotion) and tilted as a result of an articulation system at the base of the limb. In contrast to the percarids, where most of the flexibility at the base of the limb stems from the co.–ba., here it results from body–co. and co.–ba. combined. Because their hinge lines are perpendicular to each other, and because the intervening coxa is short, they form a universal joint, like a gimbal which connects drive shaft to crank shaft in an automobile. Such a system allows the limb to be moved in any direction.

In a variety of decapods the movement of the walking limbs and skeletal system that permits it are as in *Palaemon*, although in some of them there is fusion of ba.–i. These others include: *Homarus vulgaris*, *Nephrops norvegicus*, *Astacus fluviatilus*, *Pandalus borealis*, *Hyas araneus*, *Lithodes maja*, *Macropodia rostrata*, *Macropipus depurator*, *Geryon tridens*, *Cancer pagurus* and *Ebalia tumefacta*.

Syncarida

Anaspides tasmanae, the least specialized of the living Syncarida, is partly ambulatory. Descriptions of walking limb morphology appear in Snodgrass (1965) and Carpentier & Barlet

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FIGURE 36. *Palaemon*. (*a*) Pereopods I–V, right. Lateral view of thorax, showing attachment of coxae, the basis of pereopod V and the entire pereopod III. The limb plane rises out of the paper to the right. Hinge lines that are oblique to the viewing plane taper as they extend away from the viewer. Those of body–co., ba.–i. and c.–p. are in the limb plane, whereas co.–ba., i.–m., m.–c. and p.–d. are perpendicular to it. (*b–d*) Pereopod III, right. Body–co. and co.–ba. articulations. (*b*) Lateral view. (*c*) Ventral view. The body–co. hinge line (a) allows promotion/remotion; that of co.–ba. (b) permits abduction/adduction. The resulting gimbal allows mobility of the distal portion of the limb. (*d*) Outline of proximal edge of basis in same view as (*c*) to show muscle insertions (see figures 37–39). (*e*) Pereopods II–IV, left. Medial view of body cavity, showing proximal portion of visible extrinsic musculature. Pereopod III is subjected to further dissection in figures 37–39 and is figured in the same view in figure 38*a*. Symbols: x, attachment opening for branchia; y, ligaments extending from posterior shelf (z) to lateral body wall; z, posterior shelf of ventral cuticle overhanging the insertion of the limb and giving origin to some extrinsic muscles.

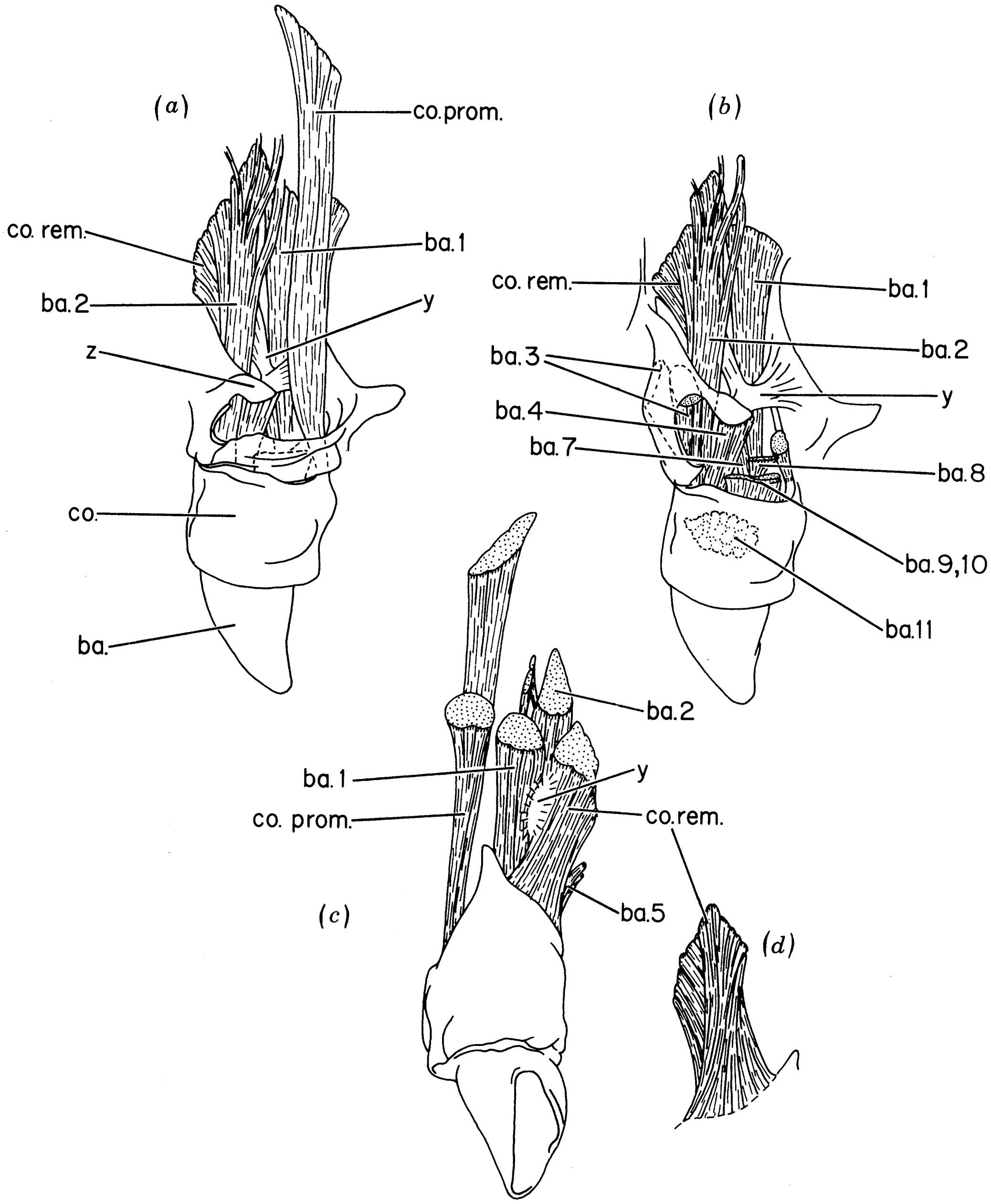

Figure 38. *Palaemon*, pereopod III, left. Coxal and basal musculature. (*a*, *b*) Medial view in advancing stages of dissection. (*a*) Portion of ventroposterior cuticle medial to posterior shelf (z) cut away. (*b*) Medial body–co., arthrodial membrane removed and most of muscle co.prom. cut away. (*c*) Lateral view, with body wall removed. (*d*) Muscle co.rem. in anterior view. Symbols: y, z, see legend of figure 36.

(1959). All eight pereopods are much alike, although they grade from anterior limbs with shorter, more robust distal podomeres to longer, more slender limbs posteriorly. This is related to the feeding activity of the anterior limbs. Pereopod VII has a reduced exopod and pereopod VIII lacks one. An intrabasal articulation present in other pereopods is missing on pereopods VII–VIII and nearly so on VI. Pereopods V–VI (figure 40) were studied because they are sufficiently posterior to minimize trophic functions, yet not so far back as to have posterior reductions.

As in previous taxa, the endopod has a pronounced limb plane (figure 40). All articulations are dicondylic. Of them, i.–m., m.–c. and p.–d. allow movement in the plane, whereas ba.–i. and c.–p. permit movement perpendicular to the plane. All have a pair of opposing muscle groups.

As far back as pereopods V–VI, the limb plane has an anterolateral–posteromedial slant to its primarily transverse orientation, although the plane of the coxa and basis is completely transverse. The shift in orientation is a result of the anterolateral–posteromedial positioning of the ba.–i. articular condyles. The limb plane is vertical on anterior pereopods, but is gradually tilted on posterior limbs, with the posterior surface facing upward.

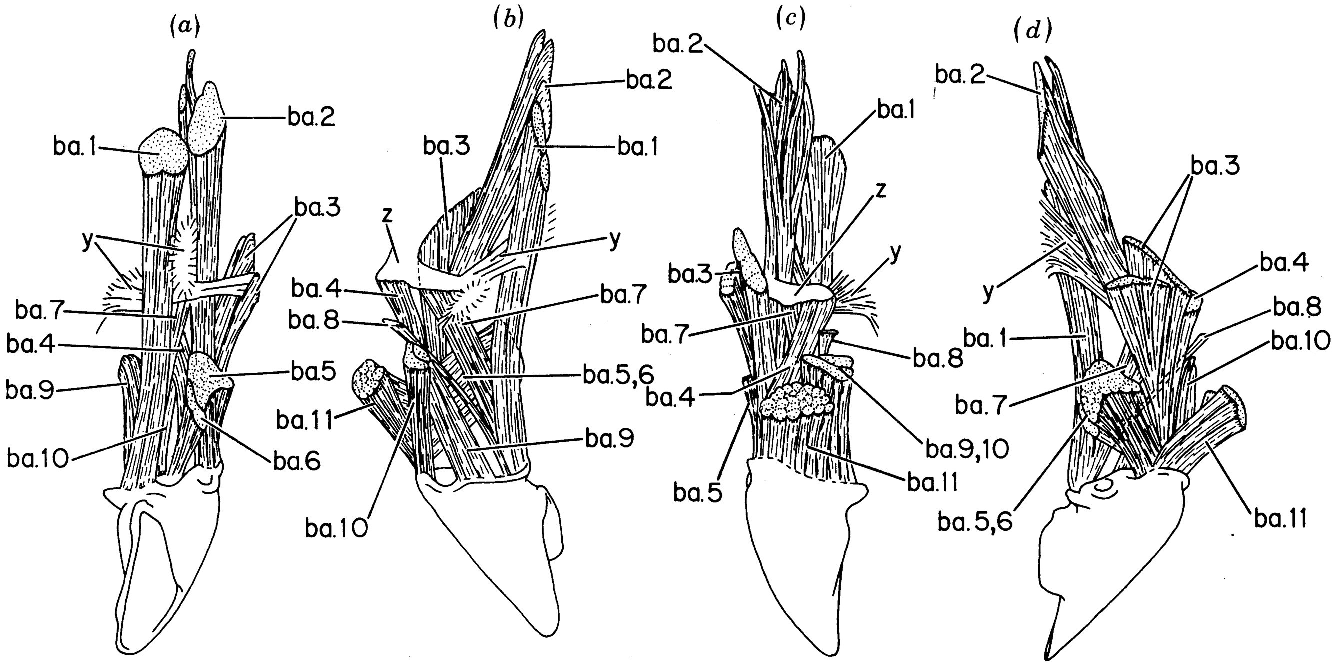

FIGURE 39. *Palaemon*, pereopod III, left. Basal musculature. (*a*) Lateral view. (*b*) Anterior view. (*c*) Medial view. (*d*) Posterior view. Muscles ba. 3, 9–11 are levators (abductors), and muscles ba. 4–8, 12–13 are depressors (adductors) according to the position of their insertions with respect to the articulating axis (figure 36*c*, *d*). Symbols: y, z, see legend of figure 36.

The junction of coxa with body forms an elongate, transverse oval, with the base of the coxa somewhat invaginated into the body, especially laterally (figure 41*a*, *c*). The arthrodial membrane is narrowest laterally and medially; only laterally is an articular condyle vaguely indicated. This, combined with the transverse elongation of the junction, suggests that promotion/remotion is the dominant movement.

The morphology of the coxa is complex. Anteriorly, it is well sclerotized. Laterally, except for a proximal rim of sclerotized cuticle that runs to the lateral condyle, it consists of a broad field of thin flexible cuticle surrounding the insertion of the epipods. A small rigid strut extends from the anterior sclerotized cuticle to the base of the anterior epipod. The medial edge of the coxa extends to the midline of the trunk, where it forms a small, setose, anteriorly directed endite. The posterior face of the coxa is deeper, but poorly sclerotized posteromedially. Its main structural element is a heavily sclerotized vertical beam that ascends from the posterior co.–ba. condyle to a large proximal apodeme (figure 41*a*, *c*: y). The latter curves up and forward to join the main ventral intersegmental tendon of the trunk at the base of the ventral longitudinal trunk muscle (figure 41*b*, *d*: x). This buttress would seem to inhibit promotion/remotion.

The coxal musculature is simple (figure 41*b*, *d*). A large muscle (co.rem.) originates on the lateral or ventrolateral body wall and descends obliquely to insert on the posterolateral face of the coxa. Anteriorly, a smaller sheet of short fibres (co.prom.) originates from the ventro-anterior body wall and descends obliquely mediad to insert on the anterior proximal rim of the coxa. A third muscle from the ventrolateral body wall at the anterior edge of the somite descends obliquely posteriad to insert with the posterior coxal muscle. The junction of the coxa with the body is too complicated for one to be certain what these muscles do.

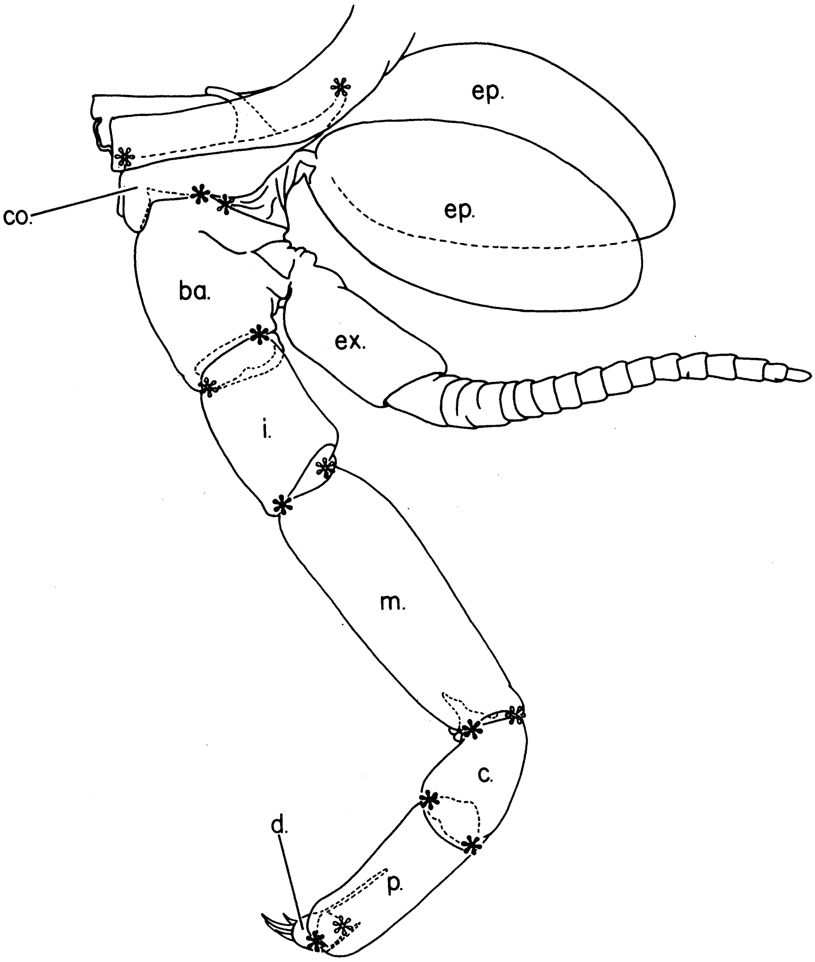

FIGURE 40. *Anaspides*, thoracopod VI, left. Anterior view showing general morphology.

The situation is further complicated by a potential zone of flexibility in the ventral body wall itself (figure 41*c*: z). This extends from posterior to the limb, dorsolaterally, and descends along the lateral wall toward the coxal margin anterior to the lateral body–co. hinge point.

The basis has distinct co.–ba. condyles in the middle of its anterior and posterior margins. Elsewhere, co.–ba. consists of ample arthrodial membrane. The result is a strong antero-posterior hinge line that allows abduction/adduction (equivalent to levation/depression). An additional zone of articulation runs transversely across the proximal quarter of the basis

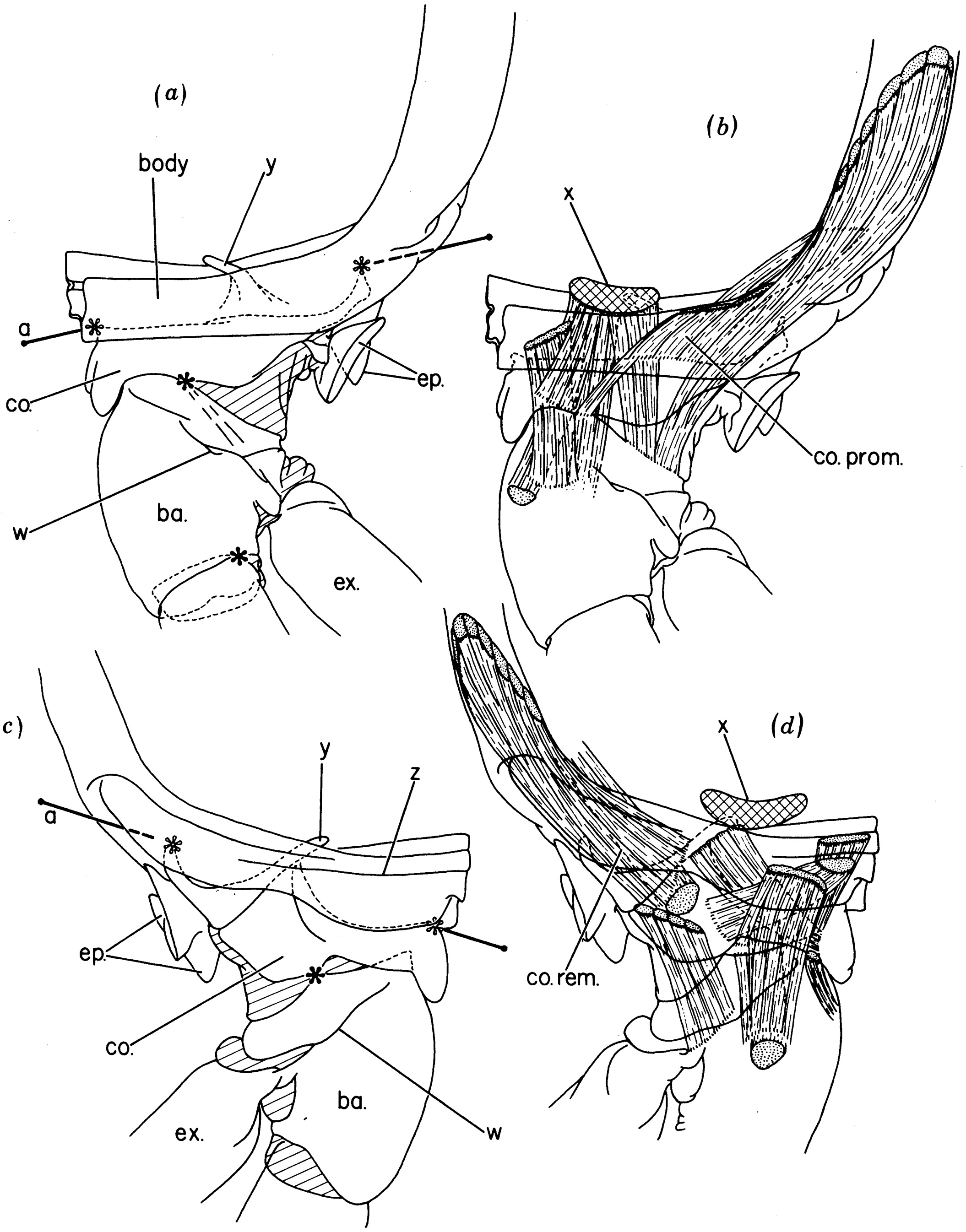

FIGURE 41. *Anaspides*, thoracopod V, left. (*a*, *b*) Anterior views. (*a*) Cuticular structures. (*b*) Anterior coxal and basal musculature. (*c*, *d*) Posterior views. (*c*) Cuticular structures. (*d*) Posterior coxal and basal musculature. Symbols: w, intrabasal articulation; x, ventral longitudinal trunk muscle; y, apodeme from posterior coxal wall, apically in close conjunction with x; z, zone of potential flexibility within posterior body cuticle.

(figure 41*a*, *c*: w). Laterally, it becomes the articulating membrane of the ba.–exopod junction. This intrabasal articulation allows a slight amount of levation/depression when moved with a probe and may simply enhance the motion of co.–ba. The musculature of the basis is so complicated that less obvious functions may also be possible.

The co.–ba. musculature originates on the lateral, ventroposterior and ventromedial body wall, on the ventral intersegmental tendon, on the posterior coxal apodeme, and on the anterior and posterior faces of the coxa itself. Most of the insertions are on the proximal margin of the basis or its walls distal to the intrabasal articulation. One muscle, however, inserts on one of the many ligaments that run between anterior and posterior faces of the podomere. The positioning of these muscles both lateral and medial to the hinge line gives ample evidence of the ability to conduct both abduction and adduction.

I observed living *Anaspides* in their natural habitat and in the laboratory. In walking, pereopodal endopods cause most of the propulsion, but the pleopods and pereopodal exopods are also active. Endopodal movement involves extension and flexion within the limb plane, primarily at i.–m. and m.–c. Promotion/remotion occurs at body–co. and at ba.–i., which unlike the similarly oriented articulation in decapods is heavily muscled.

An examination of a potassium hydroxide preparation of pereopod V from *Paranaspides lacustris* revealed the same morphology as *Anaspides*. Living *Paranaspides* moved like *Anaspides*, but had a more powerful caridoid escape reaction and spent more time swimming.

Discussion

Limb morphology and function

The preceding descriptions detail skeletomuscular patterns which vary between taxa. Conversely, assuming they were sampled randomly, the patterns display surprising constancy within orders. Except for variation in the degree of coxal fusion (to be treated below), representatives of four suborders of Isopoda were alike in all fundamental features. The monokonophoran and dikonophoran tanaidaceans were the same. Three families of gammaridean amphipods did not differ, and the base of the caprellidean limb followed the gammaridean pattern, in spite of substantial modifications in the rest of the body. Both mysidaceans were the same, as were the two anaspidacean syncarids. The same pattern reappeared monotonously within the decapods. These intraordinal similarities exist in spite of major differences in life style, of gammarideans and caprellideans, for example. Thus the distinctiveness and internal continuity of orders, which have been documented in many other ways, are repeated in pereopodal skeletomusculature.

At the most gross level, all limbs described follow a common pattern. In all, the arc of the limbs between base and tip is such that the body is suspended between them rather than resting upon them (Manton 1977). The orientation of the podomeres is such that a limb plane passes through the axis of all endopodal podomeres, usually the basis, and in decapods, even the coxa. The joints are dicondylic, and most of them form strong hinges whose orientation limits movement to flexion and extension within this limb plane.

In all peracarids except the mysidaceans, m.–c. is the only intrinsic articulation that allows distortion of the limb plane. In mysidaceans, it is i.–m. (and sometimes ba.–i.), and in decapods and syncarids, it is ba.–i., i.–m. and primarily c.–p. (List 1895; Macmillan 1975). In spite of the ability to bend part of the endopod out of the limb plane, this does not happen during walking. The distance between body and distal tip of the appendage may change, but the extension and flexion that cause it are in the limb plane. This plane may make marked changes in orientation, but for the most part it retains its integrity. The changes in orientation are permitted by articulations at the limb base.

The most reasonable explanation for articulations that result in bending of the limb plane is that they allow the animal to compensate for irregularities in the substrate and are vital in other activities, such as grooming. The relative uselessness of ba.–i. in decapods is revealed by its frequent fusion. In brachyurans i.–m. may also be immobilized.

A limb plane occurs in many non-malacostracan taxa as well. It is found in the terrestrial arthropods (Manton 1977), and in the walking limbs of mammals and birds. Amphibians and reptiles tend to be exceptions, in that the feet are at an angle to the plane that passes through upper and lower limb segments.

The principal exceptions to the presence of a limb plane occur when the appendage is additionally or exclusively used for purposes other than walking. The decapodan cheliped (thoracopod IV) can bend in a variety of directions (List 1895; Kukenthal & Krumbach 1927), allowing the manipulation of objects obtained from various positions in relation to the cephalon, and presentation of food items to the mouth field. The limb plane on a decapodan pereopod (*Astacus*, for example) may be strongly bent when it is used to groom the top of the carapace. The primate forelimb used in feeding and brachiation is an example within the vertebrates. If a pereopod is used for swimming or burrowing, its distal podomeres may be bent at angles with respect to the proximal ones, as seen in pereopods V–VII of the cumacean *Diastylis rathkeii* and the asellote isopod *Ilyarachna longicornis*. Here they are used for burrowing, and in the latter for swimming as well (personal observation). Both burrowing and swimming are different from walking; in walking, force is exerted on the surrounding medium only at the tip of the limb, whereas in swimming and burrowing more proximal limb surfaces are involved. The portion of the limb that exerts force on the surrounding medium is bent to enhance resistance; proximal to this, the limb usually is oriented in a plane.

As an animal walks, the orientation of the limb plane must change except when the base of the limb is in the same exsagittal plane as its tip, and even then the plane's angle of tilt alters if its orientation is not vertical. In eumalacostracans of this study, most pereopods are oriented so that in walking the limb plane tilts and rotates with respect to a vertical, transverse reference plane. Other demands for flexibility at the base of the limb result from the occasional need to position the limb in non-locomotory positions.

The adaptive rationale for the existence of a limb plane that moves at its base appears to be maximization of potential movement by minimum amount of limb structure. There are two types of limb action: as an extensible strut, as in punting a boat, or as a lever, as in rowing (Gray 1944). Action as an extensible strut involves flexion/extension between podomeres within the limb plane, the dominant action where the limb plane is parallel to the direction of motion. Such movements are not enhanced by bends in the limb plane. On the contrary, a joint yields the maximum amount of extension/flexion when the common plane of its component podomeres is parallel to the line running between base and tip of the limb. In lever action the whole limb plane is rotated/tilted about its base, as is usual with transversely oriented limbs. The distance covered in a single stroke is maximized if the lever arm involves the whole limb rather than a part of it. This is why locomotion that results from bending the limb plane is less effective than moving the entire plane. Thus, as a lever and as an extensible strut, a limb plane is most efficient.

When an organism is propelled at a constant rate by means of limbs, the only parts of the body that accelerate/decelerate are the limbs themselves (Alexander 1971). Energy is conserved if limb mass is minimized and if mass is concentrated toward the base. Accordingly, limbs taper towards their tips and musculature of an articulation is rarely found distal to the joint (Alexander 1971), yet another reason why levering the entire limb plane is most efficient; it allows the concomitant complex and bulky musculature to be located in the trunk rather than the limb.

Among eumalacostracans, there are two ways to achieve flexible movement at the base of the limb. Hansen saw this (1930) but he did not expand upon the observation. The first is best seen in the decapods, where the hinge line between body and coxa is primarily transverse, allowing promotion/remotion, and that between coxa and basis is longitudinal, permitting levation/depression. Because the coxa is short, these two directions of motion are nearly superimposed, and the limb distal to the coxa is gimballed to move in any direction. This system is present in all the decapods that I have been able to examine, including penaeid and caridean natantians, and palinurid, astacurid, anomurid and brachyuran reptantians, and has been previously documented for *Homarus americanus* (Macmillan 1975), *Cambarus longulus* (Snodgrass 1965) and *Astacus fluviatilis* (List 1895).

The coxal gimbal is also found in anaspidacean syncarids. This taxon is unique in having ba.–i. promotion/remotion in addition to that of body–co. This accessory promotion/remotion occurs close to the body because the coxa and basis are short, so that most of the limb still conforms to a plane. The large posterior invagination of the coxa that unites with the ventral intersegmental body tendon and the secondary zones of flexibility within the basis cannot be explained. The similarity in limb morphology of *Anaspides* and *Paranaspides* in spite of their different life styles suggests that these structures are fundamental to the group.

The second system of proximal limb flexibility is seen in all peracarids except the Mysidacea. Here, the coxa is either fused to the body or possesses limited flexibility in a single plane. The co.–ba. articulation, on the other hand, is capable of movement in any direction, and of some degree of rotation. This is because a single condyle is located near the long axis of the basis. The proximity of the condyle to the axis avoids the limitation of most monocondylic articulations by allowing muscles to insert all around it, making powerful movements possible in any direction. This system has been described incompletely and somewhat inaccurately for *Ligia oceanica* (Alexander 1972). Snodgrass (1965) illustrates the limb of *Ligyda exotica* in terms closely comparable to those described here.

Phylogeny of limb types

The Syncarida, Eucarida and Peracarida are generally regarded as composing a monophyletic assemblage (Calman 1909; Siewing 1960), the central evidence being their common possession, to some extent, of the suite of features called the caridoid facies. Of the two types of pereopod found in this complex, the most primitive is the limb with the gimballed coxa. Locomotion by means of promotion/remotion of the limb at the junction between body and coxa is basic to crustaceans (Manton 1977). It has been described for cephalocarids (Sanders 1963), branchiopods (Cannon 1928) and copepods (Perryman 1961), as well as the leptostracans (Cannon 1927), which are the most primitive living malacostracans. The presence of body–co. promotion/remotion in eumalacostracans is no more than a continuation of the basic crustacean pattern. Similarly, the existence in syncarids and decapods of a dicondylic co.–ba. that permits abduction/adduction suggests that the other demicomponent of the coxal gimbal is also primitive, at least within the Eumalacostraca.

On the other hand, the invaginated monocondylic co.–ba. of peracarids is unique among crustaceans, suggesting that it is an acquired feature. Some taxa show how the peracaridan system could have evolved from the other. The intermediate condition of the Mysidacea is particularly illuminating. The co.–ba. possesses a dicondylic, anteroposterior hinge line, as with the coxal gimbal, but the body–co. hinge line is also anteroposterior, and therefore incapable of promotion/remotion. Instead, a secondary, transverse, intrabasal articulation line allows the shortening of the anterior face of the basis, so that the limb pivots forward on the posterior condyle (figure 32*b*, *c*). The result is a flexibility of the co.–ba. region like that of other peracarids. The posterior condyle is also invaginated toward the long axis of the basis, allowing muscles to insert all around it and enabling them to power anteroposterior and transverse components of motion.

It is not difficult to imagine a gradual development of the intrabasal articulation, concomitant with the infolding of the posterior condyle, as the body–co. gradually lost its capacity for promotion/remotion. Similarly, it is but a short step from the mysidacean condition to one where the small, detached piece of basal cuticle became converted to arthrodial membrane, resulting in a limb no different from that of other peracarids. This transition involves no maladapted intermediates.

The most extreme development of the peracaridan system is found in the valviferan, oniscid and, in part, phreatoicid isopods, pereopods I–IV on cumaceans, and pereopods VI–VII on dikonophoran tanaidaceans. Here the coxa is completely fused to the body, and all proximal mobility is concentrated at co.–ba. More generally, the coxa is capable of feeble, limited movement, with only a partial promotor/remotor component. In Mysidacea, spelaeogriphaceans, amphipods and pereopods II–V of dikonophoran tanaidaceans, the body–co. hinge line is anteroposterior, an orientation opposite to that of the decapodan body–co. Here, as with the fused coxa, there is clearly no need for coxal promotion/remotion in locomotion. The body–co. hinge line of at least some limbs allows a promotor/remotor component only in cumaceans, phreatoicid and asellote isopods, and monokonophoran tanaidaceans. The mobility of body–co. in peracarids must be homologous with that of the coxal gimbal in decapods and with body–co. of Crustacea in general. However, there is insufficient evidence to decide whether the orientation permitting a promotor/remotor component in some groups is also homologous or whether it has secondarily re-evolved. The loss of this motion in mysidaceans and spelaeogriphaceans (both primitive taxa) argues for its secondary acquisition, but mosaic evolution is equally realistic.

The evolutionary significance of the dicondylic co.–ba. in pereopods II–IV of tanaidaceans and pereopods I–VII of amphipods needs consideration. With pereopods I–IV of amphipods (figures 23–26), the lateral condyle is just like other peracarids. The medial condyle is feebly developed and does not prevent the flexibility of motion seen in monocondylic pericaridan limbs. It suggests that this condyle is a secondary acquisition. The system of two flexible condyles combined with a pulley system that is seen on pereopods V–VII (figures 27, 28, 29*c*) is unique and provides no evidence as to its origins. The fact that pereopod VII can be as in other peracarids (*Gammarus*; figure 29*a*) reveals that the two systems may not be entirely unrelated. In tanaidaceans (figure 13, 16*a*), the lateral condyle of pereopods II–IV is as in other peracarids; the medial condyle has a looser articulation that is differently developed.

There are three possible explanations for the condition of amphipods and tanaidaceans. The dicondylic co.–ba. may be plesiomorphic and the peracaridan monocondylic joint is a secondary development within these taxa and therefore has evolved convergently. Secondly, the peracaridan co.–ba. might have evolved on some of their appendages, while the dicondylic co.–ba.

was retained on others. This avoids proposing convergence but requires explanation for why one condyle in a dicondylic joint is so like the peracaridan monocondyle. Thirdly, the ancestors of tanaidaceans and amphipods may have had a peracaridan system and secondarily regained a dicondylic co.–ba. as part of amphipodan and tanaidacean morphologies and life styles. The most primitive tanaidaceans, the Monokonophora, are burrowers, a habit that may require a dicondylic co.–ba. on the anterior pereopods for strong remotion. In amphipods, the adaptive significance may be related to the complex functional interrelationships that gave rise to strong lateral compression of the body (Dahl 1976).

The peracaridan orders, excluding the Amphipoda, embody various degrees of advancement from the most primitive condition, that of the caridoid facies, best developed in the lophogastrid Mysidacea (Calman 1909; Siewing 1960, 1963). Major elements in this change are the reduction of the carapace fold, with concomitant reduction of the branchial chamber and epipodal gills, reduction of the abdomen and its limbs as locomotory structures, loss of pereopodal exopods, reduction of the antennal scale, and immobilization of the eyes. On a subjective gradient, the ordination of the taxa is Mysidacea, Spelaeogriphacea/Cumacea, Tanaidacea, Isopoda. The rates of reduction of the different structures are not perfectly correlated, and each order has incorporated some specializations that preclude any being directly on the lineage of the more advanced orders. In short, they reflect grades of evolution.

Differences in proximal limb skeletomusculature seem to correlate with this gradient. Most obvious is the simplification of the co.–ba. musculature. If all muscle bundles with the same attachment and general origin are grouped as a single functional unit, it is clear that isopods (figures 8, 9) and tanaidaceans (figures 13, 14) have far fewer units than have cumaceans (figures 18, 19) or spelaeogriphaceans (figures 21, 22), and that lophogastrid mysidaceans (figures 30–32) are the most complex of all. This simplification reflects loss of ventral elements, muscles that originate from the coxa or ventral body wall. In mysidaceans, such muscles are both numerous and frequently powerful. In isopods and tanaidaceans, only a few, small muscles remain. Of all the peracarids, the Mysidacea are most similar in this respect to non-peracarids, particularly the Syncarida (figure 41), and, therefore, it is intriguing that both mysidaceans and syncarids possess a similar secondary proximal articulation on the basis (pp. 277, 288).

Speculation on the meaning of the simplification of the basal musculature within the peracarids will not be attempted here. The causes are likely to be complex and involve factors that would seem unrelated. For example, competing needs for internal space by other organ systems and the forces that caused the external shape of the thorax to evolve to its present form would have to be considered. This is beyond the scope of the present study. Evolution of hinge structures to allow a simpler, more stereotyped musculature is not the answer. The musculature of the decapodan basis is extremely complex (figure 39), even though co.–ba. is a rigid dicondylic hinge (figure 36*b*, *c*). Isopods have a far more flexible co.–ba., and yet their musculature is simpler. A detailed neuromuscular analysis of decapodan movement might solve this problem.

Adaptive significance, correlates and problems

The adaptive significance of the peracaridan limb remains to be discussed. What selective force could cause so profound a change? It must be one that would apply to all the Peracarida, in spite of their tremendous variety of morphologies and life styles. Of those few features that define the taxon, only one gives any sensible correlation: the marsupium.

Peracarids brood their young. The brood chamber, or marsupium, lies between the thoracic limbs and is formed by one to seven pairs of medially directed oostegites, each stemming from the medial surface of a pereopodal coxa (figures 2, 5*a*, 15*a*, 17*b*, 30, 31). To be effective, there must be a stable chamber. This would not be so if every time a pereopod moved the oostegite moved, but such would be the inevitable consequence of a coxa that performed promotion/remotion every time the animal took a step. The resulting movement of the oostegites would disturb the developing embryos and increase mortality rate or accidental loss..

To prevent this, the coxa had to be immobilized, which required abandonment of the coxal gimbal and the evolution of a new mechanism for allowing flexibility of motion at the base of the limb. The result was the peracaridan co.–ba.

In broad terms, this hypothesis makes good sense, but, as one would expect in a taxon this large, there are apparent inconsistencies and exceptions.

The most interesting problem arises in the asellote isopods *Janiralata* and *Asellus*. Here the coxa articulates with the body on pereopods II–VII. On males and non-brooding females, the dicondylic hinge is sufficiently transverse that promotion/remotion results. The peracaridan co.–ba. is fully developed, yet its functional potential is not fully realized because an external coxal flange restricts its ability to promote/remote. The resulting movements are similar to those of the gimballed coxa of decapods (pp. 283, 285). Abruptly, the situation changes in with fully developed oostegites and coxal promotion/remotion is no longer possible. This movement is one of the functions of the now unrestricted co.–ba. Thus, asellotes demonstrate the importance of eliminating coxal promotion/remotion in a brooding female.

Within the Peracarida, only pereopods I–IV in asellotes and pereopod V in cumaceans and monokonophorans possess a promotable/remotable coxa which bears oostegites. In other taxa, if an oostegite-bearing coxa is mobile, the movement is slight abduction/adduction. There is insufficient information to determine whether the former condition is plesiomorphic or whether it is reacquired. In either case it is hard to understand why a promotable/remotable coxa is necessary; the complete adequacy of the co.–ba. is well documented in the other isopodan suborders, where the coxa is immobile.

On more posterior pereopods, a coxa capable of some promotion/remotion is found in asellotes and phreatoicoids, monokonophoran tanaidaceans and cumaceans. Even then, the narrow arthrodial membrane and poor musculature suggest feeble motion. Observations of *Apseudes* showed that most promotion/remotion was accomplished at co.–ba. Except for pereopod V in monokonophorans and cumaceans, these limbs do not bear oostegites, and, therefore, such coxal motion does not conflict with the functioning of the marsupium. Again, it is uncertain whether this condition is plesiomorphic.

There is little reason to question the primitive nature of body–co. mobility *per se*, but in most peracarids its axis has shifted to favour abduction/adduction, and mobility is slight. Coxal abduction/adduction probably serves more than one purpose. On oostegite-bearing limbs, the resulting motion of oostegites would be levation/depression, causing expansion and contraction of the brood chamber. This would enable ventilation of the eggs, and such marsupial movement is commonly observed. In the laterally compressed amphipods and pereopods II–IV of tube or burrow-building tanaidaceans, coxal abduction would enlarge the range of positions in which the limbs can operate. In effect, the system is a functional gimbal, as in decapods, but the roles of body–co. and co.–ba. are reversed.

In peracaridan females, the peracaridan co.–ba. is present even in prebrooding instars.

This is not surprising; the differences between this and the dicondylic co.–ba. are so great that profound metamorphosis would be required for conversion. Not only the articulation would have to change, but the arrangement of muscles as well, and this would have to take place in a single ecdysis without benefit of diapause or a pupa. It is simpler or less costly to use throughout life the system that is compatible with reproduction.

Except perhaps in amphipods, the non-oostegal pereopods also possess the peracaridan co.–ba. This might have happened in two ways. Primitively, all pereopods bore oostegites, as shown in lophogastrids today. This might also be an indication of genetic economy. Genetic instructions that confer tagmatic differences between somites are acceptable when tagmosis results in adaptive improvements. If two systems are equally acceptable on one set of somites, but one is superior on another set, it would seem economical that the latter be used on both sets of somites to avoid carrying unnecessary genetic information. A similar argument can be made for why male peracarids also possess the peracaridan co.–ba., with an additional suggestion that it is unlikely that genetic information for something as basic as major locomotory mechanisms would be on the sexual chromosomes.

One last apparent exception to the correlation between oostegites and the peracaridan co.–ba. is seen in the Thermosbaenacea, where brooding takes place under the carapace fold subthoracically. If this taxon has evolved from one with a typical peracaridan marsupium (Fryer 1964), then one could argue that the peracaridan co.–ba. was retained. If it is ever proven that the ancestors of thermosbaenaceans never possessed oostegites (Siewing 1958), then one could conclude that other causes result in a similar structure. The anterior origin of the co.–ba. condyle is unique to thermosbaenaceans, supporting the argument of independent evolution.

Although the peracaridan co.–ba. system is unique within the Malacostraca it is not unique among the arthropods. A comparable configuration occurs in body–co. of some pterygote insects (Snodgrass 1935; Manton 1977). In the orthopteran *Dissosteria*, a single lateral condyle is displaced inwardly toward the limb axis, the major muscle masses descend from the dorsal or lateral body wall to insertions on all quadrants of the proximal margin of the coxa, and there are smaller oblique rotators with ventral origins (Snodgrass 1935). While this system is functionally the same, it is not homologous in the two taxa, as shown by its independent ancestry (Manton 1977) and the difference of which podomeres are involved. It is not clear why this particular mechanism has evolved in some insects. That it is unrelated to brooding does not invalidate the hypothesis of its relationship in peracarids.

The Peracarida are among the most successful crustaceans. Since eucarids are another extremely successful taxon, much of this success must be due to attributes common to the Malacostraca as a whole. It is reasonable to conclude that peracaridan traits are also critical to peracaridan success. The most important must be the ability to brood young in a ventral thoracic marsupium. In effect, larval stages have been eliminated, resulting in a shift away from larval dispersal, which is so critical in other taxa. Brood protection dramatically decreases mortality of young and therefore influences the fecundity necessary to sustain the species. Peracarids are the most successful arthropods in the deep-sea benthos, and the energy saved by brood protection in the nutrition-poor environment is surely one of the reasons.

Peracarids are also the only crustaceans to have invaded the terrestrial environment with major success. Here, the role of brood protection is obvious; peracarids are not tied to an aqueous medium for their early free-living stages. Nevertheless, the move onto land was not the stimulus for brood protection, since exclusively aqueous forms possess the ability. Rather, brood protection must be regarded as a potent preadaptation.

The driving force for the evolution of the peracaridan limb must, therefore, be measured in terms of the selective advantage of brood protection, for if the hypothesis is correct, the oostegal marsupium could not have evolved without it. This is example of the necessity of the holistic approach to the evolution of functional systems (Dahl 1976); attributes as seemingly unrelated as fecundity and locomotory ability can be inextricably coupled.

This paper is dedicated to the memory of Dr S. M. Manton, F.R.S., whose enormous productivity and critical leadership in the study of arthropod functional morphology and phylogeny will continue to be felt for decades to come.

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List of symbols and abbreviations

a	body–coxa hinge line
b	coxa–basis hinge line
abd.	abductor
add.	adductor
ant.	anterior
arth.	arthrodial membrane
ba.	basis
ba. 1–*n*	basal muscles 1–*n* (numbering of specific muscles is consistent only within an order)
c.	carpus
co.	coxa
d.	dactylus
e–g	axes of muscle contraction, explained in specific figure legend
ep.	epipod
ex.	exopod
ext.	extensor
fl.	flexor
i.	ischium
lig.	ligament
m.	merus
med.	medial
oost.	oostegite
p.	propodus
per. 1–7	pereonites 1–7
per. I–VII	pereopods I–VII
prom.	promotor
rem.	remotor
rot.	rotator
ster.	sternite
tend.	tendon
terg.	tergite
u–z	variable meaning, explained in specific figure legend
*	articulating condyle
•——— ———•	axis of articulation
diagonal shading	arthrodial membrane or cut edge of a structure