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Systematics of the Cumacea (Crustacea)

Pilar A. Haye

SYSTEMATICS OF THE CUMACEA (CRUSTACEA)

By

Pilar A. Haye

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Advisory Committee:

Irv Kornfield, Professor of Zoology, Co-Advisor

Les Watling, Professor of Biological Oceanography, Co-Advisor

Christopher Campbell, Professor of Plant Systematics

Keith Hutchison, Professor of Biochemistry

Seth Tyler, Professor of Zoology

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Thesis Co-Advisors: Dr. Irv Kornfield and Dr. Les Watling

An Abstract of the Thesis Presented
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Cumaceans are small benthic crustaceans. They have a marine cosmopolitan distribution with diversity increasing with depth. There are approximately 1,400 described species of cumaceans. Despite the fact that they offer a good model for the study of morphological evolution and biogeography, the studies on the Order Cumacea are almost restricted to work at the alpha taxonomy level. This thesis contributes to the systematics of Cumacea.

The phylogenetic relationships within the Cumacea were studied using newly obtained partial amino acid sequences from the mitochondrial gene Cytochrome Oxidase I. Among other findings, phylogenetic analyses revealed that the families Bodotriidae, Leuconidae, and Nannastacidae, characterized by the presence of a pleotelson (telson fused to last abdominal segment), form a monophyletic and derived clade. The gene tree topology suggests that some characters traditionally used in cumacean diagnoses represent homoplasies.

The cumacean family Bodotriidae is divided into three subfamilies and 34 genera with over 350 species, all of which were morphologically analyzed for 114 variable characters. Two main accomplishments were a result of this study. First, the phylogenetic relationships of the subfamilies and genera within the family were studied. The subfamily Mancocumatinae failed to resolve as a monophyletic group, the subfamily Vaunthompsoniinae are basal bodotriids, and the subfamily Bodotriinae is the most derived clade. A Tethyan origin for the bodotriid fauna is suggested, with radiation along the Atlantic Ocean during the Cretaceous. Phylogenetic and character evolution analyses support several changes to the classification of Bodotriidae. For

example, the subfamily Mancocumatinae should be incorporated into the subfamily Vaunthompsoniinae, the genus *Coricuma* should be incorporated into the Bodotriinae, and the species of the genera *Heterocuma*, *Mossambicuma*, *Pseudocyclaspis*, should be incorporated into the genera *Cumopsis*, *Eocuma* and *Cyclaspis*, respectively. Second, a comprehensive morphological work on the Family Bodotriidae was completed incorporating the suggested changes in the taxonomy. The generic review includes a dichotomous key and rediagnosis of each of the genera of the Family.

A new species of *Austrocuma* from the eastern coast of India is described. Among other characters, the uniqueness of this species relies on the presence of only four pleopods on the males.

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I need to thank undergraduate students that have been involved in my thesis work. Amber Goetz helped me by picking cumaceans from benthic samples otained in Chile. Gopinatha Alberts also assited with sorting of cumaceans, but more importantly, she helped on the generation of sequence data for the outgroup taxa. I want to thank Karen Smith who helped with PCR, electrophoresis and cloning for an extensive period of time. Finally, I would like to thank Charmaine Patel. Charmaine has been an excellent student who has become very interested and knowledgeable on cumaceans. To teach has been a very stimulating and rewarding experience.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

INTRODUCTION TO THE CUMACEA

The crustacean Superorder Peracarida (Malacostraca, Eumalacostraca) includes eight orders: Amphipoda, Cumacea, Isopoda, Mictacea, Mysidacea, Spelaeogriphacea, Tanaidacea, and Thermosbaenacea. Cumaceans have been known since 1780 when J. Lepechin described *Oniscus scorpioides* (=*Diastylis scorpioides*). Initially it was thought that cumaceans were larval decapods, until Krøyer (1841) described pregnant females, and some years later they were finally recognized as a separate taxonomic entity. By 1870, 51 species of cumaceans were known, and currently approximately 1,400 species have been described.

Cumaceans have a cosmopolitan distribution. They are a major component of the benthic fauna and demersal zooplankton (Hessler and Sanders, 1967; Quintana, 1986; Wang and Dauvin, 1994; Dauvin et al., 1995; Grabe, 1996; Cunha et al., 1997) and have been extensively reported as food items for teleosts and other macrofauna (e.g., Jaime and Kong, 1992; Cartes, 1993; Tokranov and Maksimenkov, 1994; Schlacher and Wooldridge, 1996; Olaso et al., 2000). When burrowed in the sediment most cumaceans feed by scraping sand grains (Foxon, 1936; Dixon, 1944; Bachmann and Moguilevsky, 1973).

Cumaceans are elusive to study: they are small (usually less than 1 cm), inhabit deep waters, and generally occur within the substrate. Knowledge about cumaceans is limited, and little attention has been given to the study of unique aspects of cumacean biology. The diversity of Cumacea increases with depth down the continental slope (Jones and Sanders, 1971; Rex, 1981). Future and ongoing deep-sea expeditions will undoubtedly prove that we now underestimate true cumacean diversity.

Eight families of cumaceans are currently recognized: Bodotriidae Scott (1901) with 360 species, Ceratocumatidae Calman (1905) with 85 species, Diastylidae Bate (1856) with 281 species, Gynodiastylidae Stebbing (1912) with 103 species, Lampropidae Sars (1878) with 90

species, Leuconidae Sars (1878) with 121 species, Nannastacidae Bates (1966) with 350 species, and Pseudocumatidae Sars (1878) with 29 species. Most of the published studies on Cumacea are of taxonomic work at the alpha level. Some efforts have been made to review major groups in the order: for example, Watling (1991a, b, 1998) reviewed the Family Leuconidae and some of the genera of the Nannastacidae, and Gerken (2002) reviewed the Gynodiastylidae. Phylogenetic relationships of Families within the Order have not been investigated.

Anatomy

Cumacean anatomy and sexual dimorphism have been reviewed by Sars (1900), Zimmer (1941), Jones (1963), Jones (1976), Schram (1986), Bâcescu and Petrescu (1999) and others (general anatomy depicted in Fig. 1 and Appendix C).

Malacostracans have five segments forming the head, eight forming the thorax (thoracomers) and six the abdomen or pleon (pleonites). This is known as the 5-8-6 arrangement that defines the Class Malacostraca. The five head appendages, from anterior to posterior are Antenna 1 or antennulae, Antenna 2 or antennae, Mandible, Maxilla 1 or maxillule, and Maxilla 2 or maxillae.

Cumaceans are characterized by a carapace covering the head and three thoracomers. The first three thoracomers have modified appendages, the maxillipeds, which generally assist in feeding and gas exchange. For example, maxilliped 1 has an inwardly oriented projection developed into series of plates or lobes that function as the gill. The remaining thoracomers form the peraeon and each bears a pair of peraeopods, which may be biramous or uniramous.

The cumacean carapace is very conspicuous. It is bulbous and laterally extends anteriorly in lobe-like projections that form a pseudorostrum. Inside the carapace and pseudorostrum is a well-developed and divided respiratory chamber. Cumaceans have a unique respiratory system that directs water currents within the chambers of the carapace, where the gills are found.

The eye lobes, ancestrally two in lateral position (Malzahn, 1972), are generally fused into a single median dorsal eye lobe which may or may not be pigmented or bear lenses. Some

species, particularly within the Family Bodotriidae, have very noticeable eyes that reflect light and have big central eye lenses, while members of the family Leuconidae have completely lost the eyelobe.

The pleon is long and slender and often curls under the body. Together with the carapace, it gives cumaceans their characteristic 'comma' shape. Males may have from zero to five pairs of appendages, or pleopods, on the pleon. Pleopods are usually absent in females, but females of one species have a single pair of pleopods. An articulated terminal telson may be present, or the telson may be fused to the last pleonite to form a pleotelson. The last pair of abdominal appendages is modified as styliform uropods that form a forked tail. By flexing their pleon, cumaceans use the setose uropods to clean the carapace, presumably to keep it from becoming substrate for other forms of life.

Sexual Dimorphism

There is marked sexual dimorphism within the Cumacea (e.g. Duncan, 1983). Males and females show differences in the sculpting and ornamentation of the exoskeleton, mostly associated with the increased mobility of males and the brooding capabilities of the females. Males are relatively smaller than females and much more mobile. The better-developed appendages of males allow them to be slightly superior swimmers compared to females, although cumaceans are only known to swim short distances. Males often have a higher number of peraeopods with exopods than females. These appendages are generally covered with plumose setae that serve as paddles for locomotion. Males may also have well-developed pleopods that may also bear plumose setae and assist in swimming. In addition, males generally have better developed eyes than females. Antenna 2 extends along the body and is easily distinguished in males.

Females generally outnumber males and are larger. Like all other peracarids, cumacean females brood fertilized eggs in a ventral thoracic pouch. In cumaceans, the pouch is formed by the oöstegites, inwardly directed projections, or endites, of the coxa of the thoracopods 3 to 6 (maxilliped 3, and the first three peraeopods). Because of the space requirements for brooding,

females have much bulkier carapaces than males and are almost as wide as deep. Antenna 2 is rudimentary in females.

Life History and Behavior

Cumaceans are usually burrowed in the sediment. To burrow, they use the last four pairs of peraeopods and the pleon. Habitat choice is primarily determined by sediment grain size. Within a relatively small area, individuals show a patchy distribution that corresponds well with the distribution of different grain sizes (Corey, 1970). The distribution of many shallow-water cumaceans is also influenced by temperature, salinity and water dynamics of the benthic environment (Foxon, 1936; Pike & Le Sueur, 1958; Rachor at al., 1982; Modlin & Dardeau, 1987; Vargas, 1989; Modlin, 1992).

Since feeding usually occurs in the sediment and does not require translocation, much of the locomotory behavior is thought be related to courtship and reproduction, molting of the young, and dispersion (Yoda and Aoki, 2002). Many studies have focused on the curious nocturnal vertical migrations that cumaceans exhibit (Steams and Dardeau, 1990; Macquart-Moulin, 1991; Wang and Dauvin, 1994; Dauvin and Zouhiri, 1996). During the day cumaceans are found in the sediment, while at night many are found swimming in the water column (Allredge and King, 1980). This behavior has been widely observed in Cumacea, although there are species-specific patterns of this behavior as well as seasonal variations within species (Watkin, 1941; Corey, 1970; Macquart-Moulin and Castelbon, 1990; Macquart-Moulin, 1991; Yoda and Aoki, 2002). Males and juveniles (but rarely females) of many cumacean species swim into the plankton during the night, a behavior possibly triggered by lack of light or by an endogenous circadian rhythm (Anger and Valentin, 1976; Akiyama and Yoshida, 1990; Macquart-Moulin and Castelbon, 1990; Akiyama, 1995; Akiyama, 1997). Since cumaceans lack a larval stage that allows for dispersal, swimming has been thought to be related to range expansion (Allredge and King, 1980) and for avoidance of demersal fish predators during molting, mating and hatching (Valentin, 1976). Females swim less frequently and usually for shorter periods of time, probably associated with finding a mate or hatching individuals from the marsupium. Some species show

a seasonal pattern of nocturnal vertical migrations that is associated with lunar cycles (Watkin, 1941; Akiyama, 1995; Akiyama, 1997).

Mating occurs as the female molts into the ovigerous exoskeleton when becoming mature (Valentin and Anger, 1977). Mating has been rarely observed, but based on morphological conservation throughout the Order, we can expect it to be similar in different cumacean species. During pre-copulation, males of *Almyracuma proximucoli* clasp the females by the carapace with their oversized third maxillipeds and fist peraeopods (Duncan, 1983). Clasping pairs are in parallel position to each other and in the same antero-posterior orientation, with the dorso of the female in contact with the males ventral surface. They usually remain in the sediment in clasping position, and females continue to feed normally by grasping sand grains. Clasping is continuous until the fertilization molt (up to months under laboratory conditions). Males help females with the fertilization molt by flexing their pleon and using the uropods to remove the old exoskeleton from the pleon of the female. Copulation takes place during fertilization molt (Duncan, 1983).

After fertilization the eggs are released into the brood chamber where multiple eggs are incubated for at least one, and up to three, months (Corey, 1981; Saloman, 1981; Rachor et al., 1982; Corbera et al., 2000). Cumacean fecundity is generally determined by the size of the eggs and the size of the carapace of the female and ranges from a few to 100 eggs (Corey, 1976, Corey 1981, Corey 1983; Persson, 1989; Corbera et al. 2000).

There is a direct relationship between temperature and carapace size of females that determines two basic reproductive strategies for cumaceans. Shallower temperate-water cumaceans tend to reproduce continuously, bi-, or tri- annually, and generally live for less than a year (Corey, 1969, 1981; Duncan, 1984; Roccatagliata, 1991; Yoda and Aoki, 2002). In deeper and colder waters, cumaceans tend to live longer and reproduce once a year (Krüger, 1940; Granger, et al., 1979; Corey, 1983). Depending on the environmental conditions, both these strategies may be present within one species. *Cumoposis goodsir* is distributed along much of the northeast Atlantic coasts, the Mediterranean and Black Seas, and the Vietnamese coast. The Mediterranean populations of *C. goodsir* reproduce throughout the year, whereas the Atlantic

populations in a relatively colder environment, do not reproduce during the winter (Corey, 1969; Corbera et al., 2000).

Cumaceans hatch after three molt cycles within the brood pouch, at a manca stage that resembles the adult form but is missing the last pair of peraeopods, secondary sexual characteristics, and ornamentation of the exoskeleton. Females and males undergo several molts before reaching sexual maturity (Krüger, 1940; Granger et al., 1979; Duncan, 1984; Yoda and Aoki, 2002). Females mate soon after they are mature, and after reproducing they may molt again and brood again (Corey, 1976).

The unique life cycle and biology of cumaceans needs further investigation. For example, basic questions concerning nocturnal vertical migrations, reproductive behavior and ontogeny merit scrutiny. In addition, the discovery of new species that may represent links between currently known taxa may provide insights into the morphological evolution of these charismatic elements of the marine fauna.

Chapter 2

MOLECULAR INSIGHTS INTO CUMACEAN FAMILY RELATIONSHIPS

Introduction

Cumaceans are small (1-10 mm) benthic peracarid crustaceans (Malacostraca, Eumalacostraca, Peracarida) that reside in the surface layer of the sediment of all oceans and seas. A few species inhabit brackish water. Cumaceans can be easily recognized by an inflated carapace that covers at least three thoracic somites and a long, slender, abdomen (Fig. 1A). Comparatively little is known about this diverse group. The approximately 1,400 species are currently arranged into eight widely recognized families: Bodotriidae, Ceratocumatidae, Diastylidae, Gynodiastylidae, Lampropidae, Leuconidae, Nannastacidae, and Pseudocumatidae. The Family Bodotriidae is further subdivided into three subfamilies (Bodotriinae, Mancocumatinae and Vaunthompsoniinae).

The cumacean fossil record is poor. Paleozoic forms represent an early stage in cumacean evolution: they lack a pseudorostrum and have lobed eyes (Schram, 1986). Fossils from the early Jurassic do not differ from extant forms (Bâcescu and Petrescu, 1999).

Phylogenetic hypotheses for relationships among cumacean families are difficult to propose. Current family definitions consist of unique combinations of non-unique character states. Characters are variable within lineages and often overlap between families. Further, some newly discovered cumacean sfpecies cannot be easily assigned to the existing families requiring changes in the family diagnoses or generation of new taxonomic entities. For example, some authors recognize a ninth cumacean family, the Archaeocumatidae (Bâcescu, 1972a). As proposed, it would be monotypic, differing only slightly from the Lampropidae. In the *Archaeocuma*, females have one pair of pleopods, a state considered plesiomorphic. However, presence of pleopods in the females could represent a reversal. In addition, males bear a rudimentary penis, another plesiomorphic state, but a few other genera, including the genus

Campylaspensis in the Nannastacidae, share this character state. In other respects, *Archaeocuma* fits into the Lampropidae. As suggested by Bâcescu (1972a), who erected the Archaeocumatidae and described *Archaeocuma*, the definition of the Lampropidae can be slightly modified to accommodate the genus *Archaeocuma* (Jones, 1976).

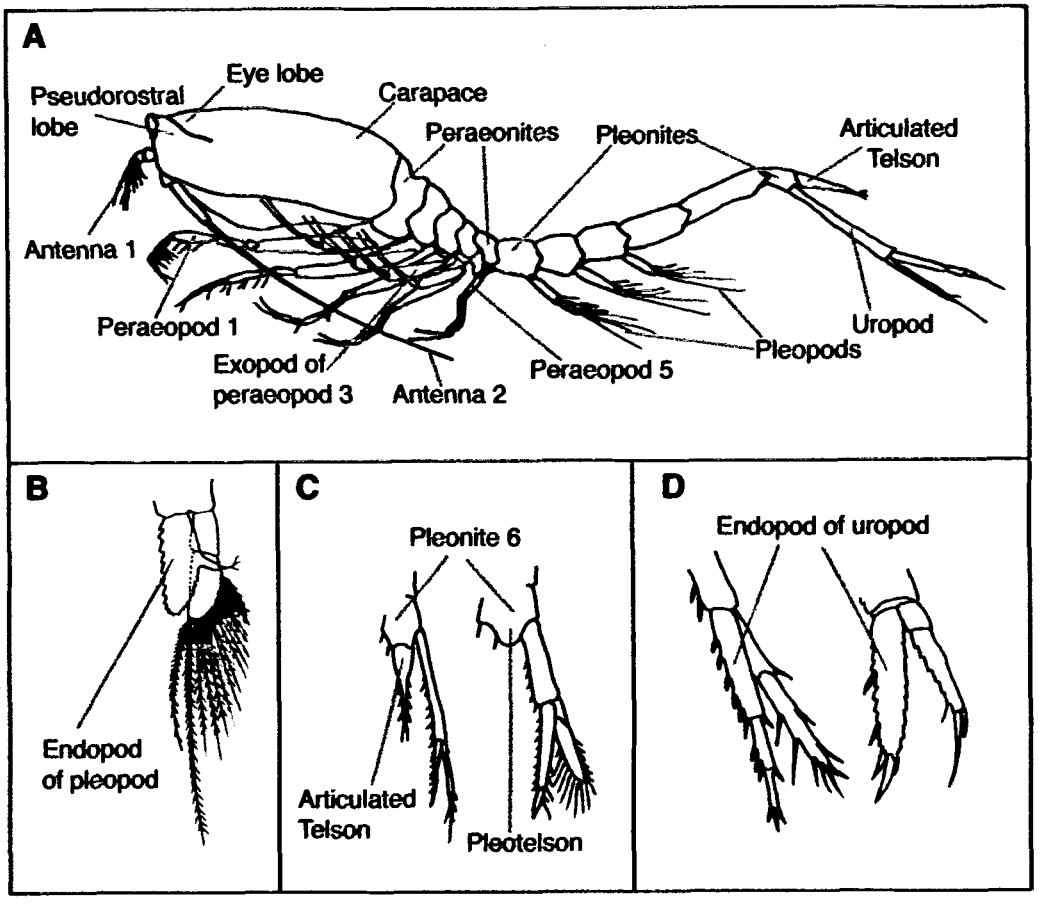

Figure 1. External morphology of cumaceans. A. Lateral view of the whole body of an adult male. B. Rami of a pleopod showing the presence of a process on the inner wall of the endopod. C. Dorsal view of the last abdominal segment (pleonite 6). *Left*, with articulated telson; *right*, telson has been fused to the last pleonite forming a pleotelson. One of the uropods has also been drawn (appendage originating on the last pleonite). D. Rami of the uropod. *Left*, tri-articulated endopod; *right*, uni-articulated endopod. Drawn after Sars (1900).

Tracing morphological characters along presumed cumacean familial lineages is a challenge because there are no clear patterns of character distribution among taxa (see Appendix A). For example, three families include species in which males bear a process on the endopod of the pleopod, while the other five families lack a process (Fig. 1B). However, a different combination of five families includes species that have an articulated telson, whereas the telson has been fused to form a pleotelson in the other three families (Fig. 1C).

The presence or absence of a telson is monomorphic within each family. In the currently accepted classification (Schram, 1986), it is assumed that telson fusion occurred at most three times in cumacean evolution, once in each of the three families bearing a pleotelson. However, a more parsimonious hypothesis is that the telson fusion happened once. Thus, the Bodotriidae, Leuconidae and Nannastacidae would be monophyletic. This arrangement conflicts with other morphological characters, and has yet to be validated.

Using molecular phylogenies to trace morphological characters along the lineages has contributed to the understanding of character evolution within numerous groups (e.g., McCracken *et al.*, 1999; Gatesy and Arctander, 2000; Schubart *et al.*, 2000; Cicero and Johnson, 2002; Feldman and Parham, 2002; Hooge *et al.*, 2002; Schulte *et al.*, 2002). Such studies have shown that many characters traditionally used in classification are homoplasious, representing convergences, parallelisms and/or reversals. The incorporation of molecular data into systematic analyses has provided an independent perspective from which for deciphering the evolution of taxa and their morphological characters. In the present study, we use molecular data from the mitochondrial gene encoding for subunit I of the Cytochrome c Oxidase protein (COI) to construct a phylogenetic hypothesis for cumaceans and trace changes in morphological characters among lineages. Our phylogenetic hypothesis challenge current familial taxonomy.

Materials and Methods

Outgroup Choice. The Superorder Peracarida (Calman, 1904) has characteristically included eight orders: Amphipoda, Cumacea, Isopoda, Mictacea, Mysidacea, Spelaeogriphacea, Tanaidacea and Thermosbaenacea, diagnosed by their common possession of a ventral brood pouch formed by oostegite extension of the legs and bear a mandibular lacinia mobilis. However, additional evidence suggests that this suit of characters may not be sufficient for defining the Peracarida. Although it was originally described as homologous, development of the marsupium suggests it is homoplasious within the Peracarida. Thermosbaenaceans lack the epipodal brood pouch that characterizes other peracarid orders (Siewing, 1958). On the other hand, the lacinia mobilis is present in all peracarids but is also present in syncarids (Eumalacostraca, Syncarida) and some eucarid larvae (Eumalacostraca, Eucarida), two superorders related to the peracarids (Dahl, 1982). Other characters suggest a narrowing of the membership in the Peracarida. For example, isopods, tanaidaceans, cumaceans, mictaceans and thermosbaenaceans develop within the marsupium until they reach the unique crawl-away manca stage. A manca is the earliest post-hatching stage where development is almost complete, but the last pair of peraeopods have not yet appeared. Also, five of the eight peracarid orders possess an epipod with ventilatory functions on the first maxilliped (first thoracopod), but this is absent in Isopoda, Amphipoda and Mictacea (Sieg, 1983). In addition, unique sperm morphology is shared by amphipods, cumaceans, isopods and mysids (Jamieson, 1991). The validity of the Peracarida as a natural group has yet to be confirmed.

Although some members of the Peracarida may be included by possession of homoplasious characters, several of the sister-relationship of orders within the Superorder are well supported. Siewing (1963) proposed cumaceans to be sister taxa to a clade formed by Tanaidacea and Isopoda (see also Hessler and Newman, 1975; Sieg, 1983). Based on the evolution of the carapace as a respiratory structure, Watling (2000) suggested Cumacea and Tanaidacea as sister taxa, with isopods diverging more basally (see also Nylund *et al.*, 1987). Schram (1986) also placed cumaceans in close proximity to tanaids, and closely related to

Spaleogriphaceans. Therefore, although resolution is not complete, several lines of evidence indicate that cumaceans are close to isopods and tanaids. Sequence data for the mitochondrial gene Cytochrome Oxidase II (COII), shows that cumaceans and isopods share a unique deletion of five amino acids; while no COII sequence is available for tanaidaceans, this deletion is not present in amphipods or other non-peracarid crustaceans (Haye and Kornfield, unpublished data). There is strong support for the monophyly of the clade formed by cumaceans, isopods and tanaids. Based on this information, tanaids and isopods were used as outgroup taxa in this study.

Gene Choice. Cumaceans represent a relatively old lineage which probably diversified during the Paleozoic. Only conserved genes can provide adequate information for a family-level study. Several genes were explored as possible candidates for molecular phylogenetic studies. Protein-coding genes are more easily aligned and more likely to have conserved sequence than are genes that are selectively neutral. Because many cumacean samples used for analysis were degraded, we examined genes in the mitochondrial genome. The high-copy number of the mtDNA within each cell facilitated sequence acquisition.

The mitochondrial COI gene has been extensively used in phylogenetic studies on a variety of malacostracan groups (Palumbi and Benzie, 1991; Meyran *et al.*, 1997; Badwin *et al.*, 1998; Harrison and Crespi, 1999; Shank *et al.*, 1999; Duffy *et al.*, 2000; Gusmão *et al.*, 2000; Remigio and Hebert, 2000; Schubart *et al.*, 2000; Tong *et al.*, 2000; Macpherson and Machordom, 2001; Vaniola *et al.*, 2001, Williams *et al.*, 2001; Haye *et al.*, 2002; Pérez-Losada and Crandall, 2002). It has been shown to be the most conserved of the mitochondrial protein-coding genes for a wide variety of taxa (Simon *et al.*, 1994), and has been useful in elucidating phylogenetic relationships at the familial level (e.g., Siddall and Burreson, 1998; Carlini and Graves, 1999; Nylander *et al.*, 1999; Remigio and Hebert, 2000). For the family-level analyses of cumaceans presented here, we examined variation in amino acid sequence of COI.

Collection and DNA Extraction. Twenty-five species of cumaceans and two outgroup species were used for the phylogenetic analyses (Table 1). No material was obtained from members of

the least diverse and most obscure family, the Ceratocumatidae. Members of that family live at great depths, making their collection difficult. The other seven cumacean families are all represented in this study. Many samples were collected by slowly dragging a plankton net across the surface of the sediment. At night, a light trap was used to attract cumaceans with well developed eyes into the net. Alternatively, the surface sediment was sampled and sieved through a 500 μ mesh to retain all cumaceans. Deep water samples were obtained using a running-dredge with a small mesh bag. Specimens were stored in 95% ethanol for DNA preservation. Samples were sorted to genus or species level; some species are new to science and will be formally described elsewhere. Whole specimens were used for extraction of DNA using a Qiagen Tissue DNA Extraction Kit (Qiagen Inc., Chatsworth, California). Partial sequence for the COI gene was obtained using PCR (Polymerase Chain Reaction; Saiki *et al.*, 1988) with primers LCO (Folmer *et al.*, 1994) and mt9 (UBC, Biotechnol. Lab., Vancouver, British Columbia) that amplify a 700 bp. Reactions had a final volume of 25 μl and the following ingredients: 1x PCR reaction buffer with $MgCl_2$ (Roche Diagnostics Corp., Indianapolis, IN), 1x PCRx enhancer (Invitrogen Corp., San Diego, CA), 0.8 mM of deoxyribo-nucleotide triphosphate mix, 0.9 μM of each primer (Qiagen Operon, Alameda, CA); 3 μl of template DNA, and 0.75 Units of Platinum *Taq* (Invitrogen Corp., San Diego, CA). Once in the thermo-cycler, reactions started with 5 min of denaturization at 94°C and were followed by 35 cycles of 45 sec at 94°C, 45 sec at 40°C, and 90 sec at 72°C. Lastly, there was an extension of 15 min at 72°C to allow for the polymerase to complete unfinished segments. Amplified products were visualized on 1.5% agarose electrophoresic gels using ethidium bromide and a UV-transilluminator.

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Table 1

Scientific name[a], locality of collection and accession numbers

Taxa	Location of collection	GenBank Accession Nos.
CUMACEA		
Bodotriidae		
Bodotriininae		
Cyclaspis alba Roccatagliata, 1986	Pelluco, Chile	AF137517
Eocuma longicorne Calman, 1907	Serena Beach, Kenya	AF520445
Iphinoe trispinosa (Goodsir, 1843)	Fermain Bay, U.K.	AF137519
Mancocumatinae		
Mancocuma stelliferum Zimmer, 1943	Plum Island, MA, U.S.A.	AF137520
Vaunthompsoniinae		
Cumopsis goodsir (Van Beneden, 1861)	Cobo Bay, Guensey, U.K.	AF137518
Heterocuma sp.	Mtwapa creek, Kenya	AF520443
Leptocuma sp.	Los Molinos, Chile	AF520444

Table 1 (cont.)

Pomacuma australiae (Zimmer, 1921)	Bay of Islands, New Zealand	AF352302
Vaunthompsonia sp.	Wilea Beach, Maui, Hawaii	AF352301
Diastylidae		
Colurostylis longicaudata Jones, 1963	Nelson Bank, New Zealand	AF520446
Diastylis bispinosa (Stimpson, 1853) (sp.1)	Georges Bank, Gulf of Maine	AF137511
Diastylis rathkei (Krøyer, 1837) (sp. 2)	Langeland, Denmark	AF069764
Diastylis sculpta Sars, 1871 (sp.3)	Walpole, ME, U.S.A.	AF137510
Diastylopsis thilenuisi (Zimmer, 1902)	Summer Beach, New Zealand	AF520442
Oxyurostylis lecroyae Roccatagliata and Heard, 1995 (sp.1)	Biloxi, MS, U.S.A	AF137513
Oxyurostylis smithi Roccatagliata and Heard, 1995 (sp.2)	Biloxi, MS, U.S.A	AF137512
Gynodiastylidae		
Gynodiastylis sp.	Akaroa, New Zealand	AF520447
Lampropidae		
Hemilamprops californicus Zimmer, 1907 (sp.1)	San Diego, CA, U.S.A.	AF061781
Hemilamprops sp. (sp.2)	Pelluco, Chile	AF520448
Lamprops quadriplicatus Smith, 1879	Georges Bank, Gulf of Maine	AF352297

Table 1 (cont.)

Leuconidae		
Eudorella pusilla Sars, 1871 (sp.1)	Walpole, ME, U.S.A.	AF137516
Eudorella sp. (sp.2)	San Diego, California, U.S.A.	AF352307
Nannastacidae		
Cumella sp.	Tongoy, Chile	AF520449
Campylaspis sp.	Kimbala Reef, Kenya	AF520450
Pseudocumatidae		
Pseudocuma simile Sars, 1900	Vazon, Guernsey, U.K.	AF137514
ISOPODA		
Cyathura sp.	Woods Hole, MA, U.S.A	AF520451
TANAIDACEA		
Tanaidacea sp.	Oahu, Hawaii	AF520452

[a] For multiple species within a genus, the acronym is indicated in parenthesis after the species name.

mix, 0.9 μM of each primer (Qiagen Operon, Alameda, CA); 3 μl of template DNA, and 0.75 Units of Platinum *Taq* (Invitrogen Corp., San Diego, CA). Once in the thermo-cycler, reactions started with 5 min of denaturization at 94°C and were followed by 35 cycles of 45 sec at 94°C, 45 sec at 40°C, and 90 sec at 72°C. Lastly, there was an extension of 15 min at 72°C to allow for the polymerase to complete unfinished segments. Amplified products were visualized on 1.5% agarose electrophoresic gels using ethidium bromide and a UV-transilluminator.

Amplification products were purified (QIAquick-spin columns; Qiagen Inc, Chatsworth, CA) and ligated into the pCR® vector (TA Cloning™ System, Invitrogen Corp., San Diego, CA), followed by transformation of INVα cells. Bacterial colonies with inserts were cultured overnight in SOC media (for higher yield) followed by plasmid purification using the Plasmid Miniprep Kit (Qiagen Inc., Chatsworth, CA). Presence of the correct size insert was verified using PCR followed by agarose gel electrophoresis to visualize bands.

As an alternative to cloning, when PCR products appeared in electrophoretic gels to be in high concentration and relatively clean, the desired band was excised from the agarose gels and purified using a Gel Purification Kit (Qiagen Inc., Chatsworth, CA). Each purified plasmid or PCR-gel product was sequenced in both forward and reverse directions at the University of Maine sequencing facility. Cycle-sequencing and electrophoresis were performed on a Model 377 Automated Sequencer (Applied Biosystems Inc., Foster City, CA), using the PCR amplification primers and fluorescent dye terminators (Perkin-Elmer; Foster City, California). For each species, a consensus sequence was generated on Sequence Navigator (Applied Biosystems, version 1.0, 1994, Foster City, California).

Phylogenetic Analysis. Nucleotide sequences were translated to amino acid sequences and aligned by eye. Post-alignment sequences were truncated in order to minimize ambiguous sites at the 5' and 3' ends in all taxa.

Sequences were evaluated for rate heterogeneity using the relative ratio test available in Hi-Phy (Muse and Pond, 2000). Pairwise relative rate analyses allow for only one taxon to be designated as outgroup; analyses were done multiple times to examine results when using

alternative outgroup taxa. Sequences that showed a significantly different evolutionary rate were excluded from analyses that assume similar rates of evolution for all taxa.

Molecular phylogenetic analyses were performed at the amino acid level using Bayesian (Rannala and Yang, 1996; Mau and Newton, 1997; Yang and Rannala, 1997; Mau *et al.*, 1999; Huelsenbeck *et al.*, 2001; Lewis, 2001), maximum likelihood (Felsenstein, 1981; Huelsenbeck and Crandall, 1997; Steel and Penny, 2000) and parsimony (Camin and Sokal, 1965) approaches.

Bayesian analyses are based on the generation of posterior probabilities and have the advantage of handling a very high number of taxa. Analyses were performed with MrBayes software, which uses a Metropolis-coupled, Markov Chain Monte Carlo sampling method to calculate probabilities (Huelsenbeck and Ronquist, *in press*). Analyses started from a random tree and used the JTT empirical matrix of amino acid substitution as the model of evolution (Jones *et al.*, 1992). Four Markov chains were run simultaneously for 1,000,000 generations; trees were sampled and saved every 100 generations. The number of generations needed to reach a stable likelihood value was determined by inspection, and the trees generated from those were excluded from further analyses. The rest of the 10,000 saved trees were then imported into PAUP* (Swofford, 2000) where a 50% majority rule consensus tree was calculated. The robustness of the nodes of a consensus Bayesian tree is the proportion of saved trees that share a particular node.

Maximum likelihood analyses were performed using the software ProtML available in the Phylip package (Felsenstein, 1993). It performs maximum likelihood on amino acid data implementing the mtREV matrix of amino acid substitution for mitochondrial proteins (Adachi and Hasegawa, 1996; Yang *et al.*, 1998). Heuristic parsimony analyses were performed in PAUP* using ten replicate searches with random sequence addition, tree bisection reconnection, and were rooted using multiple outgroups. Under parsimony criteria, the data were evaluated for information content using the skewness statistic (g_1) obtained from the tree length frequency distribution of an evaluation of 100,000 random trees search using PAUP* (Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992). The robustness of tree topologies generated in PAUP using

likelihood and parsimony optimality criteria were evaluated by full-heuristic bootstrap resampling (1000 replicates; Felsenstein, 1985). Clade support was also evaluated with Bremer support values (Bremer, 1994), which were obtained in PAUP* using a command file created by MacClade 4.0 (Maddison and Maddison, 2000).

Morphological characters were explored with PAUP* for phylogenetic signal. Tree topologies were obtained using parsimony with branch and bound, and distance with neighbor-joining (Saitou and Nei, 1987).

Well supported trees obtained from the phylogenetic analyses were further explored for character evolution using MacClade. Positions of taxa were changed and the effect on tree lengths, confidence values, and character evolution were examined. Consistency indices (CI) and retention indices (RI) (Farris, 1989), were obtained from MacClade tree-topology analyses. Alternative phylogenetic hypotheses were statistically tested with the non-parametric ranked sign test of Templeton (Larson, 1994) as implemented in PAUP*.

Results and Discussion

Nucleotide Sequences. Final truncated DNA sequences consisted of 676 nucleotides yielding 225 amino acid residues. All sequences have been deposited in GenBank (Table 1).

Pairwise relative rate analyses indicated that *Campylaspis* sp. and *Lamprops quadriplicatus* failed to show similar rates of evolution compared to the other cumacean species studied ($p<0.001$). In order to obtain a better signal, the two taxa were excluded from Bayesian and likelihood analyses since these approaches assume a constant model of molecular evolution.

Molecular Phylogenetic Reconstruction. The Bayesian phylogenetic hypothesis using the tanaid outgroup suggests that the Pseudocumatidae is the most basal family, followed by Gynodiastylidae, Diastylidae, and Lampropidae. Most derived are all families with a pleotelson that resolve as a monophyletic group (Fig. 2). Within the pleotelson clade, Bodotriidae resolve paraphyletically with the Leuconidae and Nannastacidae embedded within it. Two of the bodotriid

subfamilies, Bodotriinae and Vaunthompsoniinae, appear to be polyphyletic. Using the isopod as outgroup results in a similar tree topology, but with lower support values for most of the nodes. However, the node that supports monophyly of the pleotelson groups has a higher support value than when Tanaidacea is declared as the outgroup (89% vs. 62% as shown in Fig. 2). Trees generated using maximum-likelihood as optimality criteria are consistent with the tree topology resultant from Bayesian analyses.

The data consisted of 83 parsimony-informative amino acid sites. Since the parsimony method employed here allows assignment of multiple outgroups, both isopod and tanaid sequences were used. Branch and bound parsimony analysis produced three shortest trees of 576 steps ($g1 = -0.729$, $p<0.01$; CI= 0.579). Parsimony analysis again supports the monophyly of pleotelson-bearing cumaceans and paraphyly of the Bodotriidae. Consistent with the Bayesian analysis, the Pseudocumatidae are basal and are followed by the Diastylidae, Lampropidae and the pleotelson groups. Only a few terminal nodes show bootstrap support greater than 50%: *Oxyurostylis* spp. with 91%, *Diastylopsis* and *Colurostylis* with 76%, *Mancocuma* and *Leptocuma* with 55%, *Cumopsis* and *Heterocuma* with 100%, *Eudorella* spp. with 55%, and *Campylaspis* and *Cumella* with 100% support. The consensus tree shows a slightly different topology than the one produced by Bayesian analysis: the Gynodiastylidae group within the Diastylidae, and the position of some of the pleotelson taxa is changed. Inclusion or exclusion of *Campylaspis* sp. and *Lamprops quadriplicatus* does not affect the tree topology other than by the addition of the taxa into 'predictable' locations within the tree, i.e., with their confamilials.

Constraining the molecular data for the Bodotriidae to be monophyletic results in a tree significantly longer (23 steps, $p<0.01$) than the gene tree (Fig. 2).

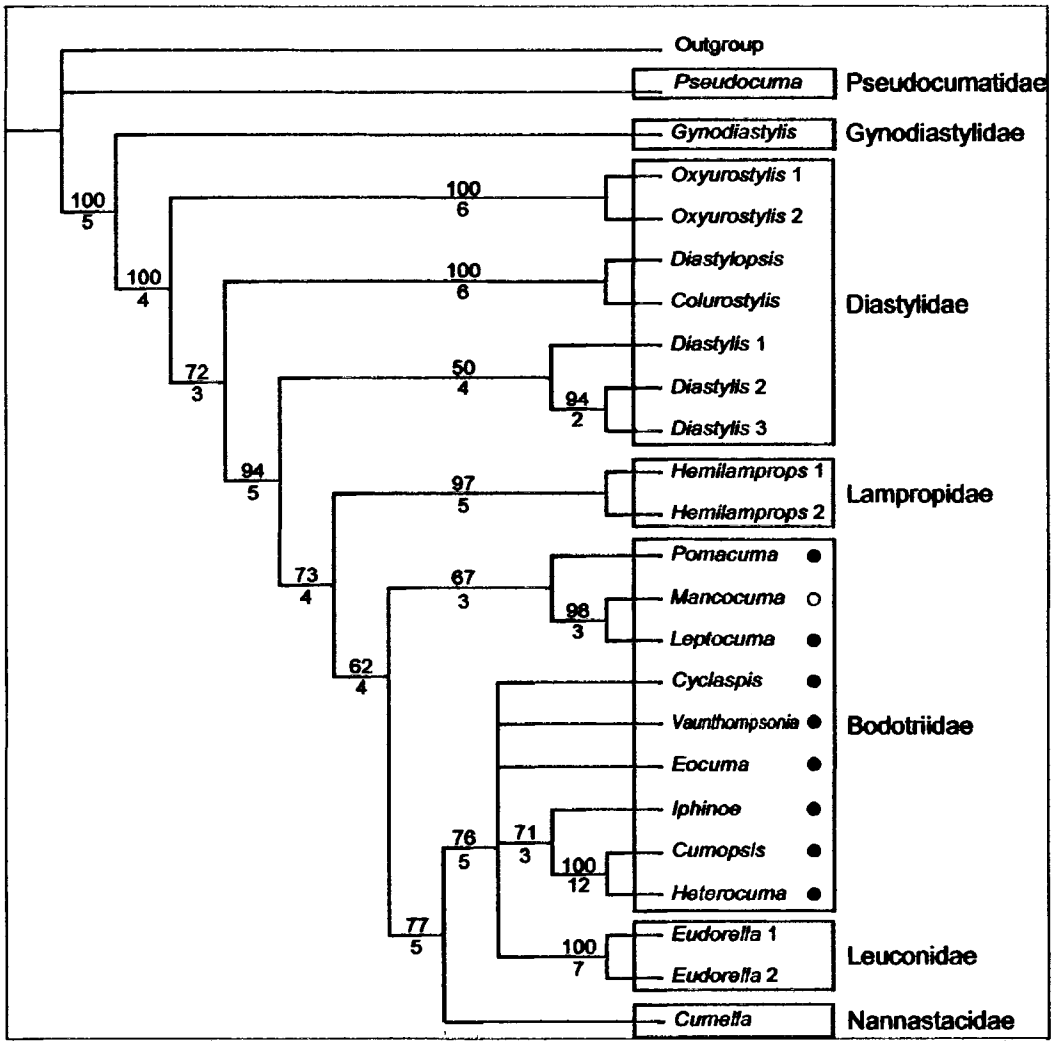


Figure 2. Bayesian phylogenetic analysis consensus tree. Within squares, numbers above branches correspond to the Bayesian score or percentage of times that node was found within the sampled trees using Tanaidacea as the outgroup. Numbers below branches are Bremer support values. The Pseudocumatidae are basal, followed by Gynodiastylidae, Diastylidae, Lampropiidae, and the pleotelson-bearing groups (Bodotriidae, Leuconidae and Nannastacidae). The Bodotriidae appears paraphyletic. Symbols indicate different subfamilies of the Bodotriidae: filled circle for Bodotriinae, empty circle for Mancocumatinae, and hatched circle for Vaunthompsoniinae.

Cumacean Morphology and Systematics. The cumacean carapace has two pseudorostral lobes extending in front of a unique mid-dorsal ocular lobe that may or may not bear ocular pigment and/or eye-lenses. Malacostracans have eight pairs of thoracopods, each associated with a thoracic segment. In cumaceans, three of those segments are fused to the head and their appendages are modified into maxillipeds (feeding appendages). The remaining five thoracopods maintain their thoracic position as peraeopods. The abdomen, or pleon, consists of six segments and may or may not each have an articulated terminal telson. Pleonites one to five may or may not have a pair of pleopods in the males (Fig.1).

The most commonly used characters for family-level discrimination are the number of peraeopods bearing exopods, the number of pleopods on males (Fig. 1A), the presence or absence of a process on the endopod of the pleopod (Fig. 1B), the presence of an articulated telson vs. presence of a pleotelson (telson fused to last pleonite) (Fig. 1C), and the number of articles of the uropodal endopod (Fig. 1D) (Zimmer, 1941; Jones, 1958, 1976; Bâcescu and Petrescu, 1999).

Since bodotriids have a full set of pleopods (five pairs), they have been considered as the most primitive cumacean family, while the Diastylidae is considered the most derived (Bâcescu and Petrescu, 1999). Because the Lampropidae have the smallest number of reductions overall (but have a slightly reduced number of pleopods), it has also been suggested that it is the most primitive family (Zimmer, 1941; Lomakina, 1958). Some of the characters that have not been reduced in lampropids include: five pairs of thoracopods with exopods, an articulated telson with three or more terminal setae, and four hepatic diverticula (Appendix A). Zimmer (1941) proposed a phylogenetic sequence starting from Lampropidae and followed by Diastylidae, Pseudocumatidae, Ceratocumatidae, Leuconidae, Nannastacidae and Bodotriidae. On the other hand, using the shape and number of hepatic diverticula, Lomakina (1958) proposed a different sequence: Lampropidae, Diastylidae, Pseudocumatidae, Ceratocumatidae, Leuconidae, Nannastacidae and Bodotriidae. These authors did not recognize the Gynodiastylidae as a separate family, but as the genus *Gynodiastylis* within the Diastylidae.

Analyses based on morphological characters (Appendix A) resulted in similar tree topologies under parsimony and distance optimality criteria. The three pleotelson-bearing families group together. The telson-bearing cumaceans group together with the Pseudocumatidae as most basal (Fig. 3A). Figure 3B contrasts molecular and morphological phylogenetic hypotheses. These two tree topologies are significantly different ($p<0.01$); fitting the morphological topology produces a tree with 15 additional steps.

The Pleotelson Clade. The presence of a clade defined by an articulated telson or a pleotelson (Fig. 1C) is revealed by the molecular phylogenetic hypotheses. It supports the monophyly of the Bodotriidae-Leuconidae-Nannastacidae clade. Although terminal nodes do not appear well resolved, the COI gene tree has adequate resolution for the deeper nodes (Fig. 2). The relationships within the pleotelson clade cannot be fully resolved using the COI data alone. Lack of an articulated telson is the main diagnostic feature of this clade. Additional characters show a distribution of states consistent with monophyly of the pleotelson groups. For example, the number of bristles on the palp of maxilla 1 shows a unique state developed in the pleotelson groups: the presence of two bristles, though they may also show other states. In addition, the number of hepatic diverticula shows unique reductions within the pleotelson groups.

The Bodotriidae, Nannastacidae and Leuconidae have several morphological differences that have justified their taxonomic separation (Appendix A; TableA1). For example, nannastacid males do not have pleopods. Bodotriid males generally have five pairs of pleopods with a process on the endopod (zero to three pairs may be found in the subfamilies Mancocumatinae and Vaunthompsoniinae, and the process of the pleopodal endopod may be absent). Leuconids have from zero to two pairs of pleopods without a process (Fig. 1B). Mandible structure also differs: bodotriids have a naviculoid mandible, while leuconids have a truncated mandible, and nannastacids may have either kind. They also show differences in the number of thoracopods that bear an exopod. Females often show reduced exopods on peraeopod 2 in the Bodotriidae, while in the Leuconidae exopods are always present and in the Nannastacidae exopods are generally absent. Nannastacids

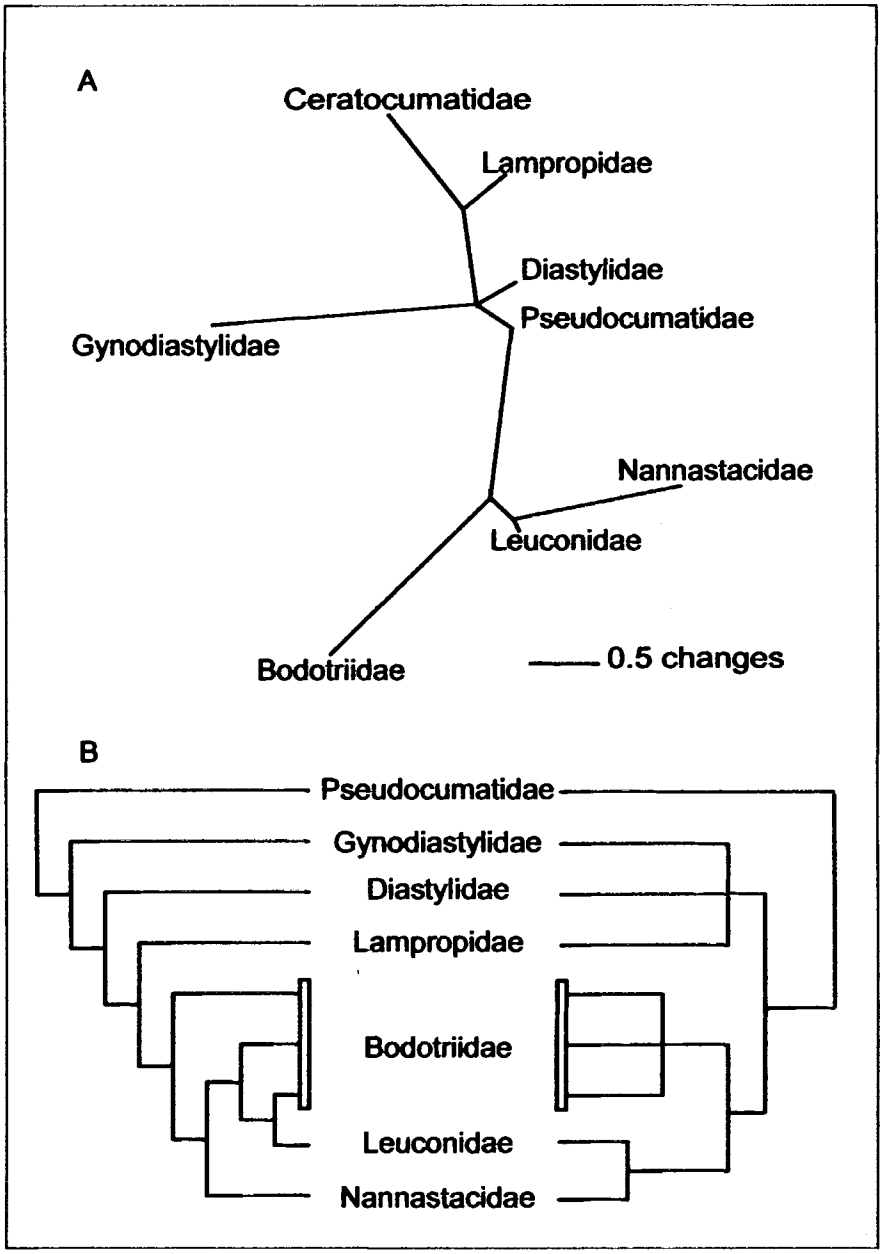


Figure 3. Parsimony analysis of the morphological data (Appendix A). A. Consensus of two shortest trees represented as an unrooted phylogram. Morphological data suggest monophyly of the pleotelson-bearing groups. B. Contrasting phylogenetic hypotheses generated with molecular (*left*) and morphological data when arbitrarily rooting with Pseudocumatidae as the basal taxon (*right*).

may represent an intermediate group between the Leuconidae and more derived Bodotriidae, judging from the mandible structure. Characters that represent reductions are more likely to be homoplasious as suggested by their high polymorphism within lineages.

The molecular data presented here suggest that the Nannastacidae and Leuconidae belong within the Bodotriidae. This result should be evaluated with additional studies that incorporate higher taxon representation. The molecular data set employed here is skewed with respect to taxon sampling of Nannastacidae and Leuconidae as compared to Bodotriidae (Table 1). Since the effects of taxon sampling are greater when few taxa are used to infer high-level relationships and when the amount of data is relatively small (Poe and Swofford, 1999; Yoder and Irwin, 1999), a greater number of characters as well as better taxon representation are needed to confirm the positioning of the groups within the pleotelson clade.

Bodotriids are distinguished from other cumacean families by a combination of characters including: pleopods generally with a process on the endopod, absence of articulated telson, naviculoid mandible, gill elements plates absent, and hepatic diverticula with four lobes (Appendix A). The distinction between bodotriid subfamilies is based on the number of pleopods, number of peraeopods with exopods, and structure of antenna 2 in males and females, among other characters (Appendix A). The present study raises questions about the validity of the subfamilies, but does not provide sufficient resolution for generic discrimination. The paraphyly of the Bodotriidae may be a consequence of the positioning of the Nannastacidae and Leuconidae, and although suggested by the data, needs further support. Analyses including additional morphological characters for all 34 genera of bodotriids should provide information on the validity of bodotriid subfamilies.

Homoplasic Morphological Characters. The gene tree topology suggests that many of the characters traditionally used in cumacean diagnoses are homoplastic. For example, the number of pleopods in males (Fig. 1A) is a variable character that most likely has undergone several reductions and reversals. Males use the pleopods to swim, and it is likely that their total number and development affects the degree of their mobility. Pseudocumatids, suggested here as the

basal lineage of cumaceans, have two pairs of pleopods that are somewhat rudimentary and without an endopod. Pleopods are missing in the Gynodiastylidae. Males of the Diastylidae and Lampropidae generally bear two and three pairs of pleopods, respectively. Although, members of both these later families may lack pleopods and the diastylids may have two pairs. Within the pleotelson clade, the number of pleopods is also variable. Bodotriid males often have well developed eyes and well developed pleopods with a process on the endopod (Fig. 1B), all necessary for nocturnal vertical migration. Many bodotriids display five pairs of pleopods. The genus *Austrocuma* (Bodotriininae) shows variability in the number of pleopods; males may have three or four pairs, both states being unique for the subfamily (Haye, personal observation).

The projection of the endopod of the pleopod and the number of articles on the uropodal endopod (Fig. 1D) also appear to have been reduced in several lineages. Similarly, the number of peraeopods bearing an exopod shows high variation in different familial lineages. Males of Pseudocumatidae and Lampropidae have four pairs of peraeopods with exopods, showing the least reduction within the Cumacea. The Gynodiastylidae and Diastylidae, suggested as intermediate between Pseudocumatidae and Lampropidae, show from four to no pairs of peraeopods with exopods. The same variable pattern is observed in the Bodotriidae, Leuconidae and Nannastacidae, all which show a relatively smaller number of peraeopods with exopods than the telson bearing groups.

Studies on the regulation and control of development in arthropods have shown that changes in appendage structure can be achieved with small genetic changes (Akam, 2000). For example, the change in expression of a regulatory homeotic gene or the gain or loss of transcriptional functions in Hox proteins can change the identity of a body segment (Nagy, 1998). From their observations of the expression of the Ultrabithorax (Ubx)/AbdominalA class Hox proteins, Averof and Patel (1997) deduced that in crustaceans, genes encoding these proteins have been turned off in anterior thoracic segments in many crustacean groups. This loss of expression is correlated with the development of appendages as maxillipeds. Further, proteins that are regulated by Hox genes may acquire new functions. It has been recently demonstrated that expression of the Hox protein Ubx is compatible with limb development in crustaceans and

onychophorans, but acts as an abdominal limb repressor in insects (Grenier and Carroll, 2000; Levine, 2002; Ronshaugen *et al.*, 2002). Because of the way that morphological evolution takes place, it is reasonable that within the Cumacea, plastic morphological traits, like the presence of a particular segment, the structure of an appendage, or fusion of articles within an appendage are homoplasious.

Conclusion. The phylogenetic hypothesis for cumacean families generated with partial amino acid sequence from the COI gene is well supported by phylogenetic analyses and is significantly different from alternative tree topologies. The pleotelson represents a diagnostic character for a clade composed the Bodotriidae, Leuconidae and Nannastacidae. The relationships within this clade need further resolution before taxonomic modification can be undertaken.

Chapter 3

GENERIC RELATIONSHIPS WITHIN THE CUMACEAN FAMILY BODOTRIIDAE

Introduction

Bodotriids are the most diverse of the cumacean families and have a worldwide distribution in shallow and deep marine waters. There are 364 species in the family organized into 34 genera. Many of these genera consist of only a few species or are monotypic, while others, such as *Cyclaspis,* include over one hundred species. Bodotriids are differentiated from other cumaceans by a combination of characters. They all have a pleotelson (articulated telson has been fused to last pleonite), naviculoid shape on the dorsal part of the mandible, gill elements and plates absent, and hepatic diverticula with four lobes (Appendix A). With the exception of the pleotelson, the other diagnostics are not known for all of the genera of the Bodotriidae.

The genera of the Bodotriidae are currently arranged into three subfamilies: Bodotriinae Scott 1901, Mancocumatinae Watling 1977, and Vaunthompsoniinae Sars 1878. The differences among the subfamilies relate to the number of pleopods on the males and the number of peraeopods with exopods both on males and females (Chapter 2, Fig. 1). These two characters and the corresponding character states, are based on reductions from an ancestral body plan that most likely had five pairs of pleopods on males, and four pairs of peraeopods with well developed exopods in both males and females.

The subfamily Bodotriinae is characterized by the lack of exopods on peraeopods beyond the first pair, and by five pairs of pleopods on males of most of the genera. The Mancocumatinae includes genera in which males have fewer than five pairs of pleopods and exopods beyond the first peraeopods. Lastly, the Vaunthompsoniinae includes genera in which males have five pairs of pleopods and exopods beyond the first pair of peraeopods.

Several bodotriid genera present problems for the current classification. For example, *Picrocuma* bears the diagnostic characters for the Vaunthompsoniinae, but in many other respects is a peculiar genus for the family and should be considered as a member of the Nannastacidae (Dr. Watling, personal communication). Most notably they have a maxilliped 3 with a leg-like structure, antenna 2 in males is modified for grasping, and males have no pleopods.

The genus *Apocuma* has been considered a member of the subfamily Bodotriinae due to general resemblance to genera within this subfamily (Bâcescu, 1988). However, when the genus was created, the author suggested it be placed in the Vaunthompsoniinae because of the presence of exopods on the second and third peraeopods, its resemblance to *Vaunthompsonia,* absence of a projection on the basis of maxilliped 3, and the three segmented Antenna 2 of females (Jones, 1973).

Other problematic genera are *Coricuma* Watling and Breedy (1988) and *Austrocuma* Day (1978). *Coricuma* was originally described as a member of the Bodotriinae based on the presence of an exopod only on the first peraeopod (Watling and Breedy, 1988). Later it was moved to the Leuconidae based on the presence of only two pairs of pleopods (Watling, 1991a), although it has a naviculoid mandible rather than a truncated one as in leuconids. While the positioning of *Coricuma* within cumacean classification has been debated, *Austrocuma*, which also shows a reduced number of pleopods, has been left within the Bodotriinae. These two genera have fewer than five pairs of pleopods and are the only exceptions within Bodotriinae.

The subfamily Mancocumatinae consists of four genera that are quite different from each other and do not have a clear synapomorphy; they all have exopods beyond the first pair of peraeopods, but in varying number, and males may have from three to zero pairs of pleopods. *Mancocuma* is characterized by the presence of two pairs of pleopods and by both males and females having fully developed exopods on peraeopods 1-3, and reduced exopods on peraeopod 4. Males of *Pseudoleptocuma* have three pairs of pleopods and fully developed exopods on the first four peraeonites, while females have three pairs of peraeopods with fully developed exopods

and the fourth peraeopod bears a reduced exopod. In *Speleocuma,* males have two pairs of pleopods as in *Mancocuma*, but differ from *Mancocuma* in that both males and females have only the first three pairs of peraeonites with exopods. Lastly, the *Spilocuma* completely lack pleopods, and both males and females have fully developed exopods on the first three peraeonites and reduced exopods on the fourth peraeonite. The exopod condition is the same for *Spilocuma* and *Mancocuma*. The relationships among the genera currently considered within the Mancocumatinae together with the other genera of the Bodotriidae need to be examined.

The goals of the present work are to shed light onto the phylogenetic relationships of all bodotriid genera by the means of a phylogenetic reconstruction based on morphological characters. This study represents the first phylogenetic analysis of the family Bodotriidae.

Materials and Methods

All genera and species of the Bodotriidae were considered for the generation of a morphological data-set. A database of 114 morphological characters was created using the software DELTA (Dallwitz, 1980; Dallwitz et al., 1993) (see Appendix B for list of characters and character states, and Appendix C for diagrams showing each of the characters and character states).

Molecular phylogenetic analyses have shown that the Bodotriidae are closely related to the other two families that lack an articulated telson, the Leuconidae and Nannastacidae. These three families form a distinct clade in the family-level phylogeny (Fig. 2). The genera *Atlantocuma* Bâcescu and Muradian (1974) and *Picrocuma* Hale (1936) have a debated position within the pleotelson clade, most probably representing genera of the Nannastacidae. They were both coded in DELTA for all of the characters in order to investigate their position relative to the bodotriid genera, and if placed outside of Bodotriidae to be used as outgroups. Additionally, one genus from the Leuconidae, *Austroleucon*, and two from Nannastacidae, *Cumellopsis* and *Scherocumella,* were coded for all the characters to be used as outgroups.

Phylogenetic analyses were performed using PAUP* (Swofford, 2000). A character which exhibited multi-states was interpreted as polymorphic, gaps were treated as missing data representing uncoded characters, and characters were equally weighted. Whenever possible characters were treated as ordered (additive or minimally connected), since ordering improves the overall resolution of the phylogenetic analysis (Slowinski, 1993; Schattuck, 1995; Sternberg and Cumberlidge, 2001). Most ordering was done assuming losses and reductions as derived condition (see Appendix B). Other characters were treated as unordered or maximally connected.

Analyses were performed using parsimony as optimality criteria with 10,000 heuristic searches to identify shortest trees. Searches were done starting from random trees using the tree bisection reconnection algorithm for branch swapping. Both 'delayed transformation' (deltran; favors convergences) and 'accelerated transformations' (acctran; favors reversals) were examined for character state optimization. Length, consistency index, and distance scores for tree topologies were obtained in PAUP*. Trees were evaluated for robustness using the DECAY index (Bremer support; Bremer, 1994). The significance of the decay values is relative to the other nodes of the tree and represents the number of steps necessary for a node to collapse. The higher the decay index, the more robust is the node. The software AutoDecay (Eriksson, 1999) was used to obtain the decay values by generating a command file with instructions for calculating the shortest tree when each of the nodes was constrained. This file was executed in PAUP*. Finally, character evolution within the resultant phylogenetic tree topology was examined using the software MacClade (Maddison and Maddison, 2000). A list of synapomorphies for each of the nodes of the most reliable tree topology was generated from the character evolution analyses.

Results

The data consisted of 86 parsimony-informative characters. In all analyses, *Atlantocuma* and *Picrocuma* grouped external to all bodotriid genera. *Atlantocuma* is sister to the two sampled nannastacid genera, *Cumellopsis* and *Scherocumella*. *Picrocuma* is external to the outgroup taxa. For the phylogenetic analyses *Atlantocuma* and *Picrocuma* were used as outgroup taxa together with the leuconid genus *Austroleucon,* and the nannastacid genera *Cumellopsis* and *Scherocumella.*

The shortest length topologies found have 1431 steps and a consistency index of 0.83. Ten equally parsimonious trees were found, the phylogram with the shortest distance score is presented in Figure 4, and a 50% majority-rule consensus tree of the ten most parsimonious trees is presented in Figure 5. The topology was the same using deltran or acctran as character state optimization. Due to the high level of character polymorphism, bootstrap resampling did not result in significant values for any of the basal nodes. Despite this limitation, decay indices provide relative support to tree nodes and are used here to establish topology.
Spilocuma weakly groups with the other members of the Bodotriidae, and based on the presented data, there are no synapomorphies that support its grouping to the rest of the bodotriid genera. Figure 5 includes all the unambiguous synapomorphies (see Maddison and Maddison, 2000) at each node. The node that groups *Speleocuma* and other bodotriids, to the exclusion of *Spilocuma*, has a decay index of three and is supported by two synapomorphies: the presence of pleopods on pleonite 1 and on pleonite 2 (characters 109 and 110, see Appendices B and C). *Spilocuma* is the only bodotriid without any pleopods.

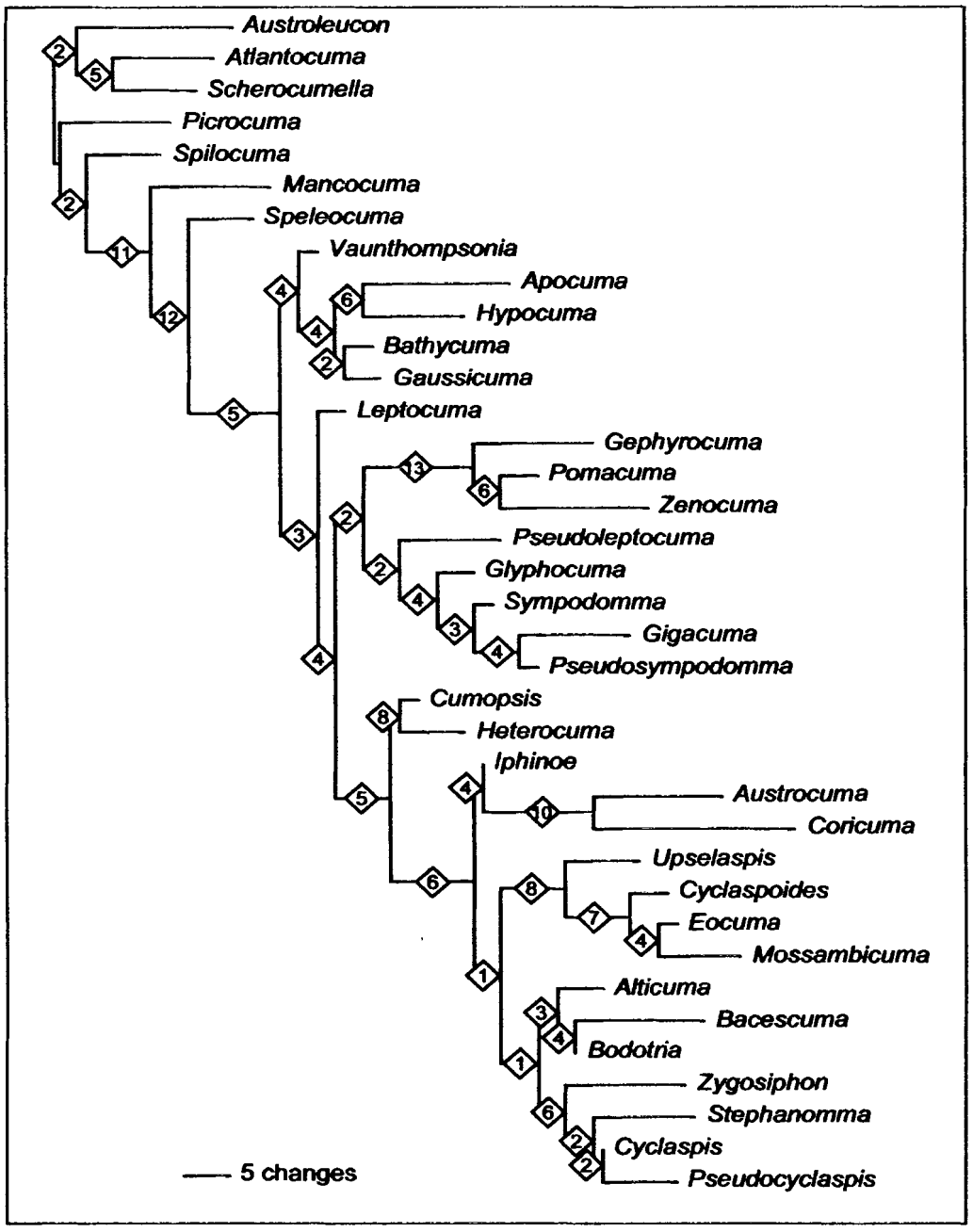


Figure 4. Phylogram of one of the ten shortest trees and the shortest-distance-score tree for all the genera of the Bodotriidae using morphological characters. *Atlantocuma*, *Austroleucon*, *Cumellopsis*, *Scherocumella* and *Picrocuma* are outgroups. Values within diamonds represent decay indices. Nodes without an index correspond to nodes that were variable across the 10 shortest trees.

The subfamily Bodotriinae forms a well-supported clade (Fig. 5) with the expected exclusion of *Apocuma* that groups with the Vaunthompsoniinae. The Bodotriinae includes *Coricuma* as sister-genus of *Austrocuma*. The subfamily has a decay index of four and is supported by eight unambiguous synapomorphies: 1) Female antenna one with one article (character 38). 2) Merus of maxilliped three extended over carpus (character 46). 3) Peraeopod 2 without an exopod in females (character 75). 4) Peraeopod 2 without an exopod in males (character 76). 5) Peraeopod 3 without an exopod in females (character 79). 6) Peraeopod 3 without an exopod in males (character 80). 7) Peraeopod 4 without an exopod in males (character 85). 8) When there are setae present on posterior margin of pleonite 6 there are only two (character 93) (Fig. 5).

There are two major clades within the Bodotriininae. In the first, *Iphinoe*, *Upselaspis*, *Cyclapsoides*, *Eocuma* and *Mossambicuma* group with decay index support of two and share the fusion of the ischium to the basis in peraeonite 2. Within this clade, there is relatively strong support for the node that groups *Upselaspis*, *Cyclapsoides*, *Eocuma* and *Mossambicuma*, in addition to two synapomorphies. The second clade of the Bodotriinae includes nine genera. *Alticuma* is the basal-most, followed by *Stephanoma* and *Zygosiphon*. All those nodes have relatively high support, and are followed by a less-supported clade that includes *Cyclaspis* and *Pseudocyclaspis* as sister-taxa. Character analyses in MacClade indicate that *Pseudocyclaspis* does not have a single diagnostic character to separate it from *Cyclaspis*. *Cyclaspis-Pseudocyclaspis* is sister to two well-supported nodes, one that leads to *Austrocuma* and *Coricuma*, and the other leading to *Bacescuma* and *Bodotria*. *Coricuma* and *Austrocuma* are characterized, among other features, by males with a short Antenna 2 that does not reach the end of the pleon (character 35), ischium missing on peraeopod 2 (character 77), and on peraeopod 4 (character 86), and by males lacking pleopods on pleonite 5 (character 113).

The subfamily Mancocumatinae, composed of the *Spilocuma*, *Speleocuma*, *Mancocuma*, and *Pseudoleptocuma*, does not resolve monophyletically. *Spilocuma* has a basal position, followed by the *Speleocuma* in a ladder-like bifurcation pattern (rather than as a clade).

Pseudoleptocuma and *Mancocuma* form a clade embedded within the Vaunthompsoniinae genera, grouping with relatively high support with the operculate genera (i.e., *Gephyrocuma*, *Pomacuma* and *Zenocuma*), sister to *Leptocuma*, and to the clade formed by *Cumopsis* and *Heterocuma*. The last two genera showed no morphological differentiation when character evolution was analyzed within MacClade. *Vaunthompsonia* is the next lineage to diverge, and is followed by a clade formed by *Apocuma* and *Hypocuma*. Lastly, sister to the Bodotriidae are the most derived members of the Vaunthompsoniinae. The basal most genera of that derived clade is *Gaussicuma*, followed by *Bathycuma*, *Glyphocuma*, *Sympodomma*, *Gigacuma* and *Pseudosympodomma* (see figure 5 for detail on the synapomorphies).

Discussion

The Monophyly of the Bodotriidae. Bodotriidae is well supported as a monophyletic group. Outgroup taxa always group together external to the bodotriid genera. *Spilocuma* is currently assigned to the Mancocumatinae, but it uniquely lacks pleopods; the presented phylogeny does not provide strong support for its placement within the Bodotriidae. The lack of grouping and absence of synapomorphies suggest that *Spilocuma* represents a basal bodotriid, or that it belongs to a different subfamily. Further analyses that include the rest of the pleotelson genera are needed to determine the accurate position of this genus.

The Bodotriinae. Monophyly of the subfamily Bodotriinae is well supported by decay index values and a series of synapomorphies. *Iphinoe* represents one of the basal genera of the subfamily. However, the body proportions and carapace ornamentation of this genus often resembles members of the *Vaunthompsonia* belonging to Vaunthompsoniinae. *Iphinoe* and *Upselaspis* are very similar but can be discriminated by the degree of visibility of the first peraeonite (never visible in *Upselaspis* and usually visible in *Iphinoe*, although sometimes only in dorsal view).

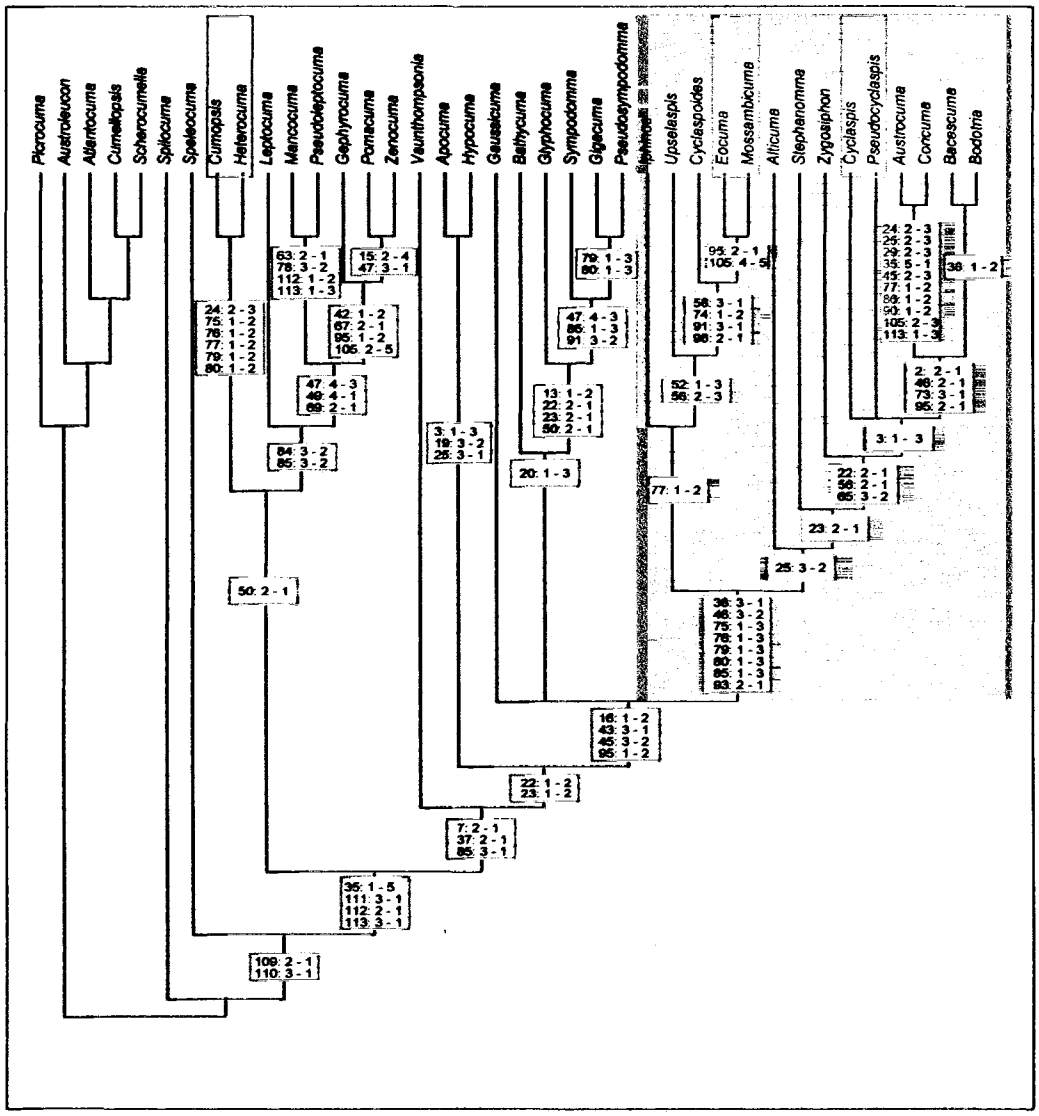


Figure 5. Majority rule (50%) consensus cladogram of the 10 most parsimonious trees obtained from 10,000 heuristic searches starting from random trees. Text boxes on branches list synapomorphies supporting the node. The first number indicates the character; after the colon, the first number indicates the plesiomorphic state and the last number the state synapomorphic for the node (see Appendices B and C for characters and character states). Shaded area corresponds to branches and nodes of the subfamily Bodotriinae. It is suggested that each pair of taxa enclosed by rectangle should be merged into one genus.

Analysis of character evolution shows that two genera of the Bodotriinae should not be separate entities and can be incorporated into other pre-existing genera. The genus *Mossambicuma* is monotypic and the species is hard to distinguish from *Eocuma* species. When Day (1978) described this new genus, she recognized that it was very similar to *Eocuma* but that the new species lacks the characteristic projection on the basis of the first peraeonite as well as the lateral horns. These two characters are common within the *Eocuma*, but not all species display them. Based on this, the species *Mossambicuma elongatum* will be placed in the genus *Eocuma* causing the generic name *Mossambicuma* to become unavailable.

Pseudocyclaspis, which was created by Radhadevi and Kurian (1981b) to include two species, reported to have a different number of eye lenses than species of *Cyclaspis*. However, number of lenses among cyclaspids is extremely variable, and the eye lenses and frontal lobe of *Pseudocyclaspis* are well within the range of *Cyclaspis* variation. Because of the lack of characters to differentiate current *Pseudocyclaspis* and *Cyclaspis* species, the two species in *Pseudocyclaspis* will be incorporated into the *Cyclaspis*, and the generic name *Pseudocyclaspis* becomes unavailable.

The results clearly show that *Austrocuma* and *Coricuma* belong to the Family Bodotriidae and represent the most divergent genera within the subfamily Bodotriinae. Since most of the members of the Bodotriidae bear five pairs of pleopods, pleopod number has been frequently used as a diagnostic character of the subfamily. However, *Austrocuma* and *Coricuma* have fewer than five pairs of pleopods but only have exopods on peraeopod 1, and thus fall within the Bodotriinae. The best synapomorphy for distinguishing the Bodotriinae is the presence of exopods restricted to the first pair of peraeopods.

In summary, the following changes to the classification of the Bodotriinae are suggested: *Apocuma* should be moved to the subfamily Vaunthompsoniinae, *Pseudocyclaspis* species should be moved into the genus *Cyclaspis*, and the monotypic *Mossambicuma* integrated into *Eocuma*. Incorporating these changes, the genera of the Bodotriinae would be: *Alticuma* Day (1978), *Austrocuma* Day (1978), *Bacescuma* Petrescu (1998), *Bodotria* Goodsir (1843),

Coricuma Watling and Breedy (1988), *Cyclaspis* Sars (1865), *Cyclapsoides* (Bonnier, 1896), *Eocuma* Marcusen (1894), *Iphinoe* Bate (1856), *Stephanoma* Sars (1871), *Upselaspis* Jones (1955), and *Zygosiphon* Calman (1907).

Diagnosis of the Subfamily Bodotriinae: Without exopods on peraeopods 2, 3 and 4. Males usually bear five pairs of pleopods. Generally without ventrolateral expansions on peraeonites 3. Females with at most two articles on Antenna 2. Basis of maxilliped three generally expanded ventrally over ischium.

The Mancocumatinae and Vaunthompsoniinae. The Mancocumatinae do not represent a monophyletic unit. The phylogenetic hypothesis presented here indicates that *Spilocuma* and *Speleocuma* diverge in a basal location to the currently recognized Vaunthompsoniinae, thus not forming a clade. Additionally, the *Pseudoleptocuma* and *Mancocuma* group within the Vaunthompsoniinae, is a clade sister to the operculate genera. Watling (1977) had compared some of the genera of Mancocumatinae and pointed out the extensive similarities between *Pseudoleptocuma* and *Mancocuma.* Since the Mancocumatinae does not represent a natural group and since there are no characters that can be used to differentiate them, members of the Mancocumatinae will be incorporated into the Vaunthompsoniinae.

Character analysis showed that *Cumposis* and *Heterocuma* lack discriminatory characters. In addition, molecular phylogenetic analyses showed that those two genera are very closely related, as much as, or more than two congeners (Chapter 2, Figs. 2 and 3). These two genera should be merged, by priority into *Cumopsis.* The following changes to the classification of the Vaunthompsoniinae are suggested. *Picrocuma* is excluded from the Vaunthompsoniinae and from the Bodotriinae. The genera currently within the Mancocumatinae (i.e., *Mancocuma*, *Pseudoleptocuma*, *Speleocuma* and *Spilocuma*), will be included in the Vaunthompsoniinae. The genus *Apocuma*, is moved from the Bodotriinae to the Vaunthompsoniinae. *Cumopsis* and *Heterocuma* are integrated into a single genus, *Cumopsis.* Thus, the Family Vaunthompsoniinae includes the following genera: *Apocuma* Jones (1973), *Bathycuma* Hansen (1895), *Cumopsis*

Sars (1878), *Gephyrocuma* Hale (1936), *Gigacuma* Kurian (1951), *Glyphocuma* Hale (1944), *Hypocuma* Jones (1973), *Leptocuma* Sars (1873), *Mancocuma* Zimmer (1943), *Pomacuma* Hale (1944), *Pseudoleptocuma* Watling (1977), *Pseudosympodomma* Kurian (1954), *Speleocuma* Corbera (2002), *Spilocuma* Watling (1977), *Sympodomma* Stebbing (1912), *Vaunthompsonia* Bate (1858), and *Zenocuma* Hale (1944)

Diagnosis of the Subfamily Vaunthompsoniinae: Exopods beyond the first pair of peraeopods. Females with at least three articles on Antenna 2. Uropod endopod generally bi-articulated.

Origin of the Bodotriidae. Bodotriids show high levels of endemism. Very few species have distributions ranging across oceans or marine bio-provinces (Day, 1978), and the majority of species are present between 20°N and 50°S latitude and absent from latitudes greater than 70° (i.e., 'negative amphipolar', Zimmer, 1941). Their latitudinal distribution suggests that bodotriids probably originated in warm-waters. Cumaceans are small, have limited mobility and lack a dispersal larval stage. They are benthic and able to swim only for short distances. Nocturnal vertical migration into the water column by males and juveniles may represent the most powerful means of the dispersal for cumaceans. For females, swimming activities are restricted to molting, hatching and copulation. The high endemism and narrow geographic range are probably due to the limited dispersal ability.

Bodotriids follow a distribution consistent with diversification in the newly forming Atlantic during the Jurassic to Cretaceous. The Jurassic followed a devastating mass-extinction, and the warm waters of the Tethys Ocean become a radiation center for many of the currently extant groups, including cumaceans. The North Atlantic started opening during the Jurassic and was still in formation in the Cretaceous, fed by a current from the Tethys Ocean (130 MYA) that may have helped cumaceans reach the Atlantic Ocean (Haq, 1984).

Based on regional diversity, Day (1978) proposed the Indo-West Pacific as the center of origin of the Bodotriidae, with subsequent dispersion into the Atlantic and Pacific Oceans. This is not compatible with the current phylogenetic scheme. Basal bodotriids inhabit the Atlantic and/or the

Indian Oceans into the Indo-West Pacific (Fig. 6). The basal most two genera, *Spilocuma*, and *Speleocuma*, only occur in the Atlantic Ocean. The current distribution of the genera can be explained by center of origin in the Atlantic Ocean or the Indian Ocean. But, since *Spilocuma* and *Speleocuma* occur in the Atlantic, and because other basal members of the Vaunthompsoniinae also inhabit the Atlantic, it is likely that bodotriids diverged from other cumaceans within the newly forming Atlantic Ocean, a view proposed for the Mancocumatinae by Corbera (2002).

The somewhat basal bodotriid clade that leads to *Cumopsis*, *Mancocuma*, *Pseudoleptocuma* and the operculate genera are currently found along coasts of Africa and Australia, in the South Atlantic, and in the Mediterranean Sea, consistent with dispersion from a common ancestor from the Atlantic Ocean. During the Cretaceous, the Atlantic was increasing in size and localized populations of cumaceans could differentiate. Over time these populations with restricted dispersion may have become the propagators/ancestors of the endemic lineages currently present in the north (Mediterranean Sea), as well as the southern Atlantic (Argentinean and African coasts) following dispersion into Australian waters. The genus *Vaunthompsonia* is widespread and its distribution can also be explained by an Atlantic origin with subsequent dispersion into Mediterranean Sea and Red Sea, West Indian Ocean, coasts of Australia, West and Indo-West Pacific, as well as SubAntarctic and Antarctic regions. The *Apocuma-Hypocuma* clade is currently restricted to the deep waters of the Atlantic Ocean. The remaining genera of the Vaunthompsoniinae and the Bodotriinae are well represented along the coasts of Africa, Indian Ocean, Australia, and Indo-West Pacific, and are also present in the Mediterranean and Red Seas, Pacific and Southern Oceans, boreal regions, oriental and Japan regions (Fig. 6).

Cumacean fossils are scarce and date back to the Carboniferous in the Paleozoic (Malzahn, 1972; Schram, personal communication). The deep-sea cumacean fauna is likely to have existed through the Mesozoic in oxygenated refuges in the deep waters, rather than the post-Mesozoic colonization of the deep sea from the Tethys Sea (Horne, 1999; Wilson, 1999). In contrast to these basal deep-sea cumaceans, the Family Bodotriidae occupies mainly temperate shallow waters, and is likely to have radiated in the newly forming Atlantic Ocean, originating in

the warm-waters of the ancient Tethys Ocean. The presence of taxa with plesiomorphic characters within the Atlantic rather than the Indo-West Pacific suggests that the dispersion route of bodotriids was from the Tethys Ocean to the Atlantic Ocean and into the Indian Ocean. Additional fossil material is needed to evaluate this hypothesis.

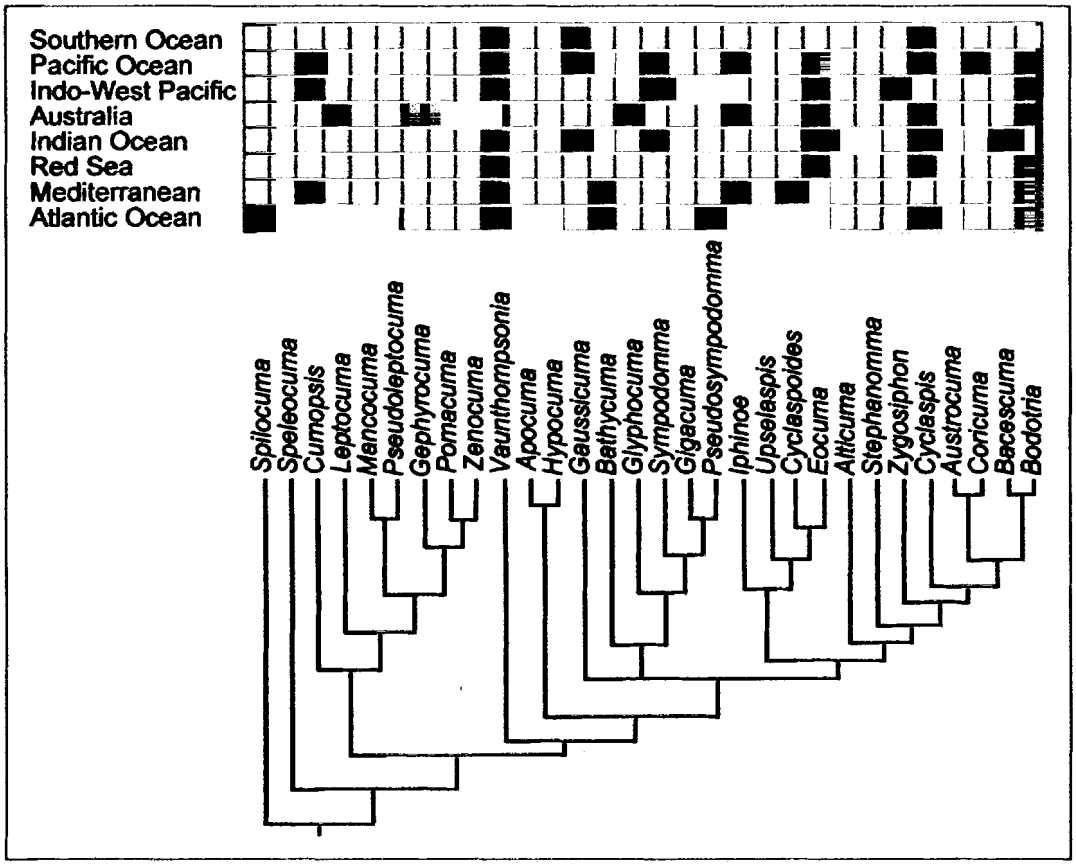


Figure 6. Geographic distribution of genera of the Family Bodotriidae. Tree topology corresponds to consensus tree from parsimony analysis. Rows of matrix above tree represent a summarized list of geographic areas (oceans, seas, or coasts) where bodotriids are well represented. Filled squares indicate presence of the genus in the area.

Chapter 4

THE GENERA OF THE BODOTRIIDAE

Introduction

The family Bodotriidae Scott (1901) is characterised by the presence of a pleotelson, naviculoid mandibles, generally five pairs of pleopods (occasionally four, three, two or zero pairs), exopods always present in third maxillipeds and in peraeopod 1, endopod of uropod uni- or bi-articulated, and branchial apparatus without gill-plates or supports.

The Vaunthompsoniinae Sars (1879) appears to be a paraphyletic group. Phylogenetic analyses reveal that the Bodotriinae Hale (1944) is a derived group of the Vaunthompsoniinae (see chapter 3, figs. 3 and 4). However, it is suggested that the subfamily Vaunthompsoniinae be retained in the classification of the Bodotriinae for taxonomic convenience. There are morphological traits that diagnose and clearly differentiate these two subfamilies. Within the subfamily Bodotriinae, species bear exopods only on peraeonite 1 and females have at the most two articles on antenna 2, while within the Vaunthompsoniinae, species bear exopods beyond the first pair of peraeopods, and females have at least three articles on antenna 2.

In this review of the Bodotriidae, the classification is slightly modified. Watling (1977) defined the subfamily Mancocumatinae to group all genera whose species had fewer than five pairs of pleopods and exopods beyond the first pair. The Subfamily Mancocumatinae is currently composed of four genera: *Mancocuma*, *Pseudoleptocuma*, *Speleocuma* and *Spilocuma*. Morphological phylogenetic analyses suggest that the Mancocumatinae is paraphyletic. The genera *Spilocuma*, and *Speleocuma* presumably are basal within the Vaunthompsoniinae. However, *Mancocuma* and *Pseudoleptocuma*, are embedded within the Vaunthompsoniinae, in a position distant from the other three genera of the Mancocumatinae. In addition, there are no

morphological characters to properly define the subfamily. In this revision, these genera are classified within the subfamily Vaunthompsoniinae.

Phylogenetic and character evolution analyses (chapters 2 and 3) suggest *Cumopsis* Sars (1878) and *Heterocuma* Miers (1879) of the Vaunthompsoniinae are closely related and lack morphological differentiation. Since there is no single character that can be used to unambiguously distinguish between these two genera, in the present work they are integrated together into the genus *Cumopsis* that has precedence over *Heterocuma.*

The genus *Apocuma* has been considered as a member of the Bodotriinae by Bâcescu (1988), although upon erection it was described as a genus of the Vaunthompsoniinae (Jones, 1973). The phylogenetic analyses confirm placement of this genus within the Vaunthompsoniinae, close to *Hypocuma*; it will be considered here as a member of the Vaunthompsoniinae.

Pseudocyclaspis Radhadevi and Kurian (1981b) was erected to include two species from the Gulf of Mexico that were thought to differ from the *Cyclaspis* by the number of lenses of the eye lobe. However, the number of lenses is extremely variable within the *Cyclaspis*, and the statements have proven to be false: there is no evidence to suggest that the species do not belong to the very diverse genus *Cyclaspis.* The two *Pseudocyclaspis* species will be incorporated into the genus *Cyclaspis.*

Several new species of the Bodotriinae were described by Day (1978), many as representatives of new monotypic genera. The genus *Mossambicuma* was erected to accommodate a species that resembles *Eocuma* species but lacks the characteristic projection on the basis of Peraeopod 1 and lateral horns. However, while both of these characters are common within the *Eocuma*, not all species have them, and thus they do not represent defining characters. *Eocuma muradianae* Petrescu (1998) also lacks the projection on the basis of Peraeopod 1, and many *Eocuma* species lack the lateral horns. The present species composition of the genus *Eocuma* does not justify having *Mossambicuma elongatum* as a

member of a separate genus since it bears all the characteristics that define a member of the *Eocuma*. In the present review, *Mossambicuma elongatum* is placed with the *Eocuma*.

Watling (1991a) moved the genus *Coricuma* from the Bodotriinae to the Family Leuconidae based on the presence of two pairs of pleopods. Here, the genus is reinserted into the Bodotriinae since it falls within its definition, and phylogenetic analyses indicate that it is very closely related to *Austrocuma*, *Bodotria* and *Bacescuma*.

Lastly, the genus *Picrocuma* has an ambiguous position within the pleotelson clade, but most likely represents a member of the Family Nannastacidae (Dr. Watling, personal communication). In this review, *Picrocuma* will not be considered as a member of the Bodotriidae.

The goals of the present work are to describe each genus of the Bodotriidae. Taxonomic keys to the subfamilial and generic level as well as redescriptions of each of the genera are provided.

The software DELTA was used as a database for all bodotriid genera. A total of 114 morphological characters (Appendix B) were coded for each genus. Characters were often coded as polymorphic since all species that compose a genus were considered in the coding. Characters and character states are depicted in Appendix C. The completed database was used to generate natural language descriptions in DELTA. A modified version of those descriptions will be presented here.

Dichotomous Key to the Subfamilies of Bodotriidae

1a- Exopods present only on first peraeopods	Bodotriinae
1b- Exopods present beyond first peraeopods	Vaunthompsoniinae

Dichotomous Key to Genera in the Subfamily Bodotriinae

1. Branchial siphons (Appendix C, character 17)	
- Long	2
- Short	3
2. Eye lenses (Appendix C, character 23)	
- Present	*Zygosiphon*
- Absent	*Cyclapsoides*
3. Basis of maxilliped 3 (Appendix C; character 43)	
- Dorso-distally projected	4
- Not projected	*Stephanoma*
4. Male, pleopods on pleonite 5 (Appendix C, character 113)	
- Present	5
- Absent	9
5. Number of articles on uropodal endopod (Appendix C, character 102)	
- One	10
- Two	6
6. Length of proximal article of peduncle of antenna 1 relative to other two articles (Appendix C, character 25)	
- Same length or longer	7
- Shorter	8

7. Lateral ridges on carapace (Appendix C, character 9) and ischium of peraeopod 2 (Appendix C, character 77)
   - Carapace with lateral ridges (sometimes only ovigerous females) or peraeopod 2 without distinct ischium — *Bodotria (Atlantobodotria)*
   - Carapace without lateral ridges and peraeopod 2 ischium present — *Alticuma*
8. Visibility of peraeonite 1 and ventrolateral expansion of peraeonite 2 (Appendix C, characters 52 and 56)
   - Peraeonite 1 not visible and ventrolateral expansion of peraeonite 2 does not override the carapace — *Upselaspis*
   - Peraeonite 1 usually visible and ventrolateral expansion of peraeonite 2 overrides carapace and/or peraeonite 1 — *Iphinoe*
9. Projection of pseudorostrum beyond frontal lobe (Appendix C, character 13)
   - Projected — *Austrocuma*
   - Not projected — *Coricuma*
10. Length of peduncle of uropods relative to rami (Appendix C, character 105)
   - Longer, equal or slightly shorter — 11
   - Much shorter — *Eocuma*
11. Mandible structure
   - Without pars incisiva and lacinia mobilis — *Bacescuma*
   - With pars incisiva and lacinia mobilis — 12

12. Lateral ridges of the carapace and degree of expansion of the merus of maxilliped three (Appendix B, characters 9 and 46)
    - Strongly marked lateral ridges or expansion of the merus of maxilliped three not reaching propodus-carpus joint — *Bodotria (Bodotria)*
    - Without strongly marked lateral ridges or expansion of the merus of maxilliped three reaching the propodus-carpus joint — *Cyclaspis*

Dichotomous Key to Genera in the Subfamily Vaunthompsoniinae

1. Modification of male antenna 2 (Appendix C, character 36)
    - Anterior margin with pad-like sensory setae — 2
    - Not modified — 3
2. Projection of basis of maxilliped 3 (Appendix C, character 43)
    - Basis projected over ischium — *Mancocuma*
    - Basis not projected over ischium — *Spilocuma*
3. Brush of setae on propodus of maxilliped 3 (Appendix C, character 50)
    - Present — 4
    - Absent — 14
4. Exopod on peraeonite 2 (Appendix C, characters 75 and 76)
    - Reduced — *Cumopsis*
    - Fully developed — 5
5. Female, exopod on peraeopod 4 (Appendix C, character 84)
    - Reduced — 6
    - Absent — 10

6. Peraeopod 1, opercularity (Appendix C, character 61)
   - Non-opercular 7
   - Opercular 8
7. Male, pleopods on pleonite 5 (Appendix C, character 113)
   - Present *Leptocuma*
   - Absent *Pseudoleptocuma*
8. Exopod on peraeopod 3 (Appendix C, characters 79 and 80)
   - Fully developed 9
   - Reduced *Gephyrocuma*
9. Pleonite 6, shape (Appendix C, character 90), and produced condition (Appendix C, character 93)
   - As long as wide, not produced between the bases of the uropods *Zenocuma*
   - Longer than wide, produced between the bases of the uropods *Pomacuma*
10. Exopod on peraeonite 3 (Appendix C, characters 79 and 80)
   - Absent 11
   - Present (fully developed or reduced) 12
11. Length of pleonite 6 relative to peduncle of uropods (Appendix C, character 91)
   - Longer or equal *Sympodomma*
   - Shorter *Glyphocuma*
12. Relative length of articles of uropodal endopod (Appendix C, character 103)
   - Proximal article equal or longer than distal article *Pseudosympodomma*
   - Proximal article shorter than distal article *Gigacuma*

13. Ocular pigment and eye lenses (Appendix C, characters 22 and 23)

    - Present 14

    - Absent 15

14. Males, pleopods (Appendix C, characters 111-113)

    - Pleopods absent on pleonites 3, 4 and 5 *Speleocuma*

    - Pleopods present on pleonites 3, 4 and 5 *Vaunthompsonia*

15. Number of articles on uropodal endopod (Appendix C, character 102)

    - One *Apocuma*

    - Two 16

16. Female, exopod on peraeopod 4 (Appendix C, characters 84)

    - Reduced *Hypocuma*

    - Absent 17

17. Shape of frontal lobe (Appendix C, character 20)

    - As wide as long *Gaussicuma*

    - Longer than wide *Bathycuma*

Implicit Characters

Unless stated otherwise, the following characteristics are implicitly assumed in the descriptions of the genera.

- Carapace not oviform posteriorly, longer than wide
- Median dorsal ridge, dorso-lateral ridges, lateral ridges, anterior transverse ridges, posterior transverse ridges, and lateral horns absent
- Branchial siphons short extending just beyond pseudorostrum
- Frontal lobe present

- Antenna 1, distal margin of peduncle, proximal article of main flagellum, and last article of main flagellum without aesthetasc; accessory flagellum reduced, without brush of setae, and without aesthetasc
- Antenna 2, not modified
- Mandible, with dorsal part to molaris naviculoid
- Maxilliped 3 (Mxp3) shows specialisation; basis of normal width, merus without dorsal projection, carpus not oviform or widened, propodus not oviform or widened, propodus without brush of setae
- Peraeonite 1 fused to carapace, well exposed
- Peraeonites 2 and 3 not fused
- Peraeonite 2 proportional in size to other peraeonites and without ventrolateral expansion
- Peraeonite 3 without ventrolateral expansion
- Peraeonite 4 without ventrolateral expansion
- Peraeopod 1 not opercular, basis without row of setae, not projected, and without inner apical angle; ischium not elongated, not modified; carpus not oviform, with no row of setae; carpus shorter than basis; propodus without setae; basis longer than propodus; dactyl with terminal setae
- Peraeopod 3 ischium present, merus of normal length, propodus and dactyl not modified
- Peraeopod 5 ischium present
- Articular pegs absent
- Pleonite 5 longer than pleonite 6
- Pleonite 6, without setae on posterior edge
- Anal plates not projected beyond posterior margin of pleonite 6 and without setae on posterior edge
- Uropod endopod and uropod exopod with terminal setae

Subfamily Bodotriinae Scott, 1901

Synonymy. Cumites Lucas, 1840; Cumacea Krŏyer, 1846; Cumadae Bell, 1851; Cumidae Sars, 1879; Bodotriidae Scott, 1901.

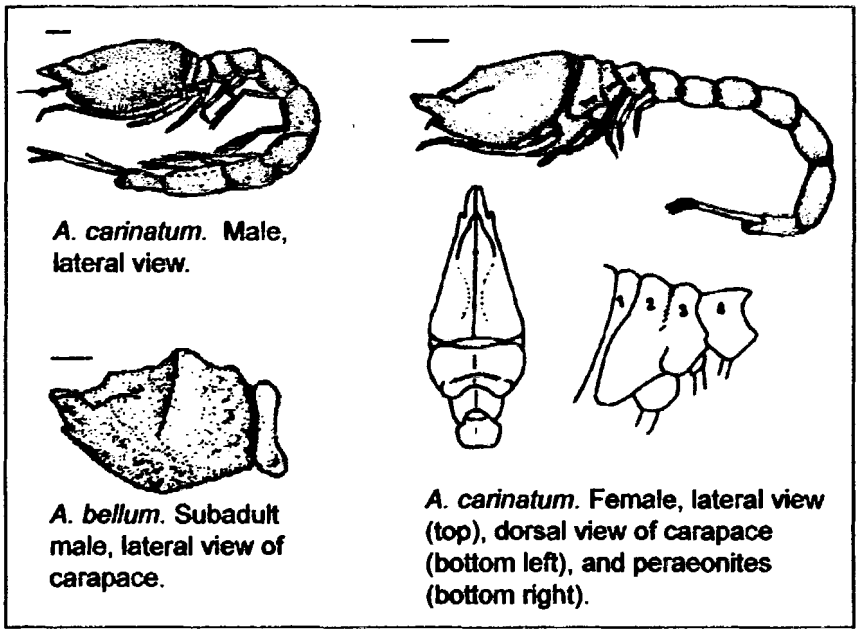
Type genus. *Bodotria* Goodsir, 1843

All genera within the Bodotriinae share the following traits: Females with one or two articles on antenna 2, and no exopods beyond the first pair of peraeopods on both females and males.

***Alticuma* Day, 1978**

Synonymy. *Cyclaspis* Zimmer, 1921.

Type species. *Alticuma carinatum* (Zimmer, 1921)



A. carinatum. Male, lateral view.

A. bellum. Subadult male, lateral view of carapace.

A. carinatum. Female, lateral view (top), dorsal view of carapace (bottom left), and peraeonites (bottom right).

Figure 7. External morphology of *Alticuma.* Figure modified from Day (1978). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as or shorter than carapace and peraeon together; carapace and peraeon similar in length.

Head. From dorsal view the carapace appears laterally compressed anteriorly and longer than wide. Carapace with mid-dorsal ridge, or mid-dorsal serration, and with or without anterior transverse ridge. Pseudorostral lappets extend or do not extend beyond frontal lobe; when extended they meet in midline. Antennal notch as a depression, subacute incision, or acute incision. Anterolateral corner with subacute or acute tooth. Frontal lobe 1/4 to 1/3 of the total carapace length; as wide as long, or longer than wide; anteriorly linguiform, or somewhat extended; without ocular pigment and without eye lenses.

Antenna 1, basal article of the peduncle geniculate or arcuate; as long as the other two articles together; males with a group of aesthetasc on distal margin of peduncle. Main flagellum uni- or bi-articulated; with one or two aesthetasc in distal-most article. Accessory flagellum uni-articulated; with or without aesthetasc. Antenna 2 in males reaching the end of the pleon.

Maxilliped 3 basis geniculate or arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium as long as merus (without considering projections). Merus extended dorso-distally over carpus. Propodus distally widened or not widened. Carpus distally widened or not widened; equal to or shorter than length of propodus and dactylus together.

Peraeon. First peraeonite well exposed, or visible only above lateral midline. Peraeonites 2 and 3 may be fused. Peraeonite 2 with or without ventrolateral expansion overriding peraeonite 3 or peraeonite 1. Peraeonite 3 with or without ventrolateral expansion overriding peraeonite 2 peraeonite 4. Peraeonite 4 with or without ventrolateral expansion overriding peraeonite 5 or peraeonite 3 and 5.

Peraeopod 1, basis arcuate; with or without row of setae. Carpus longer than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Articular pegs present or absent. Pleonite 6 longer than wide; shorter than peduncle of uropod; wide middle portion of distal end of pleonite 6 well extended past the insertion of the uropods; ending in a rounded apex. Anal plates do or do not extend posteriorly beyond distal margin of pleonite six.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than the distal one. Peduncle of uropods much longer than rami; endopod and exopod approximately same length. Males with five pairs of pleopods.

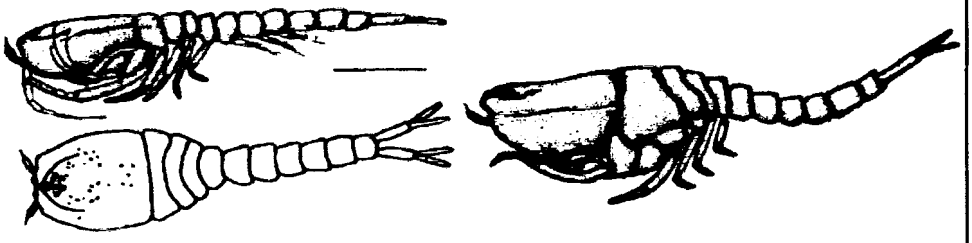
Species Included.

1. *A. bellum* Day, 1978
2. *A. carinatum* (Zimmer, 1921) (Synonymy: *Cyclaspis carinata* Zimmer, 1921; *A. carinatum* Day, 1978)

Distribution. Commonly found off the east African coast (West Indian Ocean) at depths between 100 and 1,300 m.

***Austrocuma* Day, 1978**

Type species. *Austrocuma platyceps* Day, 1978



A. platyceps. Male, lateral (top left) and dorsal (bottom left) view of body. Female, lateral view of body (right).

Figure 8. External morphology of *Austrocuma platyceps*. Figure modified from Day (1978). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen shorter than carapace and peraeon together; peraeon longer or shorter than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly and wider than long. Carapace with lateral ridges. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch as a depression, or subacute incision. Anterolateral corner bluntly rounded, or with subacute tooth. Frontal lobe 1/3 to 1/2 the total carapace length; as wide as long; slightly extended; with ocular pigment and eye lenses.

Antenna 1, basal article of the peduncle straight; shorter than the other two articles together. Main flagellum bi-articulated; with one aesthetasc in distal-most article. Accessory flagellum uni-articulated. Antenna 2 in males not reaching the end of the peraeon.

Maxilliped 3 basis geniculate or arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium shorter than merus (without considering

projections). Carpus distally widened and oviform; shorter than propodus and dactylus together. Propodus oviform.

Peraeon. First peraeonite visible only above lateral midline, or not visible. Peraeonite 2 wide; with ventrolateral expansion overriding peraeonite 1 and/or carapace and peraeonite 3, or not overriding other somites. Peraeonite 3 with or without ventrolateral expansion extended backwards overriding peraeonite 4. Peraeonite 4 with or without ventrolateral expansion overriding peraeonite 5.

Peraeopod 1, basis arcuate. Carpus equal to propodus. Peraeopod 2, ischium absent; dactyl and propodus approximately same length. Peraeopod 4, ischium absent.

Pleon. Pleonite 6 as long as wide; shorter than peduncle of uropod. Females with narrow portion of terminal end of pleonite 6 slightly extended between the base of the uropods ending in a line. Males with whole width of terminal end of pleonite 6 slightly extended between the base of the uropods; ending concave (with two projections).

Uropod endopod uni-articulated. Uropod exopod with proximal article shorter than distal one. Peduncle approximately as long as rami; endopod and exopod approximately same length. Males with three or four pairs of pleopods. Pleopodal endopod with well developed process.

Species Included.

1. *A. platyceps* Day, 1978
2. *Austrocuma* sp. Haye (to be described)

Distribution. *Austrocuma platyceps* inhabits the shallow waters (0-1 m) of the southern tip of South Africa from Muizenberg to Hout Bay on the Cape Peninsula as well as in the south-western Cape coast (Day, 1978) in the South Atlantic. *Austrocuma* sp. (see chapter 5) of the Indian Ocean inhabits shallow waters (1-5 m) in the coast of India.

***Bacescuma* Petrescu, 1998**

Type species. *Bacescuma tanzaniense* Petrescu, 1998

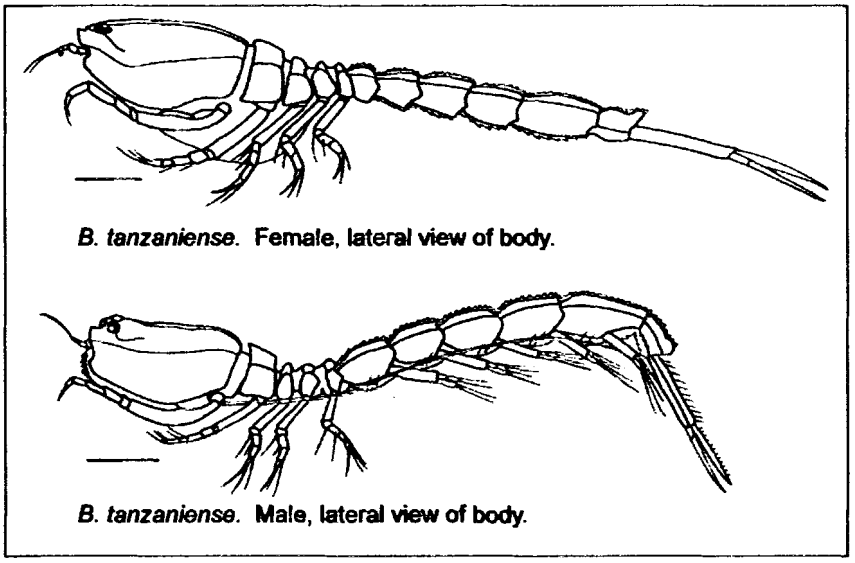


Figure 9. External morphology of *Bacescuma tanzaniense*. Figure modified from Petrescu (1998). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as carapace and peraeon together; carapace longer than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly and longer than wide. Carapace with mid-dorsal ridge and lateral ridges. Pseudorostral lappets extend beyond frontal lobe and extend towards midline but do not meet (or partially meet leaving a suture between them). Antennal notch as a depression, or as a subacute incision. Anterolateral corner bluntly rounded. Frontal lobe 1/4 of carapace length; as wide as long; anteriorly linguiform; with ocular pigment and eye lenses.

Antenna 1, basal article of the peduncle arcuate; as long as the other two articles together. Main flagellum bi-articulated; with 2 aesthetasc in distal-most article. Accessory flagellum uni-

articulated. Antenna 2 in males reaching almost the end of the pleon. Antenna 2 in females with two articles.

Maxilliped 3 basis arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium as long as merus (without considering projections). Carpus distally widened; equal to or shorter than propodus and dactylus together. Propodus proximally widened.

Peraeon. First peraeonite not visible. Peraeonite 2 proportional to or wider than other peraeonites; with ventrolateral expansion not overriding other somites.

Peraeopod 1, basis arcuate; with or without inner apical angle extended to form a convex process. Carpus longer than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; shorter than peduncle of uropod. Whole width of terminal end of pleonite 6 slightly extended between the base of the uropods; ending in a point. Anal plates extend posteriorly beyond distal margin of pleonite six.

Uropod endopod uni-articulated. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods longer than rami; endopod and exopod approximately same length. Males with five pairs of pleopods.

Species included.

1. *B. tanzaniense* Petrescu, 1998

Distribution. Coast of Tanzania in the West Indian Ocean, at 0 m in a shallow reef flat with fine sand and mud.

Notes. Modifications of Maxillipeds 1 and 2 with numerous setae and the lack of lacinia mobillis and pars incisiva on the mandible may be related to feeding on a small size particles (Petrescu, 1998).

***Bodotria* Goodsir, 1843**

Synonymy. *Cuma* Milne Edwards, 1828; *Cyma* Agassiz, 1846; *Scorpionura* Thompson, 1856; *Cumaea* Sars, 1914; *Cumoa* Sars, 1914.

Type Species. *Bodotria (Bodotria) arenosa arenosa* Goodsir, 1843

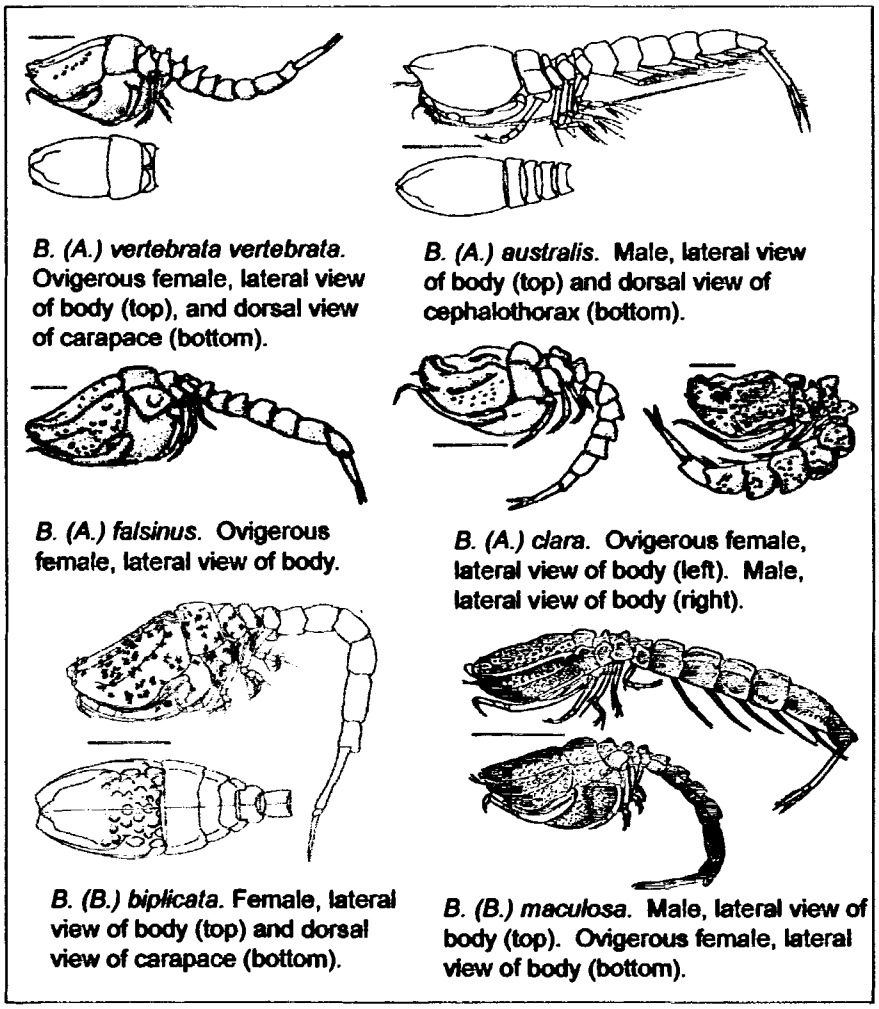


Figure 10. External morphology of *Bodotria* spp. Figure modified from Day (1978), Lee and Lee (1997), Petrescu (1998), and Tafe and Greenwood (1996). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately same length, longer, or shorter than carapace and peraeon together; carapace and peraeon similar in length, or peraeon longer or shorter than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly or not compressed and longer than wide. Carapace with or without mid-dorsal, dorso-lateral, and lateral ridges. Pseudorostral lappets extend or not beyond frontal lobe; when extended they meet in midline, extend towards midline but do not meet (or partially meet leaving a suture between them), or are widely separated. Antennal notch as a depression, subacute or acute incision. Anterolateral corner bluntly rounded, with subacute or acute tooth. Frontal lobe 1/3 to 1/2 the total carapace length; as wide as long, or wider than long; anteriorly linguiform, somewhat extended, or not extended; with or without ocular pigment and eye lenses.

Antenna 1, basal article of the peduncle geniculate, arcuate, or straight; longer or as long as the other two articles together; males with or without a group of aesthetasc on distal margin of peduncle. Main flagellum bi- or tri-articulated, with second article longer than third; with one or more aesthetasc in distal-most article; with or without two or a group of aesthetascs on proximal article of main flagellum. Accessory flagellum uni-articulated; with or without aesthetasc. Males with antenna 2 reaching the end of the pleon; with sensory setae on anterior margin of article four. Antenna 2 in females with two articles.

Maxilliped 3 basis geniculate or arcuate; slightly extended dorso-distally over ischium or projecting beyond the articulation of the ischium and merus. Ischium longer or same size as merus (without considering projections). Merus with or without dorso-distal projection over carpus. Carpus distally widened and/or oviform; longer, equal to, or shorter than propodus and dactylus together. Propodus oviform, distally widened or not.

Peraeon. First peraeonite well exposed, visible only above lateral midline, or not visible. Peraeonite 2 wide or proportional to other peraeonites; with or without ventrolateral expansion not

overriding other somites, or overriding peraeonite 1 and/or carapace, or overriding peraeonite 3, or overriding peraeonite 1 and/or carapace and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended forward overriding peraeonite 2, or extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 without ventrolateral expansion, or with ventrolateral expansion overriding peraeonite 3, or with ventrolateral expansion overriding peraeonite 5, or peraeonite 4 with ventrolateral expansion overriding peraeonite 3 and 5.

Peraeopod 1, basis arcuate or straight; with or without row of setae; with or without inner apical angle extended to form a sub-triangular tooth-like process or a convex process; with or without row of setae on the carpus; with or without setae in a linear arrangement along propodus; carpus longer than or equal to propodus. Peraeopod 2, ischium present or absent; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide, or as long as wide; shorter than peduncle of uropod; with or without two setae close to midline on posterior edge of pleonite 6. Pleonite 6 not extended between the base of the uropods, or whole width or wide portion of distal end of pleonite 6 slightly extended between the base of the uropods; ending in a point, a line, or in a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or do not project; with or without setae on posterior margin of anal plates.

Uropod endopod uni- or bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods much longer than rami; endopod and exopod approximately same length, or exopod longer than endopod. Males with five pairs of pleopods. Pleopodal endopod with well developed process, or process reduced.

Species Included.

1. *Bodotria* sp. Gamô, 1963
2. *Bodotria* sp. Toulmond and Truchot, 1964
3. *Bodotria* sp. Le Loeuff and Intès, 1972

Subgenus *Atlantobodotria* Petrescu, 1998

4. *B. (A.) australis* Stebbing, 1912
5. *B. (A.) armoricana* Le Loeuff and Intès, 1977 (Synonymy: *B. scorpioides* Fage, 1933)
6. *B. (A.) bineti* Le Loeuff and Intès, 1977
7. *B. (A.) choprai* Kurian, 1951
8. *B. (A.) clara* Day, 1978
9. *B. (A.) africana* Zimmer, 1920
10. *B. (A.) cribraria* Le Loeuff and Intès, 1972
11. *B. (A.) elevata* Jones, 1960
12. *B. (A.) falsinus* Day, 1978
13. *B. (A.) gibba* (Sars, 1878) (Synonymy: *Cuma gibba* Sars, 1878; *B. gibbus* Stebbing, 1912)
14. *B. (A.) intermedia* Le Loeuff and Intès, 1977
15. *B. (A.) lata* Jones, 1956
16. *B. (A.) magna* Zimmer, 1921
17. *B. (A.) montagui* Stebbing, 1912
18. *B. (A.) nitida* Day, 1978
19. *B. (A.) prionura* Zimmer, 1952
20. *B. (A.) pulchella* (Sars, 1878) (Synonymy: *Cuma pulchella* Sars, 1878; *B. pulchellus* Stebbing, 1912)
21. *B. (A.) scorpioides* (Montagu, 1804)
22. *B. (A.) serica* Day, 1978

23. *B. (A.) tenuis* Day, 1978

24. *B. (A.) vertebrata* Day, 1978

- *B. (A.) vertebrata semicarinata* Day, 1978

- *B. (A.) vertebrata vertebrata* Day, 1978

Subgenus *Bodotria* Goodsir, 1843

25. *B. (B.) alata* Bâcescu and Muradian, 1975

26. *B. (B.) angusta* Harada, 1967

27. *B. (B.) arenosa* Goodsir, 1843

- *B. (B.) arenosa arenosa* Goodsir, 1843 (Synonymy: *B. arenosa* Goodsir, 1843; *Bodothria arenosa* Van Beneden, 1861a; *Cuma pusilla* Sars, 1866; *Cuma scorpioides* Sars, 1899; *Bodotria arenosus* Stebbing, 1912; *Bodotria scorpioides typica* Steuer, 1936; *B. scorpioides septentrionalis* Steuer, 1936; *B. arenosa typica* Lomakina, 1958; *B. arenosa arenosa* Bâcescu, 1988)

- *B. (B.) arenosa leloeuffi* Corbera and Garcia-Rubies, 1998

- *B. (B.) arenosa mediterranea* (Steuer, 1936) (Synonymy: *Cuma edwardsi* Marcusen, 1867; *Bodotria* sp. Ostroumov, 1899; *B. scorpioides* Derzhavin, 1925; *B. scorpioides mediterranea* Steuer, 1936; *Bodotria arenosa mediterranea* Bâcescu, 1949)

28. *B. (B.) armata* Tafe and Greenwood, 1996

29. *B. (B.) biocellata* Radhadevi and Kurian 1989

30. *B. (B.) biplicata* Gamô, 1964b (Synonymy: *Bodotria* sp. Gamô, 1963)

31. *B. (B.) carinata* Gamô, 1964b

32. *B. (B.) cochinensis* Radhadevi and Kurian, 1989

33. *B. (B.) depressa* Harada, 1967

34. *B. (B.) dispar* Harada, 1967

35. *B. (B.) glabra* Jones, 1955

36. *B. (B.) iroensis* Harada, 1967

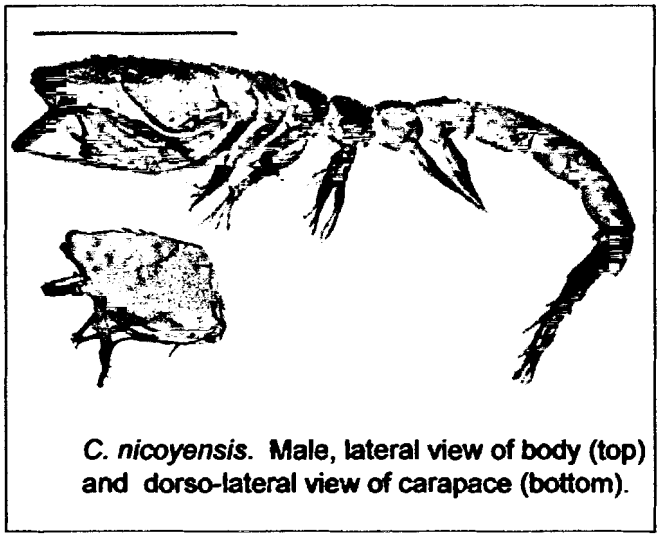
37. *B. (B.) laevigata* Le Loeuff and Intès, 1977 (Synonymy: *B. africana* Fage, 1928)
38. *B. (B.) maculosa* Hale, 1944
39. *B. (B.) minuta* Kurian, 1961
40. *B. (B.) nuda* Harada, 1967
41. *B. (B.) ovalis* Gamô, 1965
42. *B. (B.) ozolinshi* Tzareva and Vassilenko, 1993
43. *B. (B.) parva* Calman, 1907 (Synonymy: *B. chinensis* Lomakina 1960)
44. *B. (B.) platybasis* Radhadevi and Kurian, 1981a
45. *B. (B.) pulex* (Zimmer, 1903) (Synonymy: *Cuma pulex* Zimmer, 1903)
46. *B. (B.) rugosa* Gamô, 1963
47. *B. (B.) serrata* Harada, 1967
48. *B. (B.) serrulata* Gamô, 1965
49. *B. (B.) setoensis* Harada, 1967
50. *B. (B.) similis* Calman, 1907 (Synonymy: *B. siamensis* Calman, 1907; *Bodotria* sp. Calman, 1907; *Bodotria pumilio* Zimmer, 1921)
51. *B. (B.) spinifera* Gamô, 1986
52. *B. (B.) sublevis* Calman, 1907
53. *B. (B.) tosaensis* Harada, 1967
54. *B. (B.)* sp. nov.1 Tafe and Greenwood, 1996

Distribution. The sugenus *Atlantobodotria* is most commonly found in the Eastern Atlantic Ocean and Mediterranean Sea. They can also be found in the Indo-West Pacific and Indian Ocean. Generally found in sand at depths lower than 80 m, but some species are found at depths of up to 550 m. The subgenus *Bodotria* mostly found in the shallow waters of the West Pacific between 50 and 300 m. Only one species, *Bodotria (Bodotria) arenosa*, is distributed in the North-East Atlantic Ocean and Mediterranean and Black Seas.

Remarks. *Bodotria minuta* Kurian (1961) is the only species within the genus in which males bear only four pairs of pleopods. A re-description of this species will most likely reveal that it belongs in a different genus. Petrescu (1998) divided the genus *Bodotria* into two subgenera. Species where the endopod of the uropod is uni-articulated are within the *Bodotria (Bodotria)*, and the ones with the endopod of the uropod bi-articulated are within the *Bodotria (Atlantobodotria)*.

***Coricuma* Watling and Breedy, 1988**

Type species. *Coricuma nicoyensis* Watling and Breedy, 1988



C. nicoyensis. Male, lateral view of body (top) and dorso-lateral view of carapace (bottom).

Figure 11. External morphology of *Coricuma nicoyensis*. Figure modified from Watling and Breedy (1988). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as carapace and peraeon together; peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly and longer than wide. Carapace with mid-dorsal serration. Pseudorostral lappets do not extend beyond the frontal lobe. Antennal notch as a subacute incision. Anterolateral corner with subacute tooth. Frontal lobe half of carapace length; longer than wide; anteriorly linguiform; without eye lenses.

Antenna 1, basal article of the peduncle straight; shorter than the other two articles together. Main flagellum tri-articulated; with second article longer than third; with one aesthetasc in distal-most article. Accessory flagellum uni-articulated. Antenna 2 in males not reaching the end of the peraeon; posterior margin modified for grasping. Antenna 2 in females with one article.

Maxilliped 3 basis arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium shorter than merus (without considering projections). Merus slightly expanded laterally; equal to or shorter than propodus and dactylus together.

Peraeon. Peraeonite 2 wide or proportional to other peraeonites.

Peraeopod 1, basis arcuate; with inner apical angle extended to form a convex process; carpus longer than propodus. Peraeopod 2, dactyl longer than propodus. Peraeopods 2 to 5, ischium absent.

Pleon. Pleonite 6 as long as wide; shorter than peduncle of uropod. Pleonite 6 slightly extended between the base of the uropods.

Uropod endopod bi-articulated; proximal article shorter than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle approximately as long asrami; exopod longer than endopod. Males with two pairs of pleopods. Pleopodal endopod without process.

Species Included.

1. *C. nicoyensis* Watling and Breedy, 1988

Distribution. Gulf of Nicoya (western Costa Rica) in a tidal mud flat.

***Cyclaspis* Sars, 1865**

Synonymy. *Pseudocyclaspis* Radhadevi and Kurian, 1981.

Type species. *Cyclaspis quadriplicata* Sars, 1865

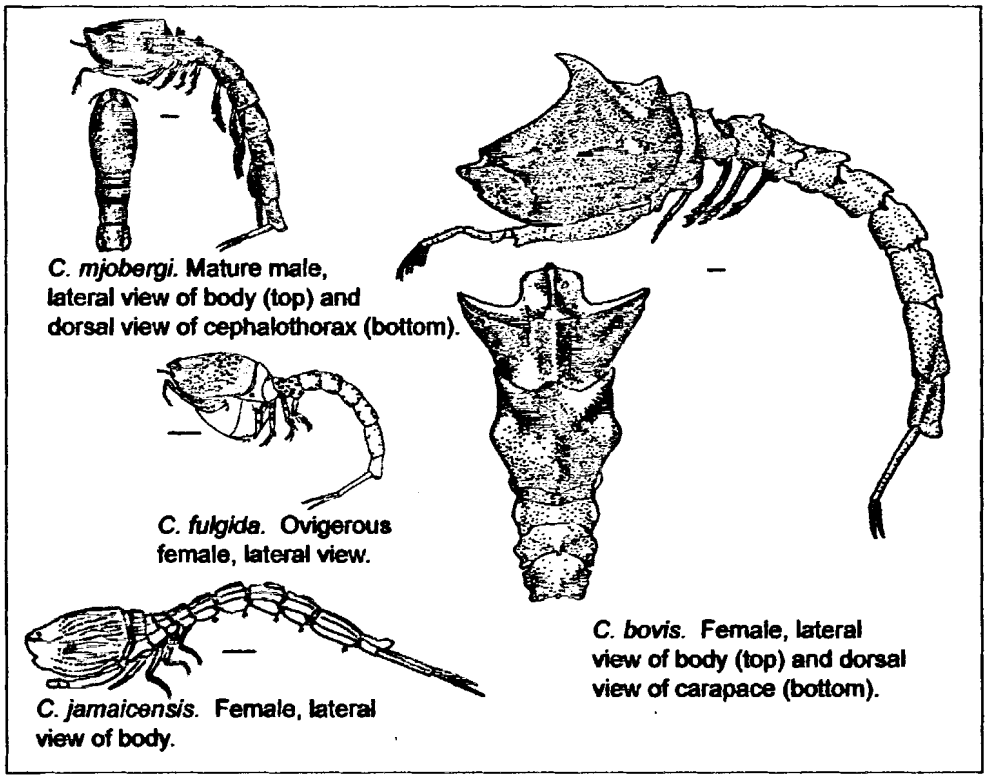


Figure 12. External morphology of *Cyclaspis* spp. Figure modified from Hale (1928, 1944) and Petrescu, Illife and Sarbu (1993). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace longer than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly, posteriorly, or in the medial portion, or not to be laterally compressed; oviform, or not oviform posteriorly and longer than wide. Carapace with or without mid-dorsal ridge, or with mid-dorsal serration, with or without dorso-lateral, lateral, anterior transverse, and posterior transverse ridges. Pseudorostral

lappets extend beyond or do not extend beyond frontal lobe; when extended they meet in midline, extend towards midline but do not meet (or partially meet leaving a suture between them), or are widely separated. Antennal notch as a depression, a subacute incision, an acute incision, or not distinct. Anterolateral corner bluntly rounded, with subacute tooth, or with acute tooth. Frontal lobe may be from 1/5 or less to half of the carapace length; as wide as long, or longer than wide; anteriorly linguiform, or somewhat extended; with or without ocular pigment and with eye lenses.

Antenna 1, basal article of the peduncle geniculate, arcuate, or straight; longer, shorter, or as long as the other two articles together. Main flagellum uni-, bi-, or tri-articulated; with second article longer than third; with one or more aesthetasc in distal-most article. Accessory flagellum reduced or absent. When present, accessory flagellum is uni- or bi-articulated; with or without aesthetasc. Antenna 2 in males reaching almost the end of the pleon, or reaching the end of the pleon; with sensory setae on anterior margin of article four. Antenna 2 in females with one or two articles.

Maxilliped 3 basis geniculate, arcuate, or straight; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium as long as or shorter than merus (without considering projections). Merus extended dorso-distally over carpus or expanded laterally. Carpus oviform, distally widened, or not widened; longer or equal to or shorter than propodus and dactylus together. Propodus oviform or distally or proximally widened, or not widened; with or without a brush of setae on propodus.

Peraeon. First peraeonite well exposed, or visible only above lateral midline, or not visible. Peraeonite 2 narrow, or proportional to other peraeonites; with or without ventrolateral expansion; expansion not overriding other somites, or overriding peraeonite 1 and/or carapace, or overriding peraeonite 3, or overriding peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended forward overriding peraeonite 2, or extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4.

Peraeonite 4 without ventrolateral expansion, or peraeonite 4 with ventrolateral expansion overriding peraeonite 5, or peraeonite 4 with ventrolateral expansion overriding peraeonite 3 and 5.

Peraeopod 1, basis arcuate, or straight; with or without row of setae; with basis slightly projected ventrally, or without projection; with or without inner apical angle extended to form a sub-triangular tooth-like process, or forming a convex process; with or without a brush (3 or more) of long setae on the propodus (setae longer than carpus), or with or without setae in a linear arrangement along propodus; carpus longer, equal to or shorter than propodus. Peraeopod 2, ischium present; dactyl and propodus approximately same length, or dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Articular pegs present, or absent. Pleonite 6 longer than wide; longer, same length, or shorter than peduncle of uropod. Pleonite 6 may or may not be slightly or well extended between the base of the uropods. When extended, whole width of terminal end of pleonite 6 extended ending in a point, concave (with two projections), or a rounded apex, or wide or narrow portion of the distal end of pleonite 6 extended ending in a point, a line, or in a rounded apex. Anal plates may or may not extend posteriorly beyond distal margin of pleonite six.

Uropod endopod uni-articulated. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods much longer, slightly longer, as long as or shorter than rami, endopod and exopod approximately same length, or endopod longer than exopod, or exopod longer than endopod. Endopod with or without terminal setae. Exopod with or without terminal setae. Males with five pairs of pleopods. Pleopodal endopod process well-developed, reduced, or without process.

Species Included.

1. *C. affinis* Lomakina, 1968
2. *C. agrenosculpta* Tafe and Greenwood, 1996
3. *C. alba* Roccatagliata, 1986
4. *C. alveosculpta* Tafe and Greenwood, 1996
5. *C. amamiensis* Gamô, 1963
6. *C. andersoni* Tafe and Greenwood, 1996
7. *C. antipai* Petrescu, 1995
8. *C. argus* Zimmer, 1902 (Synonymy: *C. bistriata* Zimmer, 1902; *C. biplicata* Calman, 1907; *C. pusilla* Stebbing, 1913)
9. *C. aspera* Hale, 1944
10. *C. australis* Sars, 1886
11. *C. australora* Day, 1978
12. *C. bacescui* Omholt and Heard, 1982
13. *C. bengalensis* Kurian, 1954
14. *C. bicornis* Zimmer, 1921
15. *C. bidens* Gamô, 1962
16. *C. bituberculata* Donath-Hernández, 1988
17. *C. bovis* Hale, 1928
18. *C. brevipes* Hale, 1948
19. *C. cana* Hale, 1944
20. *C. candida* Zimmer, 1921
21. *C. candidoides* Bâcescu, 1992
22. *C. caprella* Hale, 1936
23. *C. chaunosculpta* Tafe and Greenwood, 1996
24. *C. cheveyi* Fage, 1945
25. *C. cingulata* Calman, 1907

26. *C. clarki* Hale, 1944
27. *C. coelebs* Calman, 1917
28. *C. concepcionensis* Donath-Hernández, 1988
29. *C. concinna* Hale, 1944
30. *C. cooki* Tafe and Greenwood, 1996
31. *C. costata* Calman, 1904
32. *C. cottoni* Hale, 1937
33. *C. cretata* Hale, 1944
34. *C. cristulata* Gamô, 1987
35. *C. daviei* Tafe and Greenwood, 1996
36. *C. dentifrons* Zimmer, 1944
37. *C. dolera* Zimmer, 1944
38. *C. elegans* Calman, 1907
39. *C. exsculpta* Sars, 1877
40. *C. formosae* Zimmer, 1921
41. *C. fulgida* Hale, 1944
42. *C. gezamuelleri* Petrescu, 1998
43. *C. gibba* Hale, 1944
44. *C. gigas* Zimmer, 1907 (Synonymy: *C. glacialis* Hansen, 1908)
45. *C. globosa* Hale, 1944
46. *C. goesii* Sars, 1871 (Synonymy: *S. goësii* Bâcescu 1988; *Stephanoma goesii* Sars, 1871)
47. *C. granulata* Radhadevi and Kurian, 1981b (Synonymy: *Pseudocyclaspis granulata* Radhadevi and Kurian, 1981b)
48. *C. granulosa* Hale, 1944

49. *C. hermandi* Calman, 1904

- *C. hermandi hermandi* Calman, 1904 (Synonymy: *C. herdmani* Calman, 1904; *C. hermandi hermandi* Bâcescu, 1988)

- *C. hermandi annamensis* Fage, 1945

50. *C. indoaustralica* Bâcescu, 1992

51. *C. hornelli* Calman, 1904

52. *C. iphinoides* Bâcescu and Muradian, 1975 (Synonymy: *C. picta iphinoides* Bâcescu and Muradian, 1975)

53. *C. jamaicensis* Petrescu, Illife and Sarbu, 1993

54. *C. jonesi* Roccatagliata, 1985

55. *C. juxta* Hale, 1948

56. *C. kerguelenensis* Ledoyer, 1977

57. *C. levis* Thomson, 1892 (Synonymy: *C. laevis* Sars, 1899; *C. calmani* Hale, 1944)

58. *C. linguiloba* Lin and Lin, 1990

59. *C. longicaudata* Sars, 1865

60. *C. longipes* Calman, 1907

61. *C. lucida* Hale, 1944

62. *C. marisrubri* Bâcescu and Muradian, 1973 (Synonymy: *C. maris rubri* Bâcescu and Muradian, 1973; *C. marisrubri* Bâcescu and Muradian, 1975)

63. *C. mawsonae* Hale, 1944

64. *C. mexicansis* (Radhadevi and Kurian, 1981b) (Synonymy: *Pseudocyclaspis mexicansis* Radhadevi and Kurian, 1981b)

65. *C. micans* Roccatagliata, 1985

66. *C. mjoebergi* Zimmer, 1921 (Synonymy: *C. mjöbergi* Zimmer, 1921; *C. mjoerbergi* Hale, 1944)

67. *C. mollis* Hale, 1944

68. *C. nalbanti* Petrescu, 1998

69. *C. munda* Hale, 1944
70. *C. nitida* Hale, 1944
71. *C. nubila* Zimmer, 1936
72. *C. ornosculpta* Tafe and Greenwood, 1996
73. *C. oxyura* Roccatagliata and Moreira, 1987
74. *C. perelegans* Roccatagliata and Moreira, 1987
75. *C. persculpta* Calman, 1905
76. *C. peruana* Zimmer, 1943
77. *C. picta* Calman, 1904
78. *C. pinguis* Hale, 1944
79. *C. platymerus* Zimmer, 1944
80. *C. prolifica* Bàcescu, 1990
81. *C. pruinosa* Hale, 1944
82. *C. pura* Hale, 1936
83. *C. purpurascens* Gamô, 1964b
84. *C. pusilla* Sars, 1887
85. *C. pustulata* Zimmer, 1943
86. *C. popescugorji* Petrescu, 1998
87. *C. quadrituberculata* Zimmer, 1907
88. *C. quadruplicata* Kurian, 1951
89. *C. reticulata* Roccatagliata, 1985
90. *C. roccatagliatae* Petrescu, 1995
91. *C. rudis* Hale, 1948
92. *C. sabulosa* Hale, 1944
93. *C sallai* Tafe and Greenwood, 1996
94. *C. scissa* Day, 1978
95. *C. sculptilis* Roccatagliata and Moreira, 1987

96. *C. sheardi* Hale, 1944

97. *C. sibogae* Calman, 1905

98. *C. similis* Calman, 1907

99. *C. simonae* Petrescu, Illife, and Sarbu, 1993

100. *C. simula* Hale, 1944

101. *C. spectabilis* Zimmer, 1908

102. *C. spilotes* Hale, 1928

103. *C. stocki* Bâcescu, 1990

104. *C. striata* Roccatagliata and Moreira, 1987

105. *C. strigilis* Hale, 1944

106. *C. strumosa* Hale, 1948

107. *C. subgrandis* Jones, 1969

108. *C. sublevis* Hale, 1948

109. *C. supersulpta* Zimmer, 1921

110. *C. tasmanica* Jones, 1969

111. *C. testudinum* Zimmer, 1943

112. *C. thomsoni* Calman, 1907

113. *C. tranteri* Tafe and Greenwood, 1996

114. *C. tribulis* Hale, 1928

115. *C. triplicata* Calman, 1907

116. *C. unicornis* Calman, 1907

117. *C. uniplicata* Calman, 1907 (Synonymy: *Cyclaspis* sp. Calman, 1904)

118. *C. usitata* Hale, 1932

119. *C. variabilis* Roccatagliata 1986

120. *C. varians* Calman, 1912

121. *Cyclaspis* sp. Kurian, 1954

122. *Cyclaspis* sp. Lomakina, 1968

123. *Cyclaspis* sp. Gladfelter, 1975

124. *Cyclaspis* sp. A Dexter, 1979

125. *Cyclaspis* sp. B Dexter, 1979

126. *Cyclaspis* sp. nov.1 Tafe and Greenwood, 1996

127. *Cyclaspis* sp. nov.2 Tafe and Greenwood, 1996

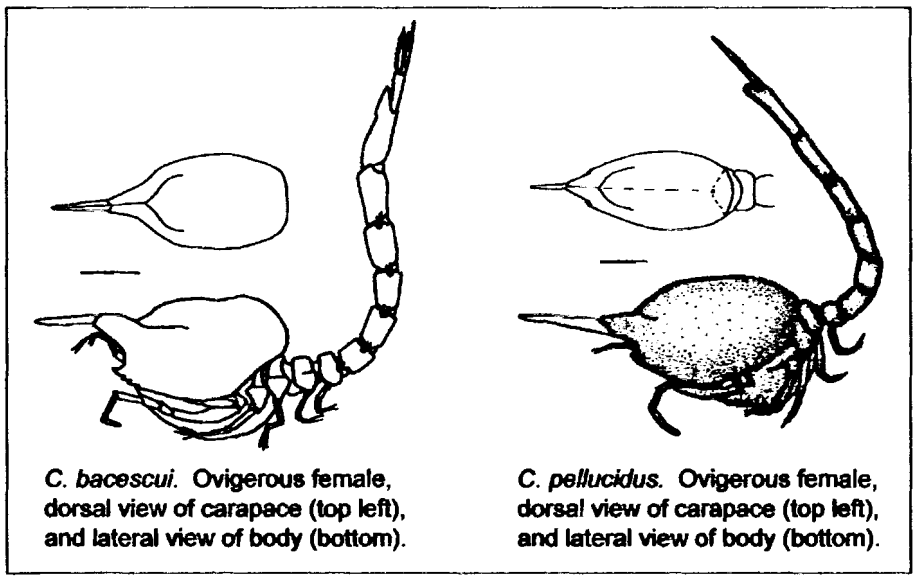
Distribution. Present in all the oceans. Most common at depths lower than 50 m in temperate latitudes of the Southern Hemisphere, particularly in the Indo-West Pacific and Australian coasts.

Remarks. *Cyclaspis* is the most specious of the bodotriid genera. *Cyclaspis* species are not easily diagnosed. This genus had been a 'grab bag' for species of the Bodotriinae that share some of a suite of characters, including: pseudorostral lappets not extending beyond the frontal lobe, well developed eye lenses, distal article of main flagellum of antenna1 with at least one aesthetasc, basis of maxilliped 3 extended dorso-distally over ischium beyond the articulation of the ischium and merus, peraeopod 2 and 4 with ischium present, articular pegs in the abdomen, pleonite 6 longer than wide, and uropod endopod uni-articulated. There is great morphological variability within the genus *Cyclaspis* and needs to be divided into several related genera.

***Cyclaspoides* Bonnier, 1896**

Synonymy. *Cyclospoides* Bonnier, 1896

Type species. *Cyclapsoides sarsi* Bonnier, 1896



C. bacescui. Ovigerous female, dorsal view of carapace (top left), and lateral view of body (bottom).

C. pellucidus. Ovigerous female, dorsal view of carapace (top left), and lateral view of body (bottom).

Figure 13. External morphology of *Cyclapsoides* spp. Figure modified from Day (1978) and Petrescu (1995). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as or longer than carapace and peraeon together; carapace longer than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly; oviform, or not oviform posteriorly, and longer than wide. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch as a depression, or as a subacute incision. Anterolateral corner bluntly rounded, with subacute tooth, or with acute tooth. Branchial siphons long, extending much beyond pseudorostrum. Frontal lobe approximately 1/4 of carapace length; as wide as long; somewhat extended, or not extended; without ocular pigment or eye lenses.

Antenna 1, basal article of the peduncle arcuate, or straight; shorter than the other two articles together. Main flagellum uni-, or tri-articulated; with second article longer than third; with 2 aesthetasc in distal-most article. Accessory flagellum uni-articulated.

Maxilliped 3 basis arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium as long as merus (without considering projections). Merus extended dorso-distally over carpus. Carpus equal to or shorter than propodus and dactylus together.

Peraeon. Peraeonite 1 to 3 covered by carapace.

Peraeopod 1, basis arcuate; with or without row of setae; carpus equal to propodus. Peraeopod 2, ischium present or absent; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Articular pegs present or absent. Pleonite 5 as long as or shorter than pleonite 6. Pleonite 6 longer than wide; longer than peduncle of uropod. Whole width of pleonite 6 is well extended between the base of the uropods; ending in a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or do not project.

Uropod endopod uni-, or bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle approximately as long as rami, or peduncle slightly shorter than exopods of rami (equal length to endopod); endopod and exopod approximately same length, or exopod longer than endopod. Males with five pairs of pleopods. Pleopodal endopod with well developed process.

Species Included.

1. C. *bacescui* Petrescu, 1995
2. *C. pellucidus* Day, 1978
3. *C. sarsi* Bonnier, 1896
4. *Cyclapsoides* sp. Calman, 1905

Distribution. Off the coasts of South Africa, Mediterranean Sea, and Pacific Ocean at depths greater than 400 m (up to 1,900 m).

Notes. The single specimen of *Cyclapsoides* sp. Calman (1905) was found in the atrial cavity of a tunicate, possibly indicating an endosymbiotic life-style.

***Eocuma* Marcusen, 1894**

Synonymy. *Cyclaspis* Kossman, 1880; *Mossambicuma* Day, 1978.

Type species. *Eocuma hilgendorfi* Marcusen, 1894

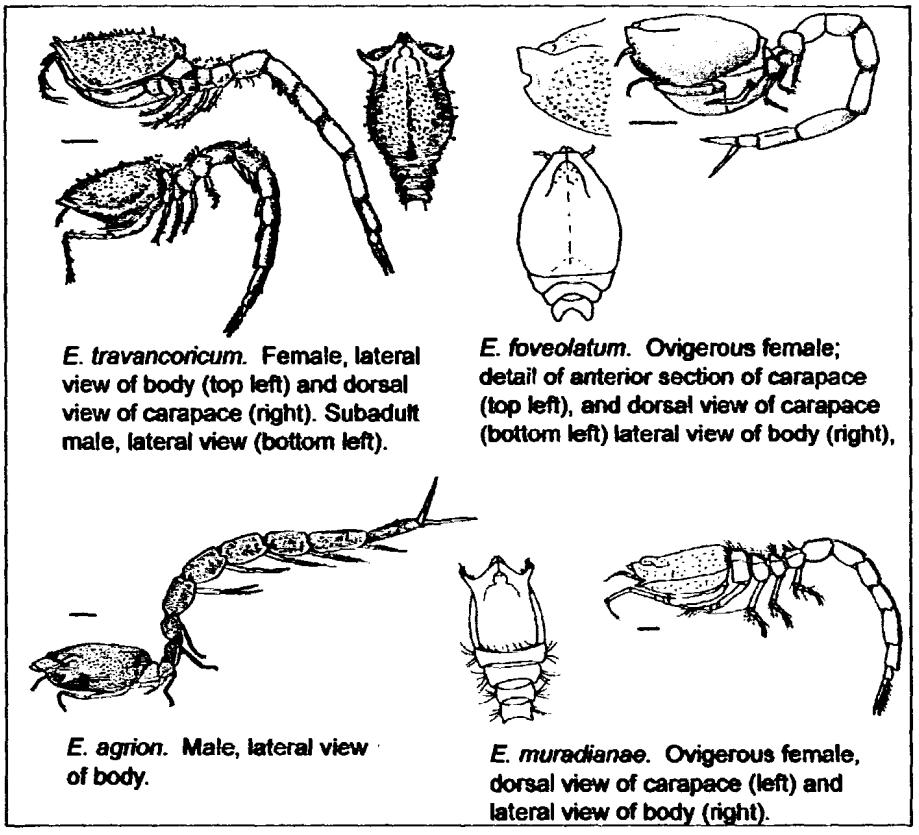


Figure 14. External morphology of *Eocuma* spp. Figure modified from Day (1978), Gamô (1967), Sars (1878), and Stebbing (1913). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace longer than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly or posteriorly, or not laterally compressed; oviform, or not oviform posteriorly and longer than wide. Carapace

with or without mid-dorsal ridge; with or without dorso-lateral ridges; with or without lateral ridges; with or without lateral horns. Pseudorostral lappets extend beyond frontal lobe; meet in midline, or extend towards midline but do not meet (or partially meet leaving a suture between them). Antennal notch not distinct, or as a depression, a subacute incision, or an acute incision. Anterolateral corner bluntly rounded, with subacute tooth, or with acute tooth. Frontal lobe from 1/5 or less to more than half of the carapace length; as wide as long, or wider than long, or longer than wide; anteriorly linguiform, or somewhat extended, or not extended; with or without ocular pigment; with or without eye lenses.

Antenna 1, basal article of the peduncle arcuate, or straight; as long as or shorter than the other two articles together. Main flagellum uni-, or bi-, or tri-articulated; with second and third article approximately same length; one, two, or three or more aesthetasc in distal-most article; with or without two aesthetascs on proximal article of main flagellum. Accessory flagellum reduced, or absent; uni-articulated; with or without brush of setae; with or without aesthetasc. Antenna 2 in males reaching half length or end of the pleon; with sensory setae on anterior margin of article four. Antenna 2 in females with one or two articles.

Maxilliped 3 basis geniculate, arcuate, or straight; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium longer, as long as or shorter than merus (without considering projections). Merus extended dorso-distally over carpus. Carpus distally widened, or not widened; equal to or shorter than propodus and dactylus together. Propodus oviform, distally widened, or not widened; with or without brush of setae.

Peraeon. First peraeonite well exposed, or visible only above lateral midline, or not visible. Peraeonite 2 narrow, wide, or proportional to other peraeonites; with or without ventrolateral expansion; ventrolateral expansion not overriding other somites, or overriding peraeonite 3, or overriding carapace and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended backwards overriding peraeonite 4. Peraeonite 4 without ventrolateral expansion, or peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Peraeopod 1, basis arcuate or straight; with or without row of setae; with dorso-distal projection on the basis totally or partially covering the ischium; with or without inner apical angle extended to form a sub-triangular tooth-like process or a convex process; with or without row of setae on the carpus; carpus shorter, equal or longer than basis; with or without a brush (3 or more) of long setae on the propodus (setae longer than carpus), or setae in a linear arrangement along propodus; basis longer than or equal to propodus; carpus longer or equal than propodus. Peraeopod 2, ischium absent; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Articular pegs present, or absent. Pleonite 6 longer than wide; longer than peduncle of uropod. Pleonite 6 not extended between the base of the uropods, or extended between the base of the uropods. Whole width of terminal end of pleonite 6 may be extended between uropods; ending in a point, a line, or a rounded apex. Alternatively, a narrow or wide portion of the terminal end of pleonite 6 may be projected; ending in a line, or a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or do not project.

Uropod endopod uni-articulated. Uropod exopod with proximal article shorter than distal one. Rami longer than peduncle; endopod and exopod approximately same length. Endopod with or without terminal setae. Exopod with or without terminal setae. Males with five pairs of pleopods. Pleopodal endopod with well developed or reduced process, or without process.

Species included.

1. *E. acuelatum* Day, 1978
2. *E. affinis* Calman, 1904 (Synonymy: *E. affine Stebbing, 1913*)
3. *E. agrion* Zimmer, 1914
4. *E. amakusense* Gamô, 1967
5. *E. cadenati* Fage, 1950
6. *E. calmani* Fage, 1928
7. *E. cochlear* Le Loeuff and Intès, 1972

8. *E. dimorphum* Fage, 1928 (Synonymy: *E. dimorpha* Fage, 1928; *E. dimorphum* Bâcescu, 1988)
9. *E. dollfusi* Calman, 1907
10. *E. elongatum* (Day, 1978) (Synonymy: *Mossambicuma elongatum* Day, 1978)
11. *E. ferox* (Fischer, 1872) (Synonymy: *Bodotria ferox* Fisher, 1872; *Cyclaspis cornigera* Sars, 1878; *Cyclapsoïdes ferox* Bonnier, 1896)
12. *E. foveolatum* Day, 1978
13. *E. gorgasiae* Mühlenhardt-Siegel, 1996
14. *E. hilgendorfi* Marcusen, 1894
15. *E. kempi* Kurian, 1954
16. *E. lanatum* Le Loeuff and Intès, 1972 (Synonymy: *E. lanata* Le Loeuff and Intès, 1972; *E. lanatum* Bâcescu, 1988)
17. *E. latum* Calman, 1907 (Synonymy: *E. lata* Calman, 1907)
18. *E. longicornis* Calman, 1907 (Synonymy: *E. longicorne* Stebbing, 1913; *E. producta* Stebbing, 1913)
19. *E. muradiannae* Petrescu, 1998
20. *E. sanguineum* Kurian and Radha Devi, 1983 (Synonymy: *E. sanguinea* Kurian and Radha Devi, 1983; *E. sanguineum* Bâcescu, 1988)
21. *E. sarsii* (Kossmann, 1880) (Synonymy: *Cyclaspis sarsii* Kossmann, 1880; *Cyclapsoides cornigera* Walker, 1901)
22. *E. spiniferum* Gamô, 1967 (Synonymy: *E. spinifera* Gamô, 1967; *E. spiniferum* Bâcescu, 1988)
23. *E. stellifera* Calman, 1907 (Synonymy: *E. stelliferum Stebbing*, 1913)
24. *E. striatum* Kurian and Radha Devi, 1990 (Synonymy: *E. striata* Kurian and Radha Devi, 1990; *E. striatum* Bâcescu, 1988)
25. *E. taprobanica* Calman, 1904 (Synonymy: *E. taprobanicum* Stebbing, 1913)
26. *E. travancoricum* Kurian, 1951

27. *E. winri* Day, 1978

28. *Eocuma* sp. Bâcescu, 1972 (Synonymy: *E.* affinis[a] *travancoricum* Bâcescu, 1972)

29. *Eocuma* sp. Day, 1978

Distribution. West Indian Ocean, Indo-West Pacific and West Pacific, South-West Australia, South-West Atlantic, Mediterranean Sea, Red Sea. They are most commonly found at less than 100m, although *Eocuma acuelatum* may be found up to 550m.

[a] Having affinity with taxon

***Iphinoe* Bate, 1856**

Synonymy. *Halia* Bate, 1856; *Venilia* Bate, 1856; *Iphinoë* Bate, 1856; *Cyrianassa* Bate, 1856; *Iphithoë* Norman, 1866; *Sphinoe* Koehler, 1885; *Epinoë* Caspers, 1957; *Ephinoë* Caspers, 1957.

Type species. *Iphinoe trispinosa* (Goodsir, 1843)

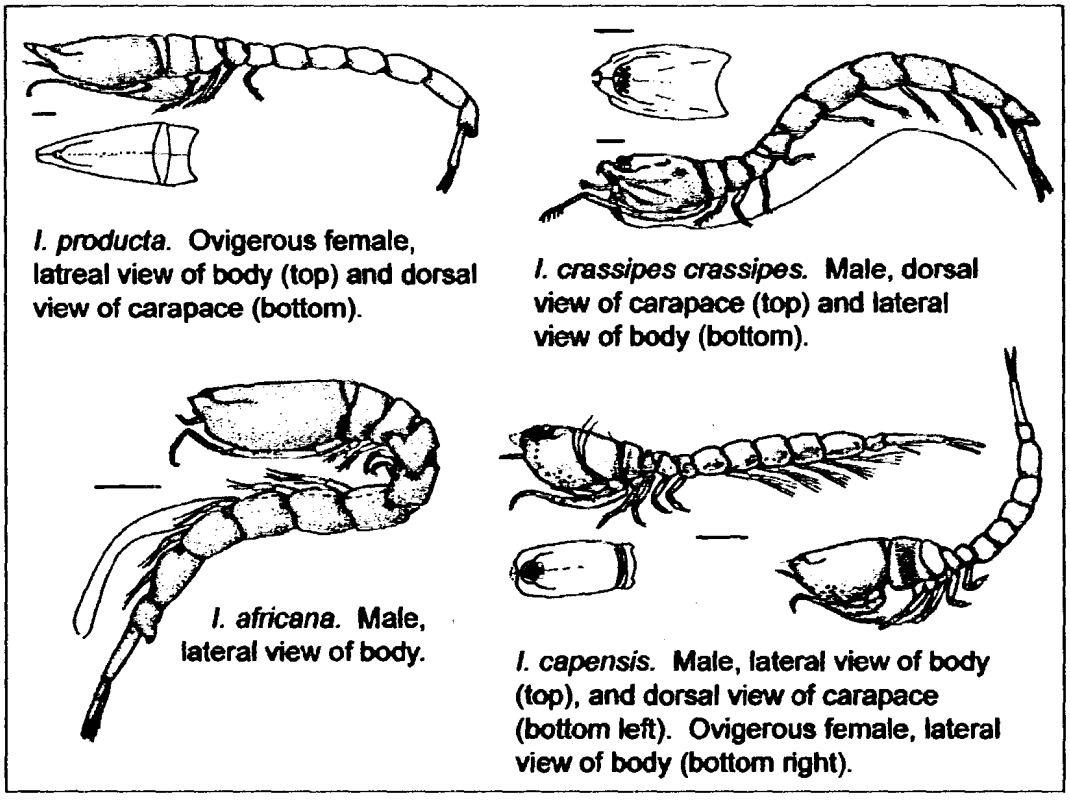


Figure 15. External morphology of *Iphinoe* spp. Figure modified from Day (1978). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long ascarapace and peraeon together; carapace and peraeon similar in length, or peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly or posteriorly, or not laterally compressed; longer than wide. Carapace with or without mid-dorsal ridge, or with mid-dorsal serration; with or without dorso-lateral ridges; with or without anterior transverse ridge; with or without posterior transverse ridge. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch as a depression, or as a subacute incision. Anterolateral corner bluntly rounded, as subacute tooth, or acute tooth. Frontal lobe from 1/4 to 1/2 of the total carapace length; as wide as long, or longer than wide; anteriorly linguiform, or somewhat extended, or not extended; with or without ocular pigment; with or without eye lenses.

Antenna 1, basal article of the peduncle arcuate, or straight; shorter than the other two articles together. Main flagellum uni-, bi-, or tri-articulated; with one, two, three or more aesthetasc in distal-most article; with or without two or a group of aesthetascs on proximal article of main flagellum. Accessory flagellum uni- or bi-articulated; with or without aesthetasc. Antenna 2 in males approximately reaching half length of pleon, or reaching the end of the pleon; with sensory setae on anterior margin of article four. Antenna 2 in females with one or two articles.

Maxilliped 3 basis geniculate, arcuate, or straight; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium longer, as long as or shorter than merus (without considering projections). Merus with dorso-distal projection over carpus. Carpus oviform or distally widened, or not widened; carpus equal to or shorter than propodus and dactylus together. Propodus oviform, distally widened, or not widened.

Peraeon. First peraeonite well exposed or visible only above lateral midline. Peraeonite 2 wide or proportional to other peraeonites; with or without ventrolateral expansion overriding peraeonite 1 and/or carapace, or overriding peraeonite 1 and/or carapace and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 without ventrolateral expansion, or peraeonite 4 with ventrolateral expansion overriding peraeonite 3, or

peraeonite 4 with ventrolateral expansion overriding peraeonite 5, or peraeonite 4 with ventrolateral expansion overriding peraeonite 3 and 5.

Peraeopod 1, basis arcuate, or straight, with or without row of setae; ischium elongate (often longer than merus) or not elongate; carpus shorter or equal length than basis; with or without setae in a linear arrangement along propodus; carpus longer or equal to propodus. Peraeopod 2, ischium absent; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Articular pegs present or absent. Pleonite 6 longer than wide, or as long as wide; as long as or shorter than peduncle of uropod; with or without two setae close to midline on posterior edge of pleonite 6. Pleonite 6 slightly extended, well extended, or not extended between the base of the uropods. Whole width of terminal end of pleonite 6 may be extended, ending in a point, a line, or a rounded apex. Alternatively, a wide portion of distal end of pleonite 6 extended; ending in a point, a line, or a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or anal plates not projected; with or without setae on posterior margin of anal plates.

Uropod endopod uni-, or bi-articulated; two articles approximately same length, or proximal article longer than distal one, or proximal article shorter than distal one. Uropod exopod with proximal article shorter than distal one, or with proximal and distal articles approximately same size. Peduncle approximately as long as or longer than rami, or peduncle slightly shorter than exopods of rami (equal length to endopod); endopod and exopod approximately same length, or endopod longer or shorter than exopod. Males with five pairs of pleopods. Pleopodal endopod with well developed or reduced process.

Species Included.

1. *I. acutirostris* Ledoyer, 1965
2. *I. adriatica* Bâcescu, 1988 (Synonymy: *Iphinoe* sp. Zimmer, 1942)
3. *I. africana* Zimmer, 1908 (Synonymy: *Iphinoë brevipes* (pro parte[b]) Stebbing, 1910)
4. *I. armata* Ledoyer, 1965
5. *I. brevipes* Hansen, 1895
6. *I. calmani* Fage, 1945
7. *I. capensis* (Zimmer, 1921) (Synonymy: *Bodotria capensis* Zimmer, 1921; *Iphinoe brevidactyla* Hale, 1953)
8. *I. crassipes* Hansen, 1895

- *I. crassipes crassipes* Hansen, 1895 (Synonymy: *Iphinoë crassipes* Hansen, 1895; *Iphinoë macrobranchium* Calman, 1904; *I. crassipes crassipes* Bâcescu, 1988)
- *I. crassipers haifae* Bâcescu, 1961

9. *I. dayi* Jones, 1960
10. *I. douniae* Ledoyer, 1965 (Synonymy: *I. trispinosa* var. Massé, 1962)
11. *I. elisae* Bâcescu, 1950 (Synonymy: *Iphinoe* sp. Bâcescu, 1949)
12. *I. fagei* Jones, 1955
13. *I. gurjanovae* Lomakina, 1960
14. *I. hupferi* Zimmer, 1916
15. *I. inermis* Sars, 1879 (Synonymy: *Iphinoë inermis* Sars, 1879; *I. inermis* Bâcescu, 1988)
16. *I. insolita* Petrescu, 1992
17. *I. ischnura* Zimmer, 1952 (Synonymy: ? *Iphinoë* sp. Calman, 1907; *Iphinoë ischnura* Zimmer, 1952; *I. ischnura* Bâcescu, 1988)
18. *I. maculata* Ledoyer, 1965

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[b] Pro parte is a designation used to indicate that only some of the specimens referred to by a specific name in a specific reference actually represent that taxon.

19. *I. maeotica* (Sowinsky, 1894) (Synonymy: *Iphinoë gracilis* var. *maeotica* Sowinsky, 1894; *Iphinoe* gracilis Zernov, 1901; *Iphinoe serrata maeotica* Derzhavin, 1925; *I. inermis* Bâcescu, 1949; *I. serrata* Markovski, 1953; *I. maeotica* Gurjanova, 1936)
20. *I. marisrubrae* Mühlenhardt-Siegel, 1996
21. *I. parva* Bâcescu and Muradian, 1973 (nomen nudum[c])
22. *I. pellucida* Hale, 1944
23. *I. pigmenta* Kurian, 1961
24. *I. plicata* Le Loeuff and Intés, 1972
25. *I. pokoui* Le Loeuff and Intés, 1972
26. *I. producta* Day, 1978
27. *I. rhodaniensis* Ledoyer, 1965
28. *I. robusta* Hansen, 1895
29. *I. sagamiensis* Gamô, 1958
30. *I. sanguinea* Kemp, 1916 (Synonymy: *Iphinoë sanguinea* Kemp, 1916; *I. sanguinea* Bâcescu, 1988)
31. *I. senegalensis* Jones, 1956
32. *I. serrata* Norman, 1867 (Synonymy: *Iphithoë serrata* Norman, 1867; *Iphinoë serrata* Norman, 1869; *Iphinoë gracilis serrata* Sars, 1878; *Sphinoe serrata* Koehler, 1886; Nec[d] *Iphinoe serrata* Motas and Bâcescu, 1938; *I. serrata* Bâcescu, 1988)
33. *I. stebbingi* Jones, 1956 (Synonymy: *Iphinoë brevipes* Stebbing, 1910)
34. *I. tenella* Sars, 1878 (Synonymy: *Iphinoë tenella* Sars, 1878; *Cyrianassa gracilis* Bate, 1856; *Iphinoë gracilis* Norman, 1869; *Iphithoë trispinosa* Fischer, 1873; *Ihpinoë gracilis* Sars, 1878)
35. *I. tenera* Lomakina, 1960
36. *I. trispinosa* (Goodsir, 1843).

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[c] Nomen nudum referes to a name that has become invalid because the original description using the name does not provide enough infomation to recognize the species.

[d] Nec is used to indicate that the species was wrongly called by a specific name in a particular citation

37. *I. truncata* Hale, 1953

38. *I. zimmeri* Stebbing, 1910

39. *Iphinoe* sp. Zimmer, 1920

40. *Iphinoe* sp. Kiseleva, 1964

41. *Iphinoe* sp. Mühlenhardt-Siegel, 1996

Distribution. Generally found at depths lower than 100 m, in the East Atlantic Ocean, West Pacific Ocean, and Mediterranean Sea. *Iphinoe producta* can be found at much deeper waters, between 200 to 800 m.

Remarks. *Iphinoe capense* and *I. pigmenta* lack the characteristic dorso-distal expansion of the merus of maxilliped 3, and are dubious members of the genus. Likewise, *Iphinoe crassipes* and *I. pokui* are dubious species; they share similar in the extensions of the pseudorostral lapplets beyond the frontal lobe that bear setae close to the midline. In addition, in these two species the artciles distal to the merus on maxilliped 3 are narrow.

***Stephanoma* Sars, 1871**

Type species. *Stephanoma goesii* (Sars, 1871)

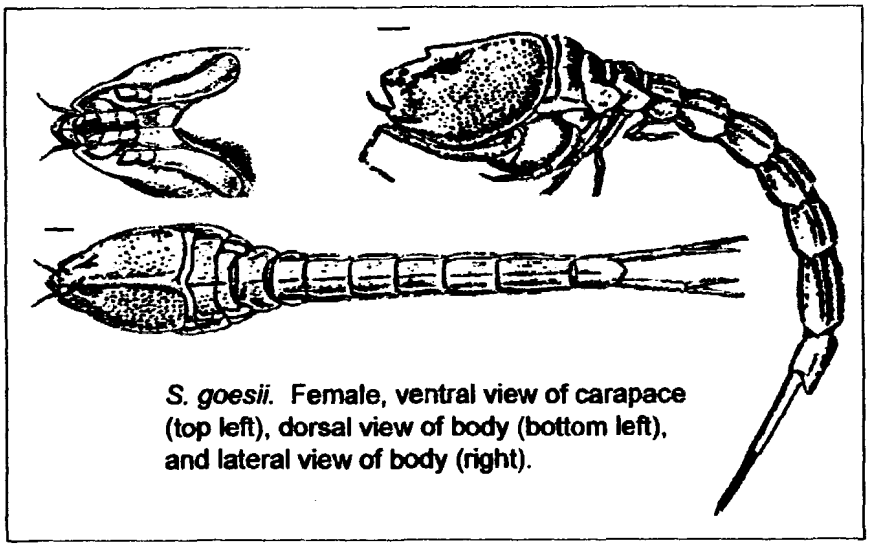


Figure 16. External morphology of *Stephanoma goesii*. Figure modified from Sars (1871). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length.

Head. From dorsal view the carapace appears laterally compressed anteriorly; longer than wide. Carapace with mid-dorsal ridge. Pseudorostral lappets do not extend beyond the frontal lobe. Antennal notch as a subacute incision. Anterolateral corner with subacute tooth. Frontal lobe 1/3 of total carapace length; as wide as long; anteriorly linguiform; without ocular pigment and with eye lenses.

Antenna 1, main flagellum tri-articulated; with second article longer than third; with 2 aesthetasc in distal-most article.

Maxilliped 3 with basis straight; not projected over ischium. Ischium as long as merus (without considering projections). Merus extended dorso-distally over carpus. Carpus oviform; equal to or shorter than propodus and dactylus together. Propodus proximally widened.

Peraeon. Peraeonite 2 with ventrolateral expansion overriding peraeonite 1 and/or carapace. Peraeonite 3 extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Peraeopod 1, basis arcuate; carpus shorter than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Articular pegs present. Pleonite 6 longer than wide; shorter than peduncle of uropod. Whole width of pleonite 6 well extended between the base of the uropods; ending in a point.

Uropod endopod uni-articulated. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods slightly longer than rami; endopod and exopod approximately same length. Endopod without terminal setae. Males with five pairs of pleopods.

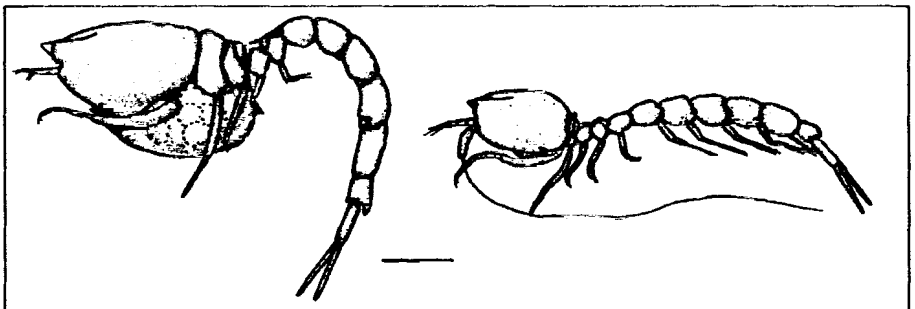
Species included.

S. goesii Sars, 1871 (*S. goesii* Bâcescu, 1988; Synonymy: *S. goēsii* Sars, 1871)

Distribution. West Indian Ocean.

***Upselaspis* Jones, 1955**

Type species. *Upselaspis caparti* (Fage, 1951)



U. caparti. Ovigerous female, lateral view of body (left). Male, lateral view of body (right).

Figure 17. External morphology of *Upselaspis caparti*. Figure modified from Day (1978). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as or longer than carapace and peraeon together; carapace as long as or longer than peraeon.

Head. From dorsal view the carapace appears not to be laterally compressed and is longer than wide. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch not distinct, or as a depression, or as a subacute incision. Anterolateral corner bluntly rounded, or with subacute tooth. Frontal lobe 1/4 to half of the total carapace length; as wide as long; somewhat extended; without ocular pigment or eye lenses.

Antenna 1, basal article of the peduncle arcuate; shorter than the other two articles together. Main flagellum bi-articulated; with 2 aesthetasc in distal-most article. Accessory flagellum uni-articulated; with brush of setae. Antenna 2 in males reaching the end of the pleon.

Maxilliped 3 basis geniculate or arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium as long as or shorter than merus (without

considering projections). Merus extended dorso-distally over carpus. Carpus equal to or shorter than propodus and dactylus together.

Peraeon. First peraeonite not visible. Peraeonite 2 with or without ventrolateral expansion; when present ventrolateral expansion overrides peraeonite 3. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Peraeopod 1, basis arcuate, with row of setae; carpus same size as propodus. Peraeopod 2, ischium absent; dactyl longer than propodus.

Pleon. Pleonite 6 as long as wide; shorter than peduncle of uropod. Wide portion of distal end of pleonite 6 well extended between the base of the uropods; ending somewhat concave. Anal plates do or do not extend posteriorly beyond distal margin of pleonite six.

Uropod endopod bi-articulated; two articles approximately same length. Uropod exopod with proximal article shorter than distal one. Peduncle slightly shorter than exopods of rami (equal length to endopod); endopod longer than exopod. Males with five pairs of pleopods.

Species Included.

1. *U. caparti* (Fage, 1951) (Synonymy: *Cyclapsoides caparti* Fage, 1951)

Distribution. Most frequently found in the coast of south-west Africa from 0 to 12 m, although it has been found at up to 78 m.

***Zygosiphon* Calman, 1907**

Type species. *Zygosiphon mortenseni* Calman, 1907

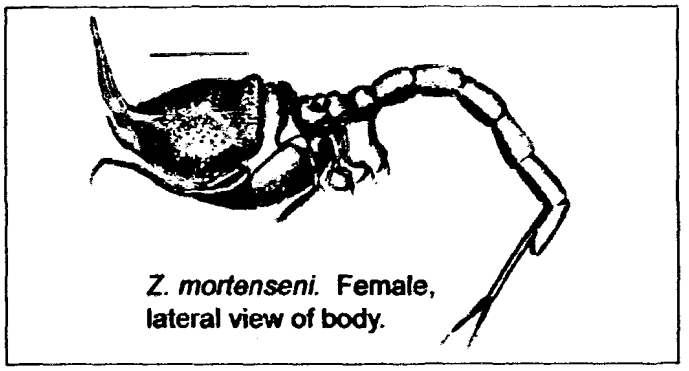


Figure 18. External morphology of *Zygosiphon mortenseni*. Figure modified from Calman (1907). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length.

Head. From dorsal view the carapace appears laterally compressed in the medial portion; longer than wide. Carapace with mid-dorsal ridge. Pseudorostral lappets extend beyond frontal lobe; the medial pair meet in midline, or partially meet leaving a suture between them. Antennal notch as a subacute or acute incision. Anterolateral corner with subacute or acute tooth. Branchial siphons long, extending much beyond pseudorostrum. Frontal lobe 1/4 to 1/3 of carapace length; wider than long; with anterior margin notched; with ocular pigment and with eye lenses.

Antenna 1, basal article of the peduncle straight; as long as the other two articles together. Main flagellum bi-articulated; with two aesthetasc in distal-most article. Accessory flagellum uni-articulated. Antenna 2 in males reaching the end of the pleon; with sensory setae on anterior margin of article four. Antenna 2 in females with one article.

Maxilliped 3 basis geniculate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium longer than merus (without considering projections). Merus extended dorso-distally over carpus. Carpus equal to or shorter than propodus and dactylus together.

Peraeon. Peraeonite 2 with ventrolateral expansion, or without ventrolateral expansion; when present the expansion does not override other somites. Peraeonite 3 extended backwards overriding peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Peraeopod 1, basis arcuate, with inner apical angle extended to form a convex process; carpus shorter than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Articular pegs present, or absent. Pleonite 5 as long or longer than pleonite 6. Pleonite 6 longer than wide; shorter than peduncle of uropod. Wide portion of distal end of pleonite 6 well extended between the base of the uropods; with rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal article. Peduncle of uropods longer than rami; exopod longer than endopod. Males with five pairs of pleopods.

Species included.

1. *Z. mortenseni* Calman, 1907 (Synonymy: Bodotriidae n.g., and sp. Calman, 1904)

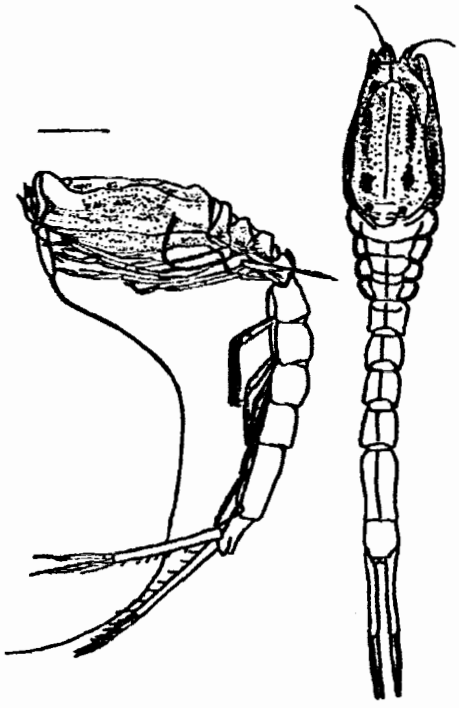
Distribution. Indo-West Pacific from 7 to 22 m.

Subfamily Vaunthompsoniinae Sars, 1878

Type genus. *Vaunthompsonia* Bate, 1858

***Apocuma* Jones, 1973**

Type Species. *Apocuma brasiliense* Jones, 1973



A. brasiliensis. Male, lateral (left) and dorsal (right) view of body.

Figure 19. External morphology of *Apocuma brasiliense*. Figure modified from Jones (1973). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as carapace and peraeon together; carapace longer than peraeon.

Head. From dorsal view the carapace appears not to be laterally compressed and longer than wide. Carapace with mid-dorsal ridge, dorso-lateral ridges, lateral ridges, and posterior transverse ridge. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch as a depression. Anterolateral corner bluntly rounded. Branchial siphons long, extending much beyond pseudorostrum, or short, extending just beyond carapace. Frontal lobe 1/4 of carapace length; as wide as long; somewhat extended; without ocular pigment and without eye lenses.

Antenna 1, basal article of the peduncle arcuate; longer than the other two articles together. Main flagellum bi-articulated; with 2 aesthetasc in distal-most article. Accessory flagellum uni-articulated. Antenna 2 in males reaching the end of the pleon. Antenna 2 in females with three articles.

Maxilliped 3 basis arcuate; not projected over ischium. Ischium shorter than merus. Merus slightly expanded laterally. Carpus longer than propodus and dactylus together.

Peraeon. Peraeonite 2 with ventrolateral expansion; overriding peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended backwards overlapping peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5, or peraeonite 3 and 5.

Females with exopods fully developed on peraeopods 1 and 2, and reduced exopod on peraeopod 3. Males with exopods fully developed on peraeopods 1 to 4. Peraeopod 1, basis arcuate; carpus longer than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 as long as wide; shorter than peduncle of uropod. Wide portion of distal end of pleonite 6 slightly extended between the base of the uropods; ending in a line. Anal plates extend posteriorly beyond distal margin of pleonite six.

Uropod endopod uni-articulated. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods longer than rami; endopod and exopod approximately same length. Males with five pairs of pleopods.

Species included.

1. *A. brasiliense* Jones, 1973 (Synonymy: *A. brasilensis* Jones, 1973; *Apocuma brasiliense* Bâcescu, 1988)

Distribution. South Atlantic Ocean in the coast of Brazil from 587 to 805 m.

***Bathycuma* Hansen, 1895**

Type species. *Bathycuma elongatum* Hansen, 1895

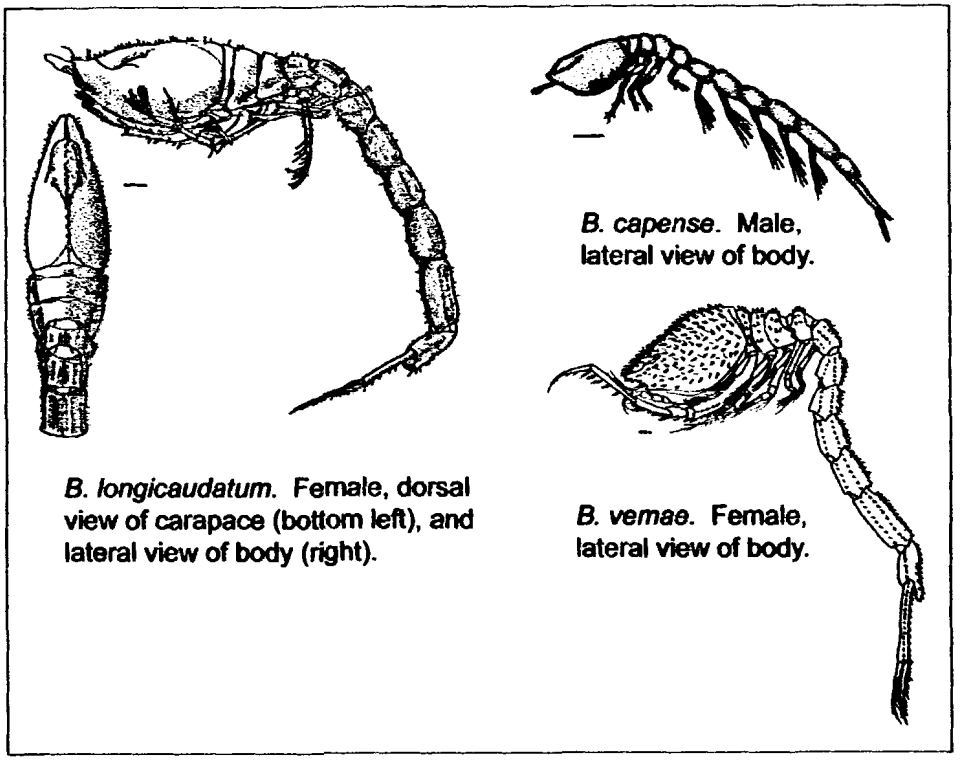


Figure 20. External morphology of *Bathycuma* spp. Figure modified from Calman (1905), Day (1975), and Petrescu (1995). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as carapace and peraeon together, or abdomen longer than carapace and peraeon together; carapace longer or same size as peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly; longer than wide. Carapace with or without mid-dorsal ridge, or with mid-dorsal serration; with or without posterior transverse ridge. Pseudorostral lappets extend beyond frontal lobe and meet in midline or extend towards midline but do not meet. Antennal notch as a depression, or as a subacute

incision. Anterolateral corner with subacute or acute tooth. Branchial siphons extend just beyond pseudorostrum, or long, extending much beyond pseudorostrum. Frontal lobe 1/3 to half of the total carapace length; longer than wide; anteriorly linguiform, somewhat extended, or not extended; without ocular pigment or eye lenses.

Antenna 1, basal article of the peduncle geniculate, arcuate, or straight; as long as or shorter than the other two articles together. Main flagellum uni-, bi-, or tri-articulated; with second and third article approximately same length, or with second article longer than third; with or without two aesthetasc in distal-most article. Accessory flagellum uni-, or bi-articulated; with or without brush of setae on accessory flagellum. Antenna 2 in males approximately reaching half length of pleon. Antenna 2 in females with three articles.

Maxilliped 3 basis arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium longer or as long as merus (without considering projections). Merus slightly expanded laterally. Carpus distally widened, or not widened; carpus equal to or shorter than propodus and dactylus together. Propodus distally widened, or not widened.

Peraeon. First peraeonite well exposed, or visible only above lateral midline. Peraeonite 2 with ventrolateral expansion, or without ventrolateral expansion; expansion not overriding other somites, or overriding peraeonite 1 and/or carapace, or overriding peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended forward overriding peraeonite 2, or extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 without ventrolateral expansion, or with ventrolateral expansion overriding peraeonite 5, or with ventrolateral expansion overriding peraeonite 3 and 5.

Females and males with exopods fully developed on peraeopods 1 to 3. Only males have exopods fully developed on peraeopod 4. Peraeopod 1, basis arcuate; with or without row of setae; with or without row of setae on the carpus; with or without setae in a linear arrangement

along propodus; carpus equal to or shorter than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; longer than peduncle of uropod, or as long as or shorter than peduncle of uropod; with or without many small setae on posterior edge of pleonite 6. Wide portion of the distal end of pleonite 6 strongly or slightly extended past the insertion of the uropods; ending in a point, or a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or do not project; setae on posterior margin of anal plates, or without setae.

Uropod endopod bi-articulated; two articles approximately same length, or proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods slightly longer or as long as rami; endopod and exopod approximately same length, or exopod longer than endopod. Males with five pairs of pleopods.

Species Included.

1. *B. brevirostris* (Norman, 1879) (Synonymy: *Leucon brevirostris* Norman, 1879; *Vaunthompsonia caeca* Bonnier, 1896; *B. brevirostre* Stebbing, 1913)
2. *B. capense* (Zimmer, 1921) (Synonymy: *Vaunthompsonia capensis* Zimmer, 1921)
3. *B. datum* Day, 1975
4. *B. declinatum* Gamô, 1989
5. *B. elongatum* Hansen, 1895 (Synonymy: *B. elongata* Hansen, 1895; *B. elongatus* Stebbing, 1912; *B. elongatum* Stebbing, 1913)
6. *B. granulatum* Gamô, 1990
7. *B. longicaudatum* Calman, 1912 (Synonymy: *B. longicaudata* Calman, 1912 *B.longicaudatus* Stebbing, 1912; *B. longicaudatum* Stebbing, 1913)
8. *B. longirostris* Calman, 1905 (Synonymy: *B. longirostre* Stebbing, 1913)
9. *B. magnum* Jones, 1969 (Synonymy: *B. magna* Jones, 1969; *B. magnum* Bâcescu, 1988)

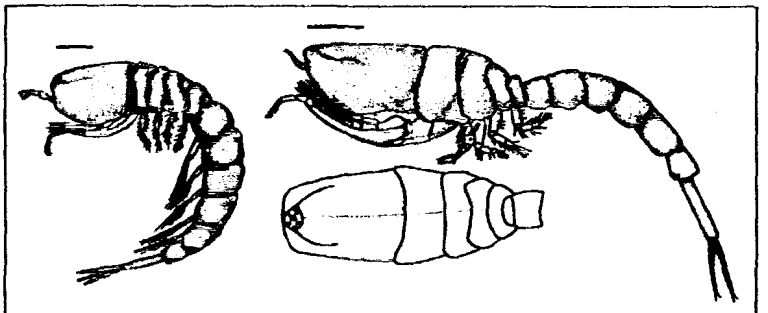
10. *B. natalensis* Stebbing, 1912 (Synonymy: *B. natalense* Stebbing, 1913)
11. *B. okinawaense* Gamô, 1989
12. *B. rotunditectorum* Gamô, 1990
13. *B. vemae* Petrescu, 1995
14. *Bathycuma* sp. Wolff, 1970

Distribution. Deep waters (up to 5,000 m) of the North Atlantic, Indian Ocean, Pacific Ocean, Mediterranean Sea, and off the coasts of South Africa.

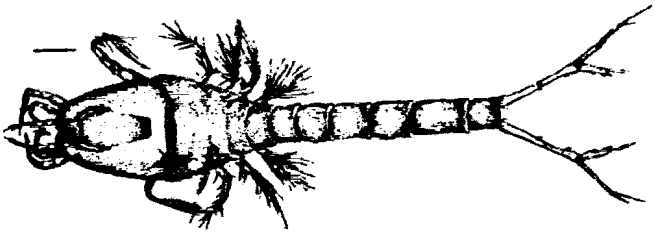
***Cumopsis* Sars, 1878**

Synonymy. *Heterocuma* Miers, 1879

Type species. *Cumopsis goodsir* Van Beneden, 1861b



C. robusta. Male, lateral view of body (left). Ovigerous female, lateral view of body (top right) and dorsal view of cephalothorax (bottom rigth).



C. fagei. Female, dorsal view of body.

Figure 21. External morphology of *Cumopsis* spp. Figure modified from Bâcescu (1956), and Day (1975). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as or longer than carapace and peraeon together; carapace and peraeon similar in length, or peraeon longer or shorter than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly, or not compressed. With or without medial dorsal ridge. With or without dorso-lateral ridges.

Pseudorostral lappets extend beyond frontal lobe and meet in midline, or extend towards midline but do not meet (or partially meet leaving a suture between them), or do not extend beyond the frontal lobe. Antennal notch not distinct, as a depression, subacute incision, or acute incision. Anterolateral corner bluntly rounded, or with subacute tooth. Frontal lobe from 1/3 to half of the total carapace length; as wide as long or longer than wide; anteriorly linguiform, somewhat extended, or not extended; with ocular pigment and with eye lenses.

Antenna 1, basal article of the peduncle straight; as long as or shorter than the other two articles together; males with or without a group of aesthetasc on distal margin of peduncle. Main flagellum uni- or bi-articulated; with two aesthetasc in distal-most article; with or without two or a group of aesthetascs on proximal article of main flagellum. Accessory flagellum uni-articulated; with or without brush of setae. Antenna 2 in males reaching the end of the pleon.

Maxilliped 3 basis geniculate, arcuate, or straight; extended dorso-distally over ischium beyond the articulation of the ischium and merus, or slightly expanded laterally, or not projected over ischium. Ischium longer, as long as or shorter than merus (without considering projections). Merus without dorsal projection, or merus extended dorso-distally over carpus, or slightly expanded laterally. Carpus may be distally widened, equal to or shorter than propodus and dactylus together. Propodus may be oviform, with or without a brush of setae.

Peraeon. First peraeonite well exposed, or visible only above lateral midline, or not visible. Peraeonite 2 with or without ventrolateral expansion overriding peraeonite 1 and/or carapace, or overriding peraeonite 3, or peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended forward overriding peraeonite 2, or overriding peraeonite 4, or overriding peraeonites 2 and 4. Peraeonite 4 without ventrolateral expansion, or with ventrolateral expansion overriding peraeonite 5, or with ventrolateral expansion overriding peraeonite 3 and 5.

Females and males with exopod fully developed on peraeopod 1 and reduced on peraeopods 2 and 3. Peraeopod 1, basis arcuate or straight; slightly projected ventrally, or without projection;

carpus may be oviform; with or without a brush (3 or more) of long setae on the propodus (setae longer than carpus) or setae in a linear arrangement along propodus; carpus longer, equal to, or shorter than propodus. Peraeopod 2, ischium absent; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide, as long as wide, or wider than long; shorter than peduncle of uropod. Pleonite 6 not extended past the insertion of the uropods, or narrow portion of distal end of pleonite 6 slightly extended past the insertion of the uropods; ending somewhat concave, or with rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or anal plates do not project.

Uropod endopod bi-articulated; two articles approximately same length or proximal article longer than distal one. Uropod exopod with proximal article same, shorter or longer than distal one. Peduncle of uropods longer, as long as or slightly shorter than rami; endopod and exopod approximately same length, or exopod longer than endopod. Males with five pairs of pleopods. Pleopodal endopod with well developed or reduced process.

Species included.

1. *C. africana* Zimmer, 1920 (Synonymy: *Heterocuma africana* Zimmer, 1920)
   - *C. africana africana* (Zimmer, 1920) (Synonymy: *Heterocuma africana* Zimmer, 1920; *H. africanum africanum* Day, 1975; *Heterocuma africana africana* Bâcescu, 1988)
   - *C. africana intermedia* (Fage, 1924) (Synonymy: *Heterocuma intermedia* Fage, 1924; *H. africana* Jones, 1965; *H. africanum intermedium* Day, 1975; *H. africana intermedia* Bâcescu, 1988)
2. *C. andamani* (Kurian, 1954) (Synonymy: *Heterocuma andamani* Kurian, 1954)
3. *C. armatum* (Kurian, 1954) (Synonymy: *Heterocuma armata* Kurian, 1954; *H. armatum* Bâcescu, 1988)
4. *C. elongata* Jones, 1956
5. *C. fagei* Bâcescu, 1956

6. *C. goodsir* (Van Beneden, 1861b) (Synonymy: *Cuma edwardsii* Bate, 1856 Nec *Cuma edwardsii* Goodsir, 1843; *Bodotria goodsir* Van Beneden, 1861b; *Bodotria goodsirii* Van Beneden, 1861b; *Cuma goodsiri* Dohm, 1869; *Cumopsis goodsiri* Sars, 1878; *Cumopsis longipes* Bâcescu, 1949; *Cumopsis goodsiri* form *longipes* Bâcescu, 1951)
7. *C. jonesi* Le Loeuff and Intés, 1972
8. *C. longipes* (Dohm, 1869) (Synonymy: *Cuma (Bodotria) longipes* Dohm, 1869; *Cumopsis laevis* Sars, 1879; Nec *Cumopsis longipes* Bâcescu, 1949; Nec *Cumopsis goodsir* form *longipes* Bâcescu, 1951)
9. *C. robusta* Day, 1975
10. *C. sarsi* Miers, 1879 (Synonymy: *Heterocuma sarsi granulata* Miers, 1879; *H. granulatum* Stebbing, 1913; *H. sarsi costata* Lomakina, 1960; *H. sarsi* Bâcescu, 1988)
11. *C. wafri* Jones, 1956
12. *Cumopsis* sp. Toulmond and Truchot, 1964

Distribution. Generally found at shallow waters between 0 and 50 m (up to 100 m) of the East Atlantic Ocean, West Pacific Ocean, and Mediterranean Sea. Only *Cumopsis sarsi* from the West Pacific Ocean is found at greater depths (up to 200 m).

***Gaussicuma* Zimmer, 1907**

Type species. *Gaussicuma vanhoeffeni* Zimmer, 1907

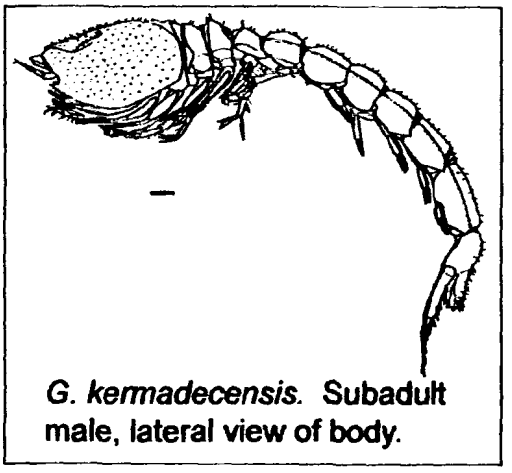


Figure 22. External morphology of *Gaussicuma kermadecensis*. Figure modified from Jones (1969). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length, or carapace longer than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly, or not laterally compressed; longer than wide. Carapace with mid-dorsal ridge, or mid-dorsal serration; with or without dorso-lateral ridges. Pseudorostral lappets extend beyond frontal lobe and meet in midline or are widely separated. Antennal notch as a depression, or as a subacute incision. Anterolateral with subacute or acute tooth. Frontal lobe from 1/3 to half the total carapace length; as wide as long; anteriorly linguiform, or somewhat extended; without ocular pigment or eye lenses.

Antenna 1, basal article of the peduncle arcuate, or straight; longer, same length, or shorter than the other two articles together. Main flagellum bi-articulated; with one or two aesthetasc in distal-most article. Accessory flagellum uni-, or bi-articulated. Antenna 2 in females with two articles.

Maxilliped 3 basis arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus, or not projected over ischium. Ischium as long as or shorter than merus (without considering projections). Merus without dorsal projection, or extended dorso-distally over carpus, or slightly expanded laterally. Carpus oviform or not widened; equal to or shorter than propodus and dactylus together. Propodus distally widened or not.

Peraeon. Peraeonite 2 with or without ventrolateral expansion; not overriding other somites, or overriding carapace and/or peraeonite 3, or overriding only peraeonite1 and/ or carapace, or overriding only peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 without ventrolateral expansion, or with ventrolateral expansion overriding peraeonite 5, or with ventrolateral expansion overriding peraeonite 3 and 5.

Peraeopod 1, females and males with exopod fully developed. Basis arcuate, or straight; with or without row of setae. Carpus equal to propodus. Peraeopod 2, females and males with exopod fully developed; ischium present; dactyl longer than propodus. Peraeopod 3, females and males with exopod fully developed. Peraeopod 4, females with no exopod; and males with exopod fully developed; ischium present.

Pleon. Pleonite 5 longer, or as long as or shorter than pleonite 6. Pleonite 6 longer than wide; longer than peduncle of uropod; with or without many small setae on posterior edge of pleonite 6. Wide portion of posterior end of pleonite 6 strongly extended past the insertion of the uropods; ending in a point, or a rounded apex.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods longer, same length, or shorter than rami; endopod and exopod approximately same length, or endopod longer. Males with five pairs of pleopods. Pleopodal endopod with well developed process.

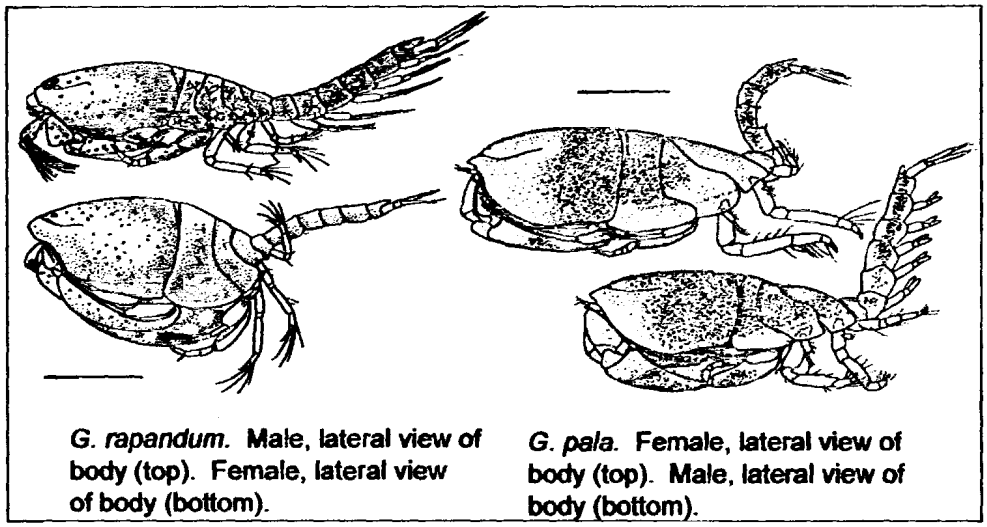
Species Included.

1. *G. dufresnae* Watling and Gerken, 1999
2. *G. gloriosae* Ledoyer, 1988
3. *G. gurjanovae* Lomakina, 1952
4. *G. kermadecense* Jones, 1969 (Synonymy: *G. kermadecensis* Jones, 1969; *G. kermadecense* Bâcescu, 1988)
5. *G. scabrum* Jones, 1969 (Synonymy: *G. scabra* Jones, 1969; *G. scabrum* Bâcescu, 1988)
6. *G. vanhoeffeni* Zimmer, 1907 (Synonymy: *G. vanhöffeni* Zimmer, 1907; G. *vanhoeffeni* Bâcescu, 1988)

Distribution. Most frequently found in the Southern Ocean at depths ranging from 3,400 to 4,600 m. Also found in the Indian and South Pacific Oceans. *Gaussicuma gurjanovae* is found in relatively shallower waters (from 42 to 105 m) in the North-West Pacific Ocean.

***Gephyrocuma* Hale, 1936**

Type species. *Gephyrocuma pala* Hale, 1936



G. rapandum. Male, lateral view of body (top). Female, lateral view of body (bottom).

G. pala. Female, lateral view of body (top). Male, lateral view of body (bottom).

Figure 23. External morphology of *Gephyrocuma* spp. Figure modified from Hale (1936), and Tafe and Greenwood (1996). Scale bars represent 0.5 mm.

General Body. Carapace approximately same length, shorter or longer than abdomen; abdomen shorter than carapace and peraeon together; carapace longer than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly; longer than wide. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch not distinct, or as a depression. Anterolateral corner bluntly rounded. Frontal lobe 1/3 to 1/2 the total carapace length; as wide as long; somewhat extended; with ocular pigment and with eye lenses.

Antenna 1, peduncle articles wide, basal article of the peduncle straight or arcuate; longer than the other two articles together. Main flagellum bi-, or tri-articulated; with second article longer than third; with three aesthetasc in distal-most article. Accessory flagellum uni-articulated; with or without brush of setae.

Maxilliped 3 basis straight; projected ventrally over ischium (opercular). Ischium shorter than merus (without considering projections). Merus slightly expanded laterally. Carpus oviform; equal to or shorter than propodus and dactylus together. Propodus distally widened, or oviform; with a brush of setae.

Peraeon. First peraeonite visible only above lateral midline. Peraeonite 2 with ventrolateral expansion; overriding peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 extended backwards overriding peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Females and males with exopods fully developed on peraeopods 1 and 2 and reduced on peraeopods 3 and 4. Peraeopod 1, opercular; basis arcuate, with ventral opercular projection; basis and carpus expanded, ischium and merus rotated to parallel positions; ischium modified as a rounded lobe with exterior concavity (opercular); carpus oviform in shape, with row of setae; brush (3 or more) of long setae on the propodus (setae longer than carpus); carpus equal to or shorter than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 3, merus enlarged (almost as large as basis). Peraeopod 4, ischium present.

Pleon. Pleonite 5 longer than pleonite 6, or as long as or shorter than pleonite 6. Pleonite 6 longer than wide; longer than peduncle of uropod. Whole width of pleonite 6 well extended past the insertion of the uropods ending in a rounded apex; or only narrow portion of distal end of pleonite 6 extended past the insertion of the uropods also ending in a rounded apex.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Rami longer than peduncle; endopod and exopod approximately same length. Males with five pairs of pleopods.

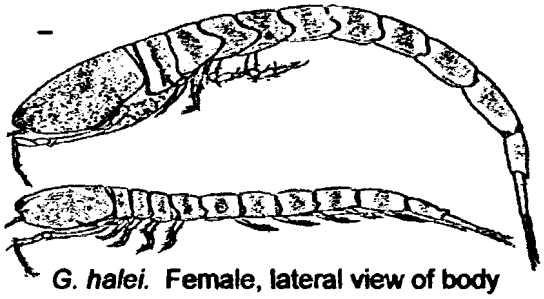
Species included.

1. *G. pala* Hale, 1936
2. *G. repandum* Hale, 1944 (Synonymy: *G. repanda* Hale, 1944; *G. repandum* Bâcescu, 1988)
3. *G. simile* Hale, 1949 (Synonymy: *G. similis* Hale, 1949; *G. simile* Bâcescu, 1988)
4. *Gephyrocuma* sp. nov.1 Tafe and Greenwood, 1996

Distribution. Shallow waters (0-75 m) of Australian coast.

***Gigacuma* Kurian, 1951**

Type species. *Gigacuma halei* Kurian, 1951



G. halei. Female, lateral view of body (top). Male, lateral view of body (bottom).

G. halei. Female, dorsal view of anterior portion of carapace (left). Male, dorsal view of anterior portion of carapace (right).

Figure 24. External morphology of *Gigacuma halei.* Figure modified from Kurian (1951). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly, or not compressed; longer than wide. Pseudorostral lappets extend beyond frontal lobe extended towards midline but do not meet (or partially meet leaving a suture between them), or do not extend beyond the frontal lobe. Antennal notch as a depression, or as a subacute incision. Anterolateral corner bluntly rounded, or with subacute tooth. Frontal lobe 1/5 or less of the carapace length; as wide as long; anteriorly linguiform; with ocular pigment and eye lenses.

Antenna 1, basal article of the peduncle straight; same length or shorter than the other two articles together. Main flagellum bi-articulated; with or without two aesthetasc in distal-most article; with or without a group of aesthetascs on proximal article of main flagellum. Accessory flagellum bi-articulated; with brush of setae. Antenna 2 in males reaching the end of the pleon; with sensory setae on anterior margin of article four. Antenna 2 in females with three articles.

Maxilliped 3 basis straight or arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium shorter or same size as merus (without considering projections). Merus expanded laterally. Carpus oviform; equal to or shorter than propodus and dactylus together. Propodus distally widened; with a brush of setae.

Peraeon. First peraeonite visible only above lateral midline. Peraeonite 2 with or without ventrolateral expansion not overriding other somites, or overriding peraeonite 1 and/or carapace. Peraeonite 3 extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Females and males with exopods fully developed on peraeopods 1 and 2. Peraeopod 1, basis arcuate, with row of setae, slightly projected ventrally; brush (3 or more) of long setae on the propodus (setae longer than carpus); carpus shorter than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; longer or as long as peduncle of uropod. Wide portion of distal end of pleonite 6 slightly extended past the insertion of the uropods; ending in a rounded apex.

Uropod endopod bi-articulated; proximal article shorter than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods slightly longer than rami; endopod and exopod approximately same length. Males with five pairs of pleopods. Pleopodal endopod without process.

Species included.

1. *G. halei* Kurian, 1951

Distribution. Indo-West Pacific, from 7 to 27 m.

***Glyphocuma* Hale, 1944**

Type species. *Glyphocuma bakeri* Hale, 1936

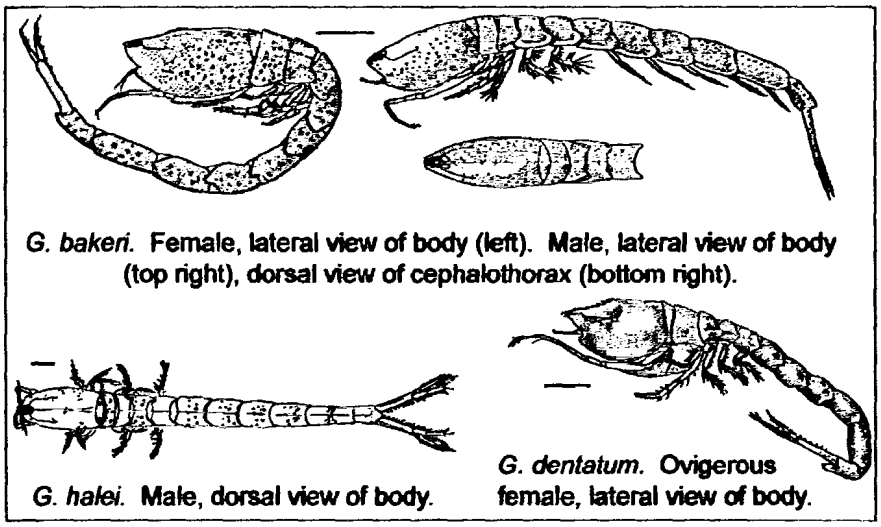


Figure 25. External morphology of *Glyphocuma* spp. Figure modified from Greenwood and Johnson (1967), Hale (1936), and Tafe and Greenwood (1996). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length, or carapace longer than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly; longer than wide. Carapace with mid-dorsal ridge, or with mid-dorsal serration; with or without dorso-lateral ridges. Pseudorostral lappets do not extend beyond the frontal lobe. Antennal notch as a depression, or as a subacute incision. Anterolateral corner bluntly rounded, or with subacute tooth. Frontal lobe from 1/3 to half of the total carapace length; longer than wide; anteriorly linguiform; with ocular pigment and eye lenses.

Antenna 1, basal article of the peduncle geniculate, or arcuate; shorter than the other two articles together. Main flagellum bi-, or tri-articulated; with second article longer than third; with or

without two or three aesthetasc in distal-most article; with or without a group of aesthetascs on proximal article of main flagellum. Accessory flagellum bi-articulated; with or without brush of setae. Antenna 2 in females with three articles.

Maxilliped 3 basis arcuate, or straight; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium longer or as long as merus (without considering projections). Carpus equal to or shorter than propodus and dactylus together. Propodus oviform, or not widened; with a brush of setae.

Peraeon. First peraeonite well exposed, or visible only above lateral midline. Peraeonite 2 wide or proportional to other peraeonites; with ventrolateral expansion; overriding peraeonite 1 and/or carapace, or overriding peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 extended forward overriding peraeonite 2, or extended backwards overriding peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5, or peraeonite 4 with ventrolateral expansion overriding peraeonite 3 and 5.

Females and males with exopods fully developed on peraeopods 1 to 3. Males also have a fully developed or reduced exopod on peraopod 4. Peraeopod 1, basis arcuate, with row of setae; with or without a brush (3 or more) of long setae on the propodus (setae longer than carpus) or setae in a linear arrangement along propodus; carpus equal to or shorter than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; shorter than peduncle of uropod. Whole width of terminal end of pleonite 6 well extended past the insertion of the uropods; ending concave (with two projections), or ending in a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or not project.

Uropod endopod bi-articulated; two articles approximately same length, or proximal article longer or shorter than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods longer or same size as rami; endopod and exopod approximately same length, or exopod longer than endopod. Males with five pairs of pleopods.

Species Included.

1. *G. bakeri* (Hale, 1936) (Synonymy: *Sympodomma bakeri* Hale, 1936)
2. *G. dentatum* Hale, 1944 (Synonymy: *G. dentata* Hale, 1944; *G. dentatum* Bâcescu, 1988)
3. *G. halei* Greenwood and Johnson, 1967
4. *G. inequale* Hale, 1944 (Synonymy: *G. inequalis* Hale, 1944; *G. inequale* Bâcescu, 1988)
5. *G. serventyi* Hale, 1944
6. *Glyphocuma* sp. Stephenson et al., 1978

Distribution. From 0 to 100 m in the Southern Australian coasts.

***Hypocuma* Jones, 1973**

Type species. *Hypocuma serratifrons* Jones, 1973

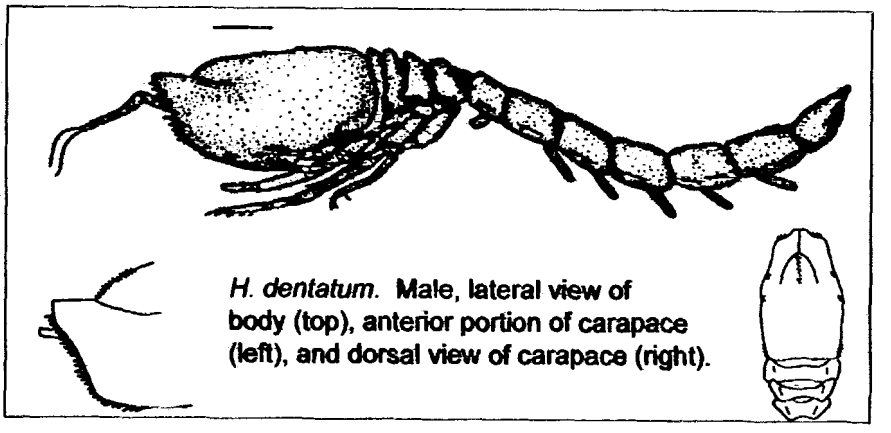


Figure 26. External morphology of *Hypocuma dentatum*. Figure modified from Day (1975). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace longer than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly; longer than wide. Carapace with mid-dorsal ridge, or with mid-dorsal serration. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch not distinct. Anterolateral corner bluntly rounded. Frontal lobe from 1/4 of carapace length; as wide as long, or wider than long; not extended; without ocular pigment or eye lenses.

Antenna 1, basal article of the peduncle arcuate, or straight; longer than the other two articles together, or as long as the other two articles together. Main flagellum uni-, or bi-, or tri-articulated; with second article longer than third; with two aesthetasc in distal-most article. Accessory flagellum uni-, or bi-articulated. Antenna 2 in males with sensory setae on anterior margin of article four. Antenna 2 in females with five articles.

Maxilliped 3 basis geniculate or arcuate; not projected over ischium. Ischium shorter than merus (without considering projections). Merus extended dorso-distally over carpus. Carpus oviform or not; equal to or shorter than propodus and dactylus together. Propodus oviform or not widened.

Peraeon. First peraeonite well exposed. Peraeonite 2 narrow or proportional to other peraeonites; with ventrolateral expansion overriding peraeonite 1 and/or carapace, or overriding peraeonite 3. Peraeonite 3 extended forward overriding peraeonite 2, or extended backwards overriding peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 3, or with ventrolateral expansion overriding peraeonite 5, or with ventrolateral expansion overriding peraeonite 3 and 5.

Females and males with exopods fully developed on peraeopods 1 to 3. Females with reduced exopods on peraeopod 4, while males have them fully developed. Peraeopod 1, basis arcuate; carpus same size as propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; shorter than peduncle of uropod. Wide portion of distal end of pleonite 6 strongly extended past the insertion of the uropods; ending in a rounded apex.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods slightly longer than rami; exopod longer than endopod. Exopod without terminal setae. Males with five pairs of pleopods. Pleopodal endopod with well developed process.

Species Included.

1. *H. dentatum* Day, 1975
2. *H. serratifrons* Jones, 1973

Distribution. *Heterocuma dentatum* is found in off the southern point of South Africa at 400 m, while *Heterocuma serratifrons* is found in the North Atlantic at depths between 1,000 and 5,000 m.

***Leptocuma* Sars, 1873**

Type species. *Leptocuma kimbergii* Sars, 1873

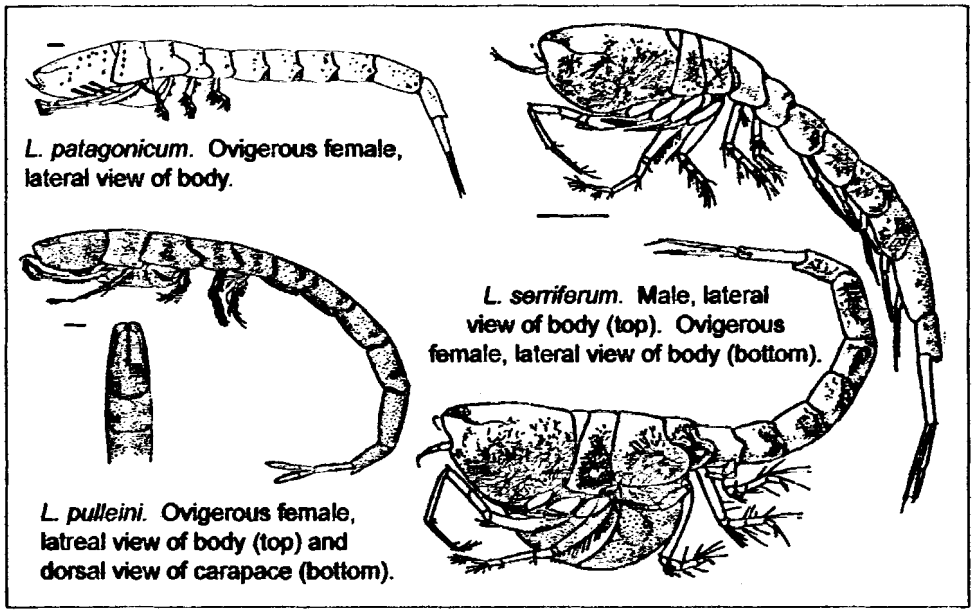


Figure 27. External morphology of *Leptocuma* spp. Figure modified from Hale (1928, 1944) and Roccatagliata (1993). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length, or peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly, or not laterally compressed; longer than wide. Carapace with or without mid-dorsal ridge. Pseudorostral lappets extend beyond frontal lobe extend towards midline but do not meet (or partially meet leaving a suture between them), or widely separated, or do not extend beyond the frontal lobe. Antennal notch as a depression, or as a subacute incision. Anterolateral corner bluntly rounded, or with subacute tooth. Frontal lobe from 1/3 to half of the total carapace length; as wide as long, or longer than wide; anteriorly linguiform, or somewhat extended; with or without ocular pigment; with or without eye lenses.

Antenna 1, basal article of the peduncle arcuate, or straight; shorter than the other two articles together; males with or without a group of aesthetasc on distal margin of peduncle. Main flagellum may have from two to five articles; with third article longer, similar length, or shorter than second; with or without two aesthetasc in distal-most article; with or without two aesthetascs on proximal article of main flagellum. Accessory flagellum uni-articulated. Antenna 2 in males reaching almost the end of the pleon. Antenna 2 in females with three articles.

Maxilliped 3 basis arcuate; not projected over ischium. Ischium shorter than merus (without considering projections). Merus extended dorso-distally over carpus, or merus slightly expanded laterally. Carpus equal to or shorter than propodus and dactylus together. Propodus with a brush of setae.

Peraeon. First peraeonite visible only above lateral midline, or not visible. Peraeonite 2 with ventrolateral expansion; overriding peraeonite 1 and/or carapace, or overriding peraeonite 1 and/or carapace and peraeonite 3. Peraeonite 3 extended forward overriding peraeonite 2, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5, or peraeonite 4 with ventrolateral expansion overriding peraeonite 3 and 5.

Females and males with exopods fully developed on peraeopods 1 to 3 and reduced on perareopod 4. Peraeopod 1, basis geniculate or arcuate, with or without row of setae; with or without a brush (3 or more) of long setae on the propodus (setae longer than carpus); carpus equal to or shorter than propodus. Peraeopod 2, ischium present; dactyl shorter, same length, or longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide, or as long as wide; as long as or shorter than peduncle of uropod. Whole width of pleonite 6 slightly or well extended past the insertion of the uropods, ending in a point, or in a rounded apex. Alternatively, only portion, wide or narrow, of distal end of pleonite 6 extended; ending in a point, or a rounded apex. Anal plates extend posteriorly

beyond distal margin of pleonite six, or do not project; with or without setae on posterior margin of anal plates.

Uropod endopod bi-articulated; two articles approximately same length, or proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods slightly longer or as long asrami, or peduncle slightly shorter than exopods of rami (equal length to endopod); endopod and exopod approximately same length, or endopod longer or shorter than exopod. Males with five pairs of pleopods.

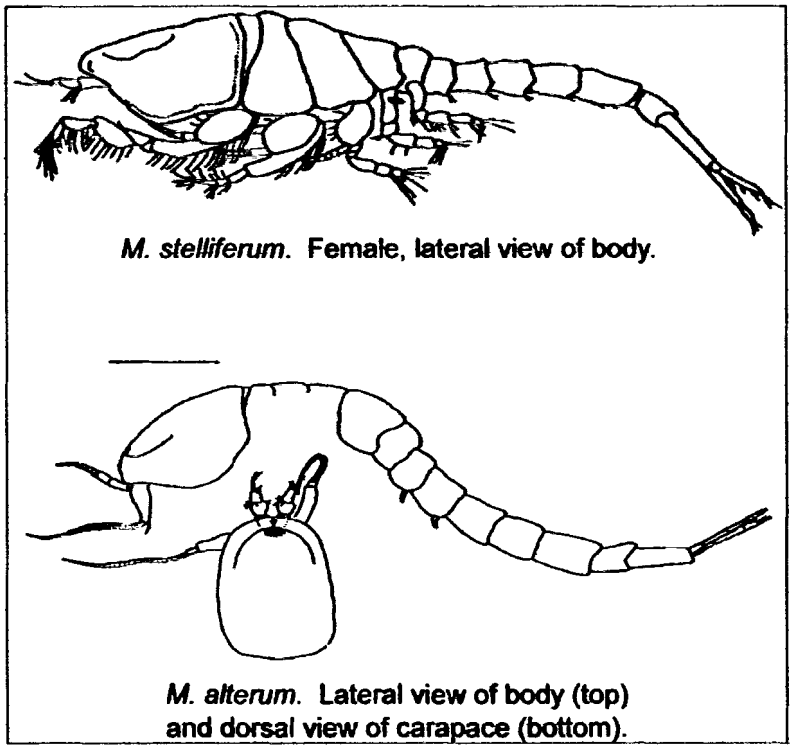
Species Included.

1. *L. barbarae* Tafe and Greenwood, 1996
2. *L. borzonei* Roccatagliata, 1997
3. *L. forsmani* Zimmer, 1943
4. *L. intermedium* Hale, 1944 (Synonymy: *L. intermedia* Hale, 1944; *L. intermedium* Bâcescu, 1988)
5. *L. kennedyi* Tafe and Greenwood, 1996
6. *L. kimbergii* Sars, 1873
7. *L. nichollsi* Hale, 1949
8. *L. obstipum* Hale, 1944 (Synonymy: *L. obstipa* Hale, 1944; *L. obstipum* Bâcescu, 1988)
9. *L. patagonicum* Roccatagliata, 1993
10. *L. pulleini* Hale, 1928
11. *L. serriferum* Hale, 1944 (Synonymy: *L. serrifera* Hale, 1944; *L. serriferum* Bâcescu, 1988)
12. *L. sheardi* Hale, 1944
13. *L. vicarium* Hale, 1944 (Synonymy: *L. vicaria* Hale, 1944; *L. vicarium* Bâcescu, 1988)

Distribution. With the exception of *Leptocuma forsmani* that is present at 10 m off the coast of California in the Noreastern Pacific Ocean, all species of *Leptocuma* are inhabitants of the Southern Hemisphere. They are found in the Australian and South American coasts between 0 and 190 m.

***Mancocuma* Zimmer, 1943**

Type species. *Mancocuma stelliferum* Zimmer, 1943



M. stelliferum. Female, lateral view of body.

M. alterum. Lateral view of body (top) and dorsal view of carapace (bottom).

Figure 28. External morphology of *Mancocuma* spp. Figure modified from Ledoyer (1972) and Watling (1979). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen shorter than carapace and peraeon together; carapace and peraeon similar in length, or peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly, or not compressed; longer than wide. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch not distinct, or as a depression. Anterolateral corner bluntly rounded.

Frontal lobe 1/4 to half the total carapace length; as wide as long, or wider than long; anteriorly linguiform, or not extended; with or without ocular pigment and lenses.

Antenna 1, basal article of the peduncle arcuate, or straight; shorter than the other two articles together. Main flagellum bi-, or tri-articulated; with second article longer than third; with zero, one or two aesthetasc in distal-most article; with or without two aesthetascs on proximal article of main flagellum. Accessory flagellum uni-articulated; with or without brush of setae. Males with antenna 2 reaching only to end of peraeon; anterior margin with pad-like sensory setae; without sensory setae on anterior margin of article four. Antenna 2 in females with three articles.

Maxilliped 3 basis arcuate; extended dorso-distally over ischium beyond the articulation of the ischium and merus, or slightly expanded dorso-distally. Ischium shorter than merus (without considering projections). Merus slightly expanded laterally. Carpus oviform and equal to or shorter than propodus and dactylus together. Propodus oviform or distally widened, with a brush of setae.

Peraeon. First peraeonite well exposed, or visible only above lateral midline. Peraeonite 2 with ventrolateral expansion overriding peraeonite 1 and/or carapace and peraeonite 3. Peraeonite 3 extended backwards overriding peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Females and males with exopods fully developed on peraeopods 1 to 3 and reduced on peraeopod 4. Peraeopod 1, opercular (with basis and carpus expanded, ischium and merus rotated to parallel positions); basis straight, with row of setae; carpus oviform in shape, with row of setae; brush of long setae (3 or more) on propodus (setae longer than carpus), or setae in a linear arrangement along propodus; carpus longer than propodus. Peraeopod 2, ischium present or absent; dactyl and propodus approximately same length. Peraeopod 3, propodus and dactyl small not articulated at the distal end of the carpus but at its side wall. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide, or as long as wide; shorter than peduncle of uropod. Whole width of terminal end of pleonite 6 slightly extended between the base of the uropods; ending in a point, or a rounded apex.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods slightly longer than rami, or peduncle approximately as long as rami; endopod and exopod approximately same length, or endopod longer than exopod. Males with two pairs of pleopods. Pleopodal endopod without a process.

Species included.

1. *M. alterum* Zimmer, 1943 (Synonymy: *M. altera* Zimmer, 1943; *M. alterum* Bâcescu, 1988)
2. *M. stelliferum* Zimmer, 1943 (Synonymy: *M. stellifera* Zimmer, 1943; *M. stelliferum* Bâcescu, 1988)

Distribution. Inhabit brackish waters on the Northwestern Atlantic Ocean up to 18m of depth.

***Pomacuma* Hale, 1944**

Type species. *Pomacuma cognatum* Hale, 1944

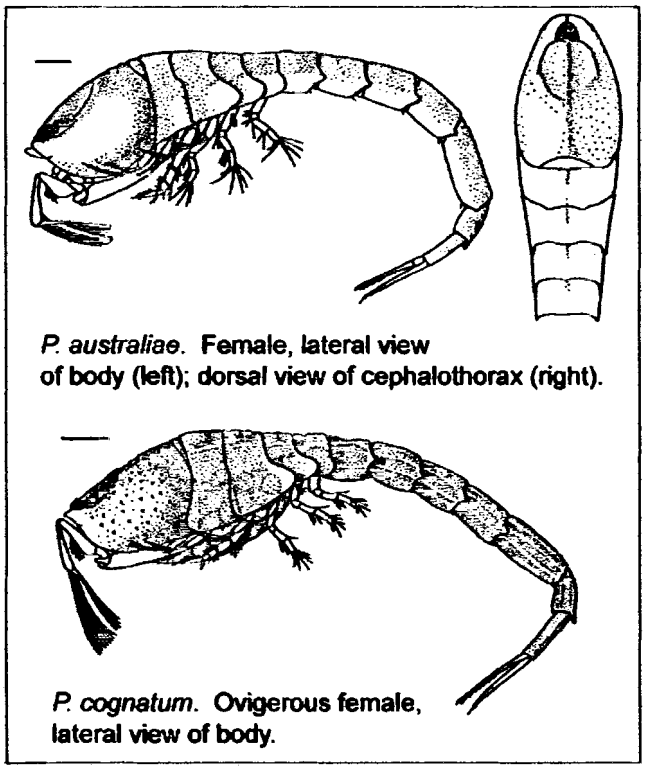


Figure 29. External morphology of *Pomacuma* spp.

Figure modified from Tafe and Greenwood (1996).

Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as or longer than carapace and peraeon together; carapace and peraeon similar in length, or peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly, or not compressed; longer than wide. Carapace with or without mid-dorsal ridge. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch as an acute incision.

Anterolateral corner bluntly rounded. Frontal lobe from 1/3 to half the total carapace length; as wide as long; anteriorly linguiform; with ocular pigment and eye lenses.

Antenna 1, basal article of the peduncle arcuate; as long as or shorter than the other two articles together. Main flagellum bi-articulated; with two, three or more aesthetasc in distal-most article. Accessory flagellum uni-articulated. Males with antenna 2 reaching the end of the pleon.

Maxilliped 3 basis geniculate or arcuate; expanded (opercular); extended dorso-distally and/or ventral over ischium; beyond the articulation of the ischium and merus. Ischium shorter than merus (without considering projections). Merus slightly expanded laterally. Carpus proximally widened; equal to or shorter than propodus and dactylus together. Propodus distally widened, or oviform; with a brush of setae.

Peraeon. First peraeonite visible only above lateral midline. Peraeonite 2 wide or proportional to other peraeonites; with ventrolateral expansion overriding peraeonite 1 and/or carapace. Peraeonite 3 extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Females and males with exopods fully developed on peraeopods 1 to 3 and reduced on peraeopod 4. Peraeopod 1, opercular (with basis-carpus expanded, ischium and merus rotated to parallel positions); basis arcuate, with or without row of setae, with dorso-distal projection totally or partially covering the ischium; ischium modified as a rounded lobe with exterior concavity (opercular); carpus oviform in shape, with row of setae; brush (3 or more) of long setae on the propodus (setae longer than carpus); carpus equal in length to propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; longer or as long as peduncle of uropod. Whole width of pleonite 6 well extended past the insertion of the uropods; ending in a point, or a rounded apex. Alternatively, a wide portion of the distal end of pleonite 6 well extended past the insertion of the uropods, ending in a rounded apex.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Rami longer than peduncle; endopod and exopod approximately same length. Males with five pairs of pleopods.

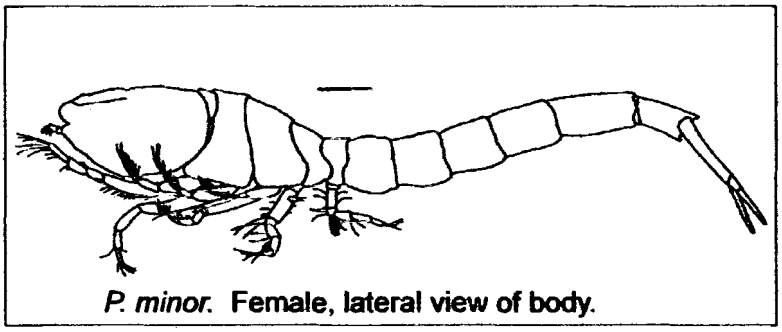
Species Included.

1. *P. australiae* (Zimmer, 1921) (Synonymy: *Vaunthompsonia australiae* Zimmer, 1921; *Leptocuma australiae* Hale, 1936; *Gephyrocuma australiae* Hale, 1944)
2. *P. cognatum* Hale, 1944 (Synonymy: *P. cognata* Hale, 1944; *P. cognatum* Bâcescu, 1988)
3. *Pomacuma* sp. nov. 1 Tafe and Greenwood, 1996

Distribution. Coasts of Asutralia and New Zealand from 0 to 75 m of depth.

***Pseudoleptocuma* Watling, 1977**

Type species. *Pseudoleptocuma minor* (Calman, 1912)



P. minor. Female, lateral view of body.

Figure 30. External morphology of *Pseudoleptocuma minor.*

Figure modified from Watling (1979). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length, or peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch as a depression, or as a subacute incision. Anterolateral corner with subacute tooth. Frontal lobe from 1/3 to half of carapace length; longer than wide; somewhat extended; with or without ocular pigment.

Antenna 1 with main flagellum bi-articulated. Accessory flagellum uni-articulated. Males with antenna 2 reaching the end of the pleon. Antenna 2 in females with three articles.

Maxilliped 3 basis arcuate; slightly expanded laterally over ischium. Ischium shorter than merus (without considering projections). Merus slightly expanded laterally. Carpus oviform; equal to or shorter than propodus and dactylus together. Propodus distally widened, or oviform, and with a brush of setae.

Peraeon. First peraeonite visible only above lateral midline. Peraeonite 2 with ventrolateral expansion; ventrolateral expansion overriding peraeonite 1 and/or carapace, or overriding peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5, or with ventrolateral expansion overriding peraeonite 3 and 5.

Females and males with exopods fully developed on peraeopods 1 to 3. Females with exopod reduced on peraeopod 4, while males have them fully developed. Peraeopod 1, basis arcuate, with row of setae; with or without row of setae on the carpus; brush (3 or more) of long setae on the propodus (setae longer than carpus), or setae in a linear arrangement; carpus equal in length to propodus. Peraeopod 2, ischium present; dactyl and propodus approximately same length. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; shorter than peduncle of uropod. Whole width of terminal end of pleonite 6 slightly extended between the base of the uropods; ending in a rounded apex.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods slightly longer than rami; endopod and exopod approximately same length, or exopod longer than endopod. Males with three pairs of pleopods. Pleopodal endopod with well developed process.

Species Included.

1. *P. minor* (Calman, 1912) (Synonymy: *Leptocuma minor* Calman, 1912; *Leptocuma minus* Stebbing, 1913)

Distribution. Northwestern Atlantic Ocean from 15 to 24 m.

***Pseudosympodomma* Kurian, 1954**

Synonymy. *Sympodomma* (part.) Stebbing, 1912

Type species. *Pseudosympodomma indicum* Kurian, 1954

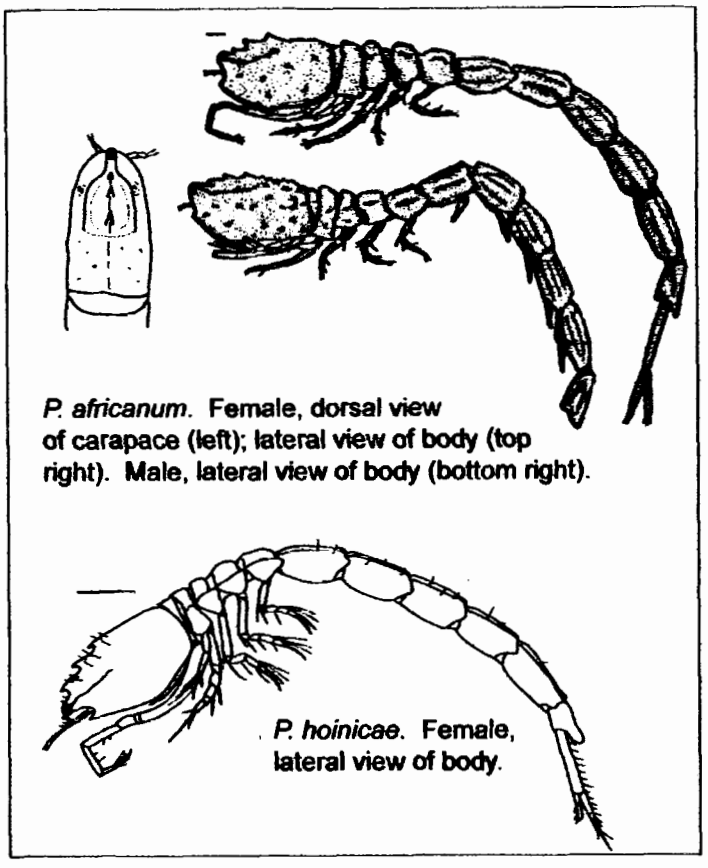


Figure 31. External morphology of *Pseudosympodomma* spp. Figure modified from Day (1975) and Petrescu (1998). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length, or peraeon longer than carapace.

Head. From dorsal view the carapace appears not laterally compressed; longer than wide. Carapace with mid-dorsal ridge, or with mid-dorsal serration; with or without anterior transverse

ridge. Pseudorostral lappets do not extend beyond the frontal lobe. Antennal notch as a depression, or as a subacute incision. Anterolateral corner with subacute tooth. Frontal lobe 1/3 to half of carapace length; longer than wide; anteriorly linguiform; with ocular pigment and eye lenses.

Antenna 1, basal article of the peduncle arcuate or straight; as long as or shorter than the other two articles together. Main flagellum bi-, or tri-articulated; with second and third article approximately same length, or with second article longer than third; with two aesthetasc in distal-most article. Accessory flagellum uni-, or bi-articulated; with or without brush of setae. Males with antenna 2 reaching the end of the pleon. Antenna 2 in females with three articles.

Maxilliped 3 basis arcuate, or straight; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium longer or as long as merus (without considering projections). Merus expanded laterally. Carpus distally widened, or oviform; equal to or shorter than propodus and dactylus together. Propodus distally widened, or not; with a brush of setae.

Peraeon. First peraeonite well exposed, or visible only above lateral midline. Peraeonite 2 with or without ventrolateral expansion not overriding other somites, or overriding peraeonite 1 and/or carapace. Peraeonite 3 without ventrolateral expansion, or extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5, or with ventrolateral expansion overriding peraeonite 3 and 5.

Females and males with exopods fully developed on peraeopods 1 and 2. Peraeopod 1, basis arcuate or straight, with or without row of setae; with or without setae in a linear arrangement along propodus; carpus shorter than propodus. Peraeopod 2, ischium present; dactyl and propodus approximately same length, or dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; as long as or shorter than peduncle of uropod. Wide portion of distal end of pleonite 6 well extended past the insertion of the uropods; ending in a point, or with rounded apex. Anal plates project posteriorly beyond distal margin of pleonite 6, or do not project; with or without setae in posterior margin of anal plates.

Uropod endopod bi-articulated; two articles approximately same length, or proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods longer or as long as rami; endopod and exopod approximately same length, or exopod longer than endopod. Males with five pairs of pleopods. Pleopodal endopod with well developed process.

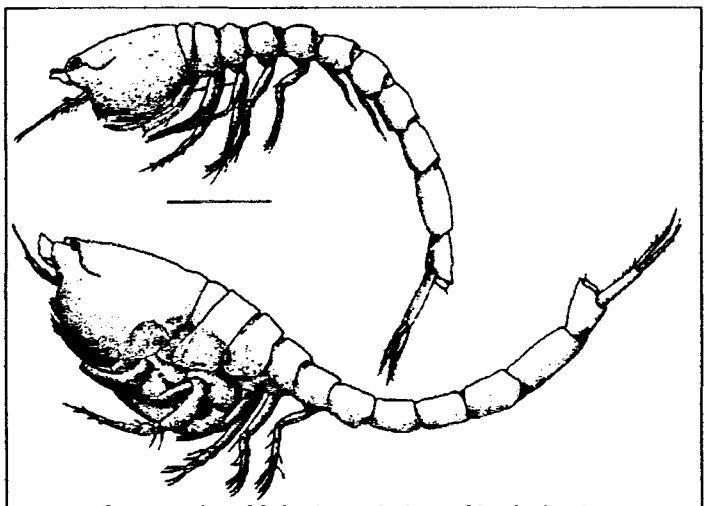
Species included.

1. *P. africanum* (Stebbing, 1912) (Synonymy: *Sympodomma africana* Hale, 1944, *P. africanum* Day, 1975; Nec *Sympodomma africanum* Hale, 1928)
2. *P. hoinicae* Petrescu, 1998
3. *P. indicum* Kurian, 1954 (Synonymy: *P. indica* Kurian, 1954; *P. indicum* Bâcescu, 1988)
4. *Pseudosympodomma* sp. Mühlenhardt-Siegel, 1996

Distribution. *Pseudosumpodomma africanum* is found off the coast of South Africa from 85 to 370 m. *Pseudosympodomma hoinicae* is found in the West Pacific Ocean (coast of Tanzania) and *P. indicum* in shallow waters (0 to 4 m) of the Indo-West Pacific.

***Speleocuma* Corbera, 2002**

Type species. *Speleocuma guanche* Corbera, 2002



S. guanche. Male, lateral view of body (top). Female, lateral view of body (bottom).

Figure 32. External morphology of *Speleocuma guanche*. Figure modified from Corbera (2002). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as or longer than carapace and peraeon together; peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly; longer than wide. Carapace with mid-dorsal serration. Pseudorostral lappets extend or not beyond frontal lobe; when extended they meet in the midline. Antennal notch as a depression. Anterolateral corner bluntly rounded, or with subacute tooth. Frontal lobe 1/3 of the total carapace length; anteriorly linguiform; with ocular pigment and with eye lenses.

Antenna 1, basal article of the peduncle arcuate; shorter than the other two articles together. Main flagellum bi-articulated; with one or two aesthetasc in distal-most article. Accessory flagellum uni-articulated. Males with antenna 2 not reaching the end of the peraeon.

Maxilliped 3 basis arcuate; not projected over ischium. Ischium shorter than merus. Merus slightly expanded laterally. Carpus oviform; equal to or shorter than propodus and dactylus together.

Peraeon. Peraeonite 2 with ventrolateral expansion; ventrolateral expansion overriding peraeonite 1 and/or carapace, or overriding peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 extended forward overriding peraeonite 2, or extended backwards overriding peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Females and males with exopods fully developed on peraeopods 1 to 3. Peraeopod 1, basis arcuate. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; shorter than peduncle of uropod. Wide portion of the distal end of pleonite 6 slightly extended past the insertion of the uropods; ending in a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six and with setae on posterior margin of anal plates.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle approximately as long as rami; endopod longer than exopod. Males with two pairs of pleopods. Pleopodal endopod without process.

Species included.

1. *S. guanche* Corbera, 2002

Distribution. Inhabit caves in the Canary Islands from 3 to 7 m of depth.

***Spilocuma* Watling, 1977**

Type species. *Spilocuma salomani* Watling, 1977

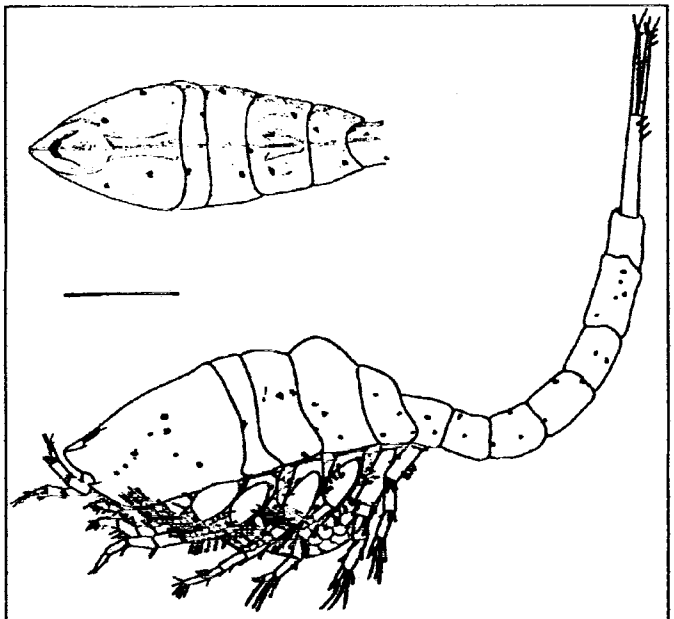


Figure 33. External morphology of *Spilocuma watlingi*. Figure modified from Omholt and Heard (1979). Scale bar represents 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen shorter or same size as carapace and peraeon together; carapace and peraeon similar in length.

Head. From dorsal view the carapace appears laterally compressed anteriorly; longer than wide. Pseudorostral lappets extend beyond frontal lobe and meet in midline. Antennal notch as a subacute or acute incision. Anterolateral corner with acute tooth. Frontal lobe from 1/5 or less to 1/4 of the carapace length; as wide as long; somewhat extended; with ocular pigment and with eye lenses.

Antenna 1, basal article of the peduncle straight; shorter than the other two articles together. Main flagellum bi-articulated; with two aesthetasc in distal-most article; with or without two aesthetasc on proximal article of main flagellum. Accessory flagellum uni-articulated; with or without brush of setae. Males with antenna 2 not reaching the end of the peraeon; anterior margin with pad-like sensory setae; without sensory setae on anterior margin of article four. Antenna 2 in females with four articles.

Maxilliped 3 basis arcuate; not projected over ischium. Ischium shorter than merus (without considering projections). Merus extended dorso-distally over carpus, or merus slightly expanded laterally. Carpus equal to or shorter than propodus and dactylus together.

Peraeon. Peraeonite 2 narrow; with ventrolateral expansion; overriding peraeonite 3, or overriding peraeonite 1 and/or carapace, and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended backwards overriding peraeonite 4. Peraeonite 4 without ventrolateral expansion, or with ventrolateral expansion overriding peraeonite 5.

Females and males with exopods fully developed on peraeopods 1 to 3 and reduced on peraeopod 4. Peraeopod 1, basis arcuate, with row of seta; with or without row of setae on the carpus; carpus longer than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 shorter than peduncle of uropods. Pleonite 6 slightly extended past the insertion of the uropods.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods slightly longer than rami; endopod and exopod approximately same length. Males without pleopods.

Species included.

1. *S. salomani* Watling, 1977
2. *S. watlingi* Omholt and Heard, 1979

Distribution. Inhabit brackish waters of the North-West Atlantic (southern coast of U.S.A.) from 0 to 3.6 m of depth.

***Sympodomma* Stebbing, 1912**

Type species. *Sympodomma diomedeae* (Calman, 1912)

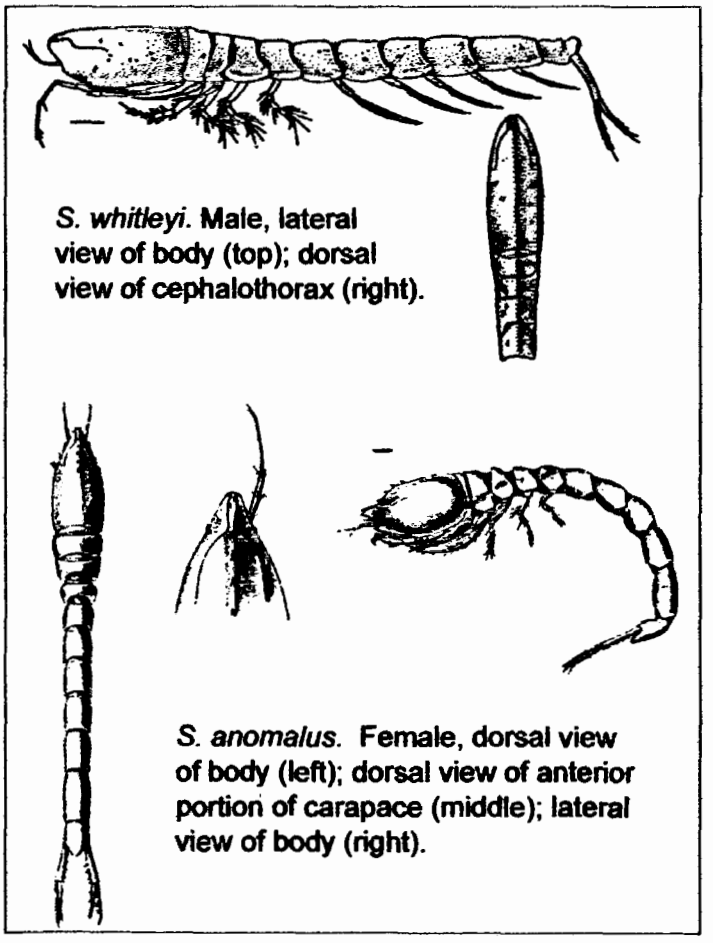


Figure 34. External morphology of *Sympodomma* spp. Figure modified from Hale (1944) and Sars (1871). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length, or carapace longer or shorter than peraeon.

Head. From dorsal view the carapace appears laterally compressed anteriorly or posteriorly; longer than wide. Carapace with mid-dorsal ridge, or with mid-dorsal serration; with or without dorso-lateral ridges; with lateral ridges; with or without anterior transverse ridge; with or without posterior transverse ridge. Pseudorostral lappets do not extend beyond the frontal lobe, or slightly extend but do not meet. Antennal notch not distinct, or as a depression, or as a subacute incision. Anterolateral corner bluntly rounded, or with subacute or acute tooth. Frontal lobe from 1/3 to 1/2 of the total carapace length; longer than wide; anteriorly linguiform; with ocular pigment and with eye lenses.

Antenna 1, basal article of the peduncle geniculate, or straight; as long as or shorter than the other two articles together. Main flagellum bi-, or tri-articulated; with second article longer than third; with two aesthetasc in distal-most article; males with or without a group of aesthetascs on proximal article of main flagellum. Accessory flagellum uni-, or bi-articulated; males with or without brush of setae; with or without aesthetasc. Males with antenna 2 reaching the end of the pleon.

Maxilliped 3 basis arcuate, or straight; extended dorso-distally over ischium beyond the articulation of the ischium and merus. Ischium as long as or longer than merus (without considering projections). Merus extended dorso-distally over carpus or expanded laterally. Carpus distally widened, or oviform; equal to or shorter than propodus and dactylus together. Propodus distally widened, or not widened; with a brush of setae.

Peraeon. First peraeonite well exposed, visible only above lateral midline, or not visible. Peraeonite 2 with or without ventrolateral expansion not overriding other somites, or overriding peraeonite 1 and/or carapace, or overriding peraeonite 3, or overriding peraeonite 1 and/or carapace and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 without ventrolateral expansion, or with ventrolateral expansion overriding peraeonite 5, or with ventrolateral expansion overriding peraeonite 3 and 5.

Females and males with exopods fully developed on peraeopods 1 to 3. Peraeopod 1, basis arcuate or straight, with or without row of setae; with or without setae in a linear arrangement along propodus; carpus shorter than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; longer or as long as peduncle of uropod; with or without many small setae on posterior edge of pleonite 6. Whole width of distal end of pleonite 6 slightly or well extended past the insertion of the uropods; ending in a point, or a line. Alternatively, wide portion of distal end of pleonite 6 extended between bases of uropods; ending in a line, or in a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or do not project; with or without setae on posterior margin of anal plates.

Uropod endopod bi-articulated; two articles approximately same length, or proximal article shorter or longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle of uropods longer or as long asrami; endopod and exopod approximately same length, or endopod shorter or longer than exopod. Males with five pairs of pleopods. Pleopodal endopod with well developed process.

Species included.

1. *S. anomalus* (Sars, 1871) (Synonymy: *Leucon anomalus* Sars, 1871; *Vaunthompsonia anomala* Sars, 1879; *S. anomalum* Stebbing, 1913)
2. *S. australiense* Foxon, 1932 (Synonymy: *S. australiensis* Foxon, 1932; *S. australiense* Bâcescu, 1988)
3. *S. diomedeae* (Calman, 1912) (Synonymy: *Heterocuma diomedeae* Calman, 1912)
4. *S. hatagumoanum* Gamô, 1969 (Synonymy: *S. hatagumoana* Gamô, 1969; *S. hatagumoanum* Bâcescu, 1988)

5. *S. incertum* Hale, 1949 (Synonymy: *S. africanum* Hale, 1928; *S. incerta* Hale, 1949; *S. incertum* Bâcescu, 1988*)*
6. *S. vitreum* Lomakina, 1967 (Synonymy: *S. vitrea* Lomakina, 1967; *S. vitreum* Bâcescu, 1988)
7. *S. weberi* (Calman, 1905) (Synonymy: *Heterocuma weberi* Calman, 1905)
8. *S. whitleyi* Hale, 1949

Distribution. West Indian Ocean (from 30 to 565 m), Indo-West and West Pacific (from 20 to 300 m), Australian coasts (from 11 to 13 m) and South Pacific (at 1,158 m).

***Vaunthompsonia* Bate, 1858**

Synonymy. *Scorpionura* Thompson, 1856

Type species. *Vaunthompsonia cristata* Bate, 1858

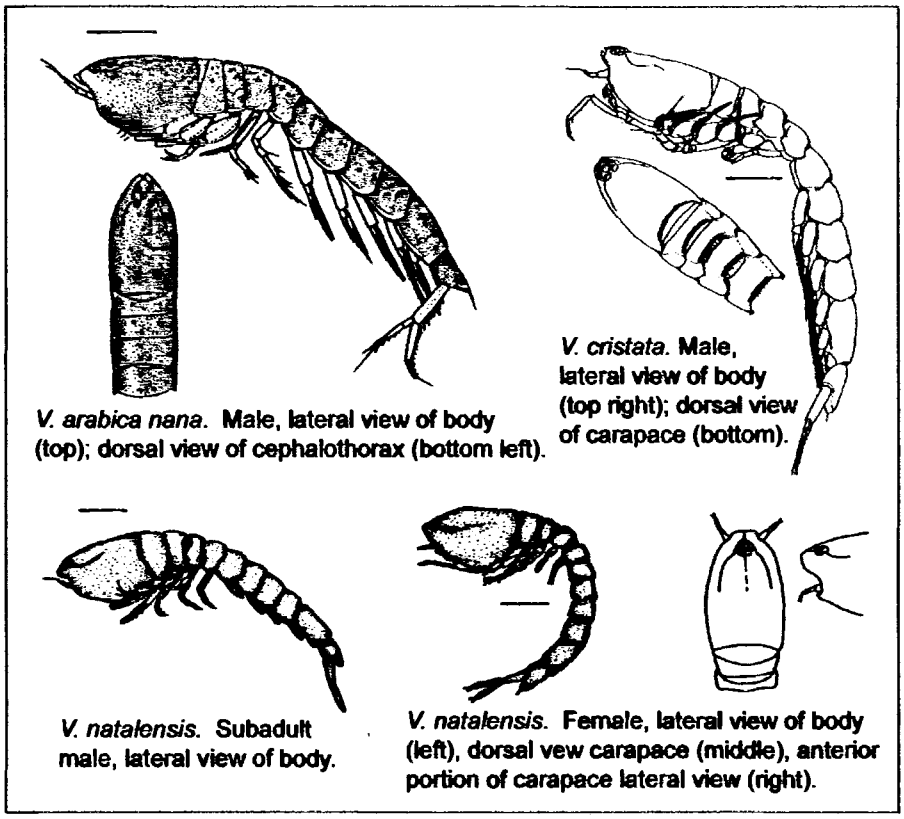


Figure 35. External morphology of *Vaunthompsonia* spp. Figure modified from Day (1975), Hale (1944), and Kang and Lee (1995). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen longer than carapace and peraeon together; carapace and peraeon similar in length, or peraeon longer than carapace.

Head. From dorsal view the carapace appears laterally compressed anteriorly; longer than wide. Carapace with mid-dorsal ridge, or with mid-dorsal serration; with or without dorso-lateral

ridges; with or without lateral ridges. Pseudorostral lappets extend beyond frontal lobe and meet in midline, or extend towards midline but do not meet (or partially meet leaving a suture between them), or are widely separated, or do not extend beyond the frontal lobe. Antennal notch not distinct, or as a depression, or as a subacute incision. Anterolateral corner bluntly rounded, or with subacute tooth. Branchial siphons extend just beyond pseudorostrum, or long, extended much beyond pseudorostrum. Frontal lobe from 1/4 to half of the total carapace length; as wide as long; anteriorly linguiform, or somewhat extended; with ocular pigment and with eye lenses.

Antenna 1, basal article of the peduncle arcuate, or straight; as long as or shorter than the other two articles together. Main flagellum uni-, or bi-articulated, or tri-articulated; with second article longer than third; with one or two aesthetasc in distal-most article. Accessory flagellum uni-articulated; with or without brush of setae. Males with antenna 2 reaching only to end of peraeon; with sensory setae on anterior margin of article four. Antenna 2 in females with two or three articles.

Maxilliped 3 basis arcuate, or straight; not projected over ischium. Ischium shorter than merus. Merus without dorsal projection, or extended dorso-distally over carpus, or slightly expanded laterally. Carpus oviform, distally widened, or not widened; equal to or shorter than propodus and dactylus together.

Peraeon. First peraeonite well exposed, or visible only above lateral midline, or not visible. Peraeonite 2 wide or proportional to other peraeonites; with or without ventrolateral expansion overriding peraeonite 1 and/or carapace, or overriding peraeonite 1 and/or carapace and peraeonite 3. Peraeonite 3 without ventrolateral expansion, or extended forward overriding peraeonite 2, or extended backwards overriding peraeonite 4, or extended forward and backwards overriding peraeonites 2 and 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5, or with ventrolateral expansion overriding peraeonite 3 and 5.

Females with exopods fully developed on peraeopods 1 to 3 and males on peraeopods 1 to 4. Peraeopod 1, basis arcuate or straight, with or without row of setae; carpus longer than, equal

to, or shorter than propodus. Peraeopod 2, ischium absent; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 longer than wide; longer, as long as or shorter than peduncle of uropod; with or without two or many setae on posterior edge of pleonite 6. Whole width of terminal end of pleonite 6 slightly or well extended past the insertion of the uropods; ending in a point or a rounded apex. Alternatively, wide portion of distal end of pleonite 6 extended between bases of uropods; ending in a point, a line, or a rounded apex. Anal plates extend posteriorly beyond distal margin of pleonite six, or do not project; with or without setae on posterior margin of anal plates.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter or longer than distal one. Peduncle of uropods longer or shorter than rami, or peduncle slightly shorter than exopods of rami (equal length to endopod); endopod longer or shorter than exopod. Males with five pairs of pleopods. Pleopodal endopod with well developed or reduced process.

Species included.

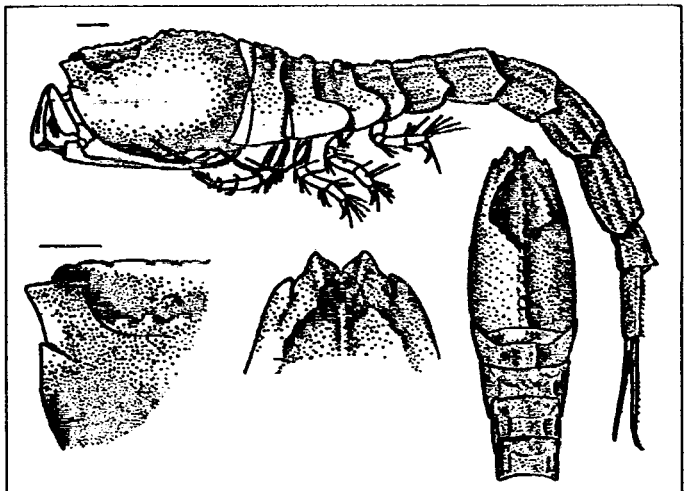
1. *V. arabica* Calman, 1907
- *V. arabica arabica* Calman, 1907 (Synonymy: *V. arabica* Calman, 1907; *V. arabica arabica* Bâcescu, 1988)
- *V. arabica nana* Hale, 1944 (Synonymy: *V. nana* Hale, 1944; *V. arabica nana* Bâcescu, 1988)
2. *V. cristata* Bate, 1858 (Synonymy: *Scorpionura vulgaris* Thompson, 1856; *Bodotria longipes* Sars, 1879)
3. *V. dawydoffi* Zimmer, 1952
4. *V. floridana* Bâcescu, 1971
5. *V. inermis* Zimmer, 1909
6. *V. laevifrons* Gamô, 1987

7. *V. media* Zimmer, 1952
8. *V. meridionalis* Sars, 1886
9. *V. minor* Zimmer, 1944 (Synonymy: *V. cristata* Calman, 1907)
10. *V. natalensis* Day, 1975
11. *V. pacifica* Zimmer, 1943
12. *V. serratifrons* Gamô, 1964a
13. *Vaunthompsonia* sp. Belyaev, 1966
14. *Vaunthompsonia* sp. Day, 1975
15. *Vaunthompsonia* sp. Mühlenhardt-Siegel, 1996

Distribution. Generally found in shallow waters (and up to 280 m) in the Mediterranean and Red Seas, Indo-West Pacific, North Pacific, Indian, and Southern Oceans. *Vaunthompsonia caeca* inhabits deeper waters (350 to 1,720 m) in the North Atlantic Ocean.

***Zenocuma* Hale, 1944**

Type species. *Zenocuma rugosum* Hale, 1944



Z. rugosum. Female, lateral view of body (top); lateral view (bottom left), and dorsal view (bottom middle) of anterior portion of carapace; dorsal view of cephalothorax (right).

Figure 36. External morphology of *Zenocuma rugosum*. Figure modified from Hale (1944). Scale bars represent 0.5 mm.

General Body. Carapace shorter than abdomen; abdomen approximately as long as carapace and peraeon together; carapace and peraeon similar in length.

Head. From dorsal view the carapace appears not to be laterally compressed; longer than wide. Carapace with mid-dorsal ridge and with anterior transverse ridge. Pseudorostral lappets extend beyond frontal lobe extended towards midline but do not meet (or partially meet leaving a suture between them). Antennal notch as an acute incision. Anterolateral corner bluntly rounded. Frontal lobe half of carapace length; as wide as long; anteriorly linguiform; with ocular pigment and eye lenses.

Antenna 1, basal article of the peduncle arcuate; as long as the other two articles together. Main flagellum bi-articulated. Accessory flagellum uni-articulated; with brush of setae.

Maxilliped 3 basis arcuate; expanded (opercular); projected ventrally over ischium. Ischium shorter than merus (without considering projections). Carpus proximally widened; equal to or shorter than propodus and dactylus together. Propodus distally widened, or oviform; with a brush of setae.

Peraeon. First peraeonite visible only above lateral midline. Peraeonite 2 with ventrolateral expansion; overriding peraeonite 1 and/or carapace and peraeonite 3. Peraeonite 3 extended backwards overriding peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

Females with exopods fully developed on peraeopods 1 to 3 and reduced on peraeopod 4. Peraeopod 1, opercular (with basis-carpus expanded, ischium and merus rotated to parallel positions); basis arcuate; ischium modified as a rounded lobe with exterior concavity (opercular); carpus oviform in shape with row of setae; brush (3 or more) of long setae on the propodus (setae longer than carpus); carpus shorter than propodus. Peraeopod 2, ischium present; dactyl longer than propodus. Peraeopod 4, ischium present.

Pleon. Pleonite 6 as long as wide; shorter than peduncle of uropod. Pleonite 6 not extended past the insertion of the uropods. Anal plates extend posteriorly beyond distal margin of pleonite six.

Uropod endopod bi-articulated; proximal article longer than distal one. Uropod exopod with proximal article shorter than distal one. Peduncle shorter than rami; endopod longer than exopod.

Species Included.

1. *Z. rugosum* Hale, 1944 (Synonymy: *Z. rugosa* Hale, 1944; *Z. rugosum* Bâcescu, 1988)

Distribution. South-East Australia from 30 to 75 m of depth.

Chapter 5

A NEW SPECIES OF *AUSTROCUMA* FROM INDIA

Because it is part of a thesis, this species description does not comply with the requirements imposed by the International Code of Zoological Nomenclature. In consequence, it should not be considered a formal species description and should not be cited as such.

Introduction

The monotypic genus *Austrocuma* was erected by Day (1978) upon her description of *Austrocuma platyceps*. This is a shallow water (0-1 m) species endemic to the coasts of South Africa from Muizenberg to Hout Bay. The uniqueness of the genus relies mainly on the presence of three pairs of pleopods, an odd feature within the subfamily Bodotriinae in which five pairs of pleopods is the general rule. The only other exception is the genus *Coricuma* whose males bear two pairs of pleopods. Additional characteristics that differentiate the genus *Austrocuma* from other members of the subfamily Bodotriinae are the dorsoventrally flattened cephalothorax, and body proportions, specifically, the carapace is as long as the peraeon and almost as long as or as long as the pleon, instead of shorter than both the peraeon and the pleon.

A new species of the genus *Austrocuma* has been found from the eastern coast of India and will be described in this chapter.

Materials and Methods

I. Kornfield collected shallow water cumaceans along the coast of India using a benthic dredge with a 425 µm mesh net bag dragged by boat. The samples were preserved in 95% ethanol. The material examined consisted of six individuals, three of each gender. An ovigerous

female has been designated as the holotype and a mature male as the paratype, and these will be sent to the National Museum of Natural History, Smithsonian Institution (USNM). One individual of each gender was dissected, and permanent preparations of each appendage were mounted using CMCP-9 (Polysciences, Inc.). The preparations were observed under a Wild compound microscope to which a *camera lucida* was attached in order to draw the detailed morphology.

Description of *Austrocuma* sp.

Material examined. Three mature males, three mature females.

Type material. Holotype, ovigerous female. Paratype, mature male.

Type locality. Lagoon separated from the Bay of Bengal by a barrier beach, 25 km South of Chennai, India (13°04'N, 80°18'E). Depth: 1-5 m.

Collection date. November 3, 2000.

Ovigerous female. Body length ranges from 1.60 to 1.75 mm. Carapace smooth, lightly pigmented brown. Carapace longer than peraeon and subequal to pleon, wider than long (Figs. 37A-B). Carapace without lateral ridges or transverse ridges and with mid-dorsal ridge. In dorsal view, lateral carinae are evident on the first two peraeonites (Fig. 37B).

Frontal lobe with eye lobe highly pigmented. Pseudorostral lobes extend antero-laterally slightly beyond frontal lobe and meet in midline forming short pseudorostrum (Fig. 37B).

Antennal notch as subacute incision, anterolateral corner with subacute tooth. Lateral margin of carapace with strongly curved concave edge along basis of maxilliped 3 (Fig. 37A).

First peraeonite visible only above lateral mid-line. Peraeonite 2 wide, with ventrolateral expansion overriding peraeonite 3. Peraeonite 3 with ventrolateral expansion overriding peraeonite 4. Peraeonite 4 with ventrolateral expansion overriding peraeonite 5.

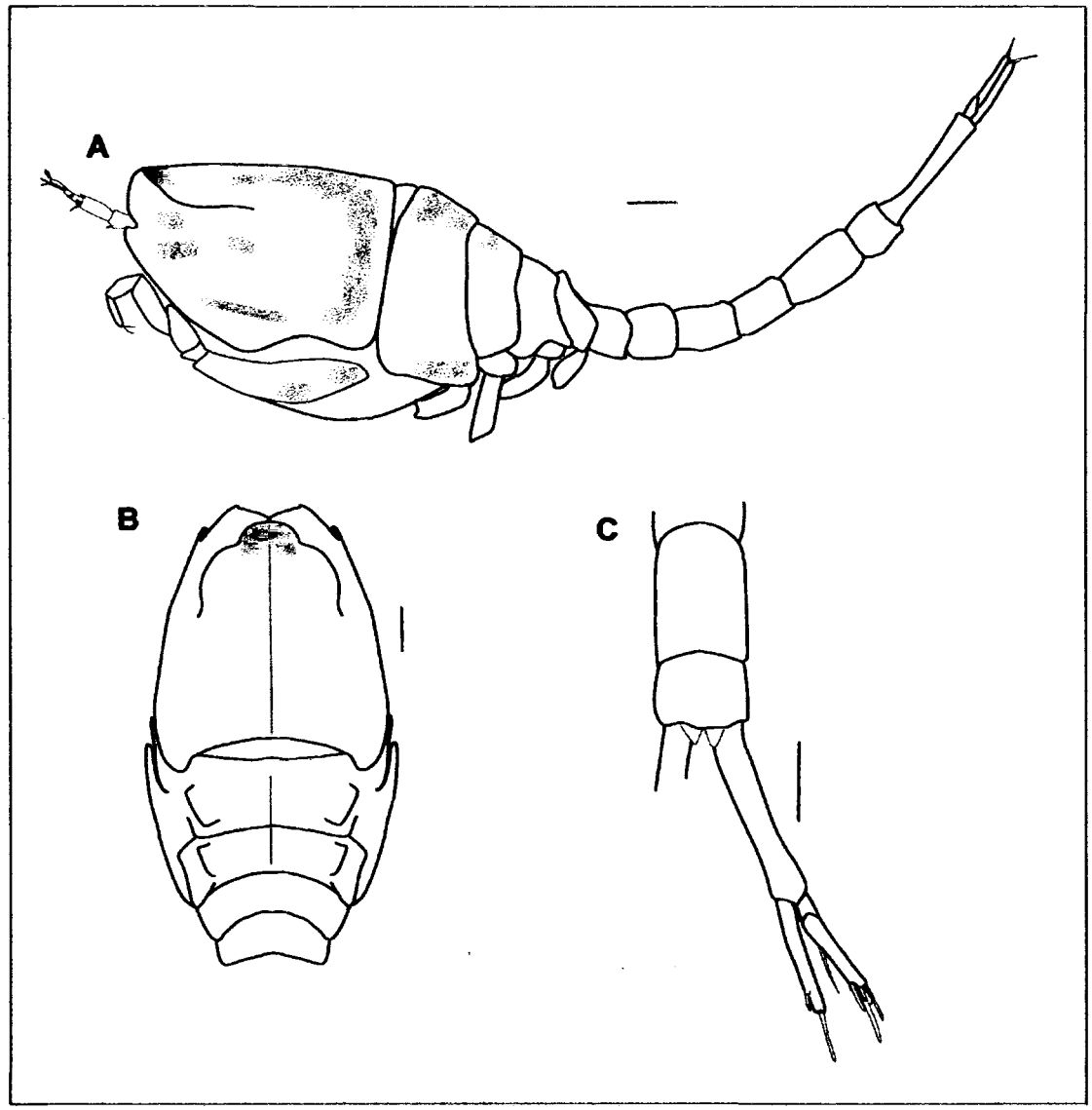


Figure 37. *Austrocuma* sp. ovigerous female, general anatomy. A. Lateral view. B. Dorsal view of cephalothorax. C. Dorsal view of pleonites 5 and 6 and uropods. Scale bars represent 0.1 mm.

Pleonite 5 approximately 1.6 times longer than pleonite 6. Anal plates extend beyond posterior margin of pleonite 6 (Fig. 37C). Pleonite 6 not extended beyond insertion of uropods.

Peduncle of Antenna 1 tri-articulated; proximal article arcuate, shorter than other two articles together. Third article longer than second. Accessory flagellum minute, uni-articulate and with

three terminal setae. Main flagellum 2-articulate with first article longer than the second. Second article with two terminal aesthetascs and one specialized cup-shaped sensory setae on distal article (Fig 38A). Antenna 2 2-articulate with three terminal setae (Fig. 38A).

Mandible with dorsal part to pars molaris naviculoid in shape. *Lacinia mobilis* on left mandible denticulate and articulated (Fig. 38B). Pars incisiva denticulate at subacute tip. Between the pars molaris and pars incisiva is single row of eight setae each bearing many small setules distally.

Maxilla 1 with two endites heavily armed distally with simple and robust setae. Palp twice length of the protopod and bears two unequally long setae adorned with occasional backwardly oriented setules.

Maxilla 2 with endites longer than protopod (Fig. 38D). Protopod and endites with distal margin heavily armed.

Maxilliped 1 basis long and stout with endite extending to articulation of merus and carpus. Ischium not visible, may be covered by basis. Carpus as long as propodus and dactylus together, armed with double row of simple setae on the inner edge, and one plumose setae distally on outer edge. Propodus with a perpendicular row of three setae. Dactyl with many simple terminal setae. Coxa with well-developed epipodite bearing gill apparatus with 11 gill lamellae. Gills without supports or plates (Fig. 38E).

Maxilliped 2 with basis almost as long as the rest of appendage, with long plumose setae distally on inner margin. Ischium very short, most clearly visible on inner side of appendage. Basis and merus with a long plumose setae along distal inner margin. Basis with two small simple setae on outer margin and with perpendicular row of three simple setae close to distal margin on dorsal side. Merus with one small setae on distal half of dorsal surface and large simple setae on the distal-most outer corner. Carpus and merus subequal in length. Carpus with two plumose setae on inner margin. Propodus with a row of setae on distal half of inner margin, and with single simple setae on its dorsal surface. Dactylus with stout terminal setae and armed with four subterminal setae (Fig. 38F).

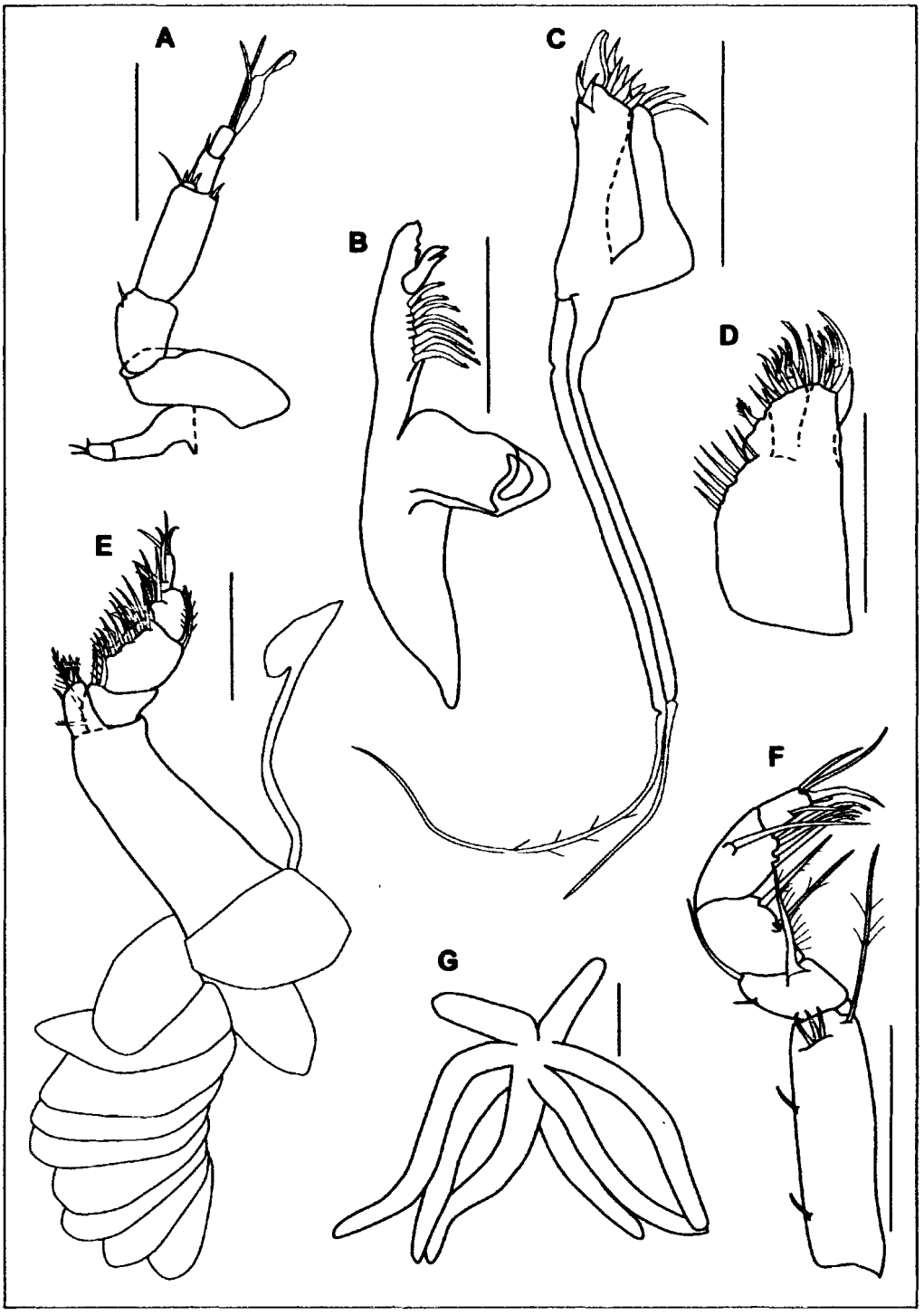


Figure 38. *Austrocuma* sp. ovigerous female, cephalothoracic structures. A. Antenna 1 and 2. B. Left mandible. C. Maxilla 1. D. Maxilla 2. E. Maxilliped 1. F. Maxilliped 2. G. Hepatic diverticula. Scale bars represent 0.1 mm.

Maxilliped 3, with exopod fully developed, armed with plumose setae. Basis of endopod very long, strongly arcuated, longer than all other articles together. Distal portion of outer margin with row of small setae. Basis with dorso-distal extension reaching beyond articulation of ischium and merus and armed with long plumose setae. Merus longer than ischium and subequal in length to dactylus. Merus as long as propodus and carpus together, laterally widened and armed with row of simple setae on inner margin. Propodus laterally widened and with row of setae increasing in size distally on its inner margin. Propodus armed with four terminal setae and one simple seta along inner margin (Fig. 39A).

Peraeopod 1 with exopod fully developed, armed with plumose setae. Basis of endopod slightly arcuate, stout in middle area, subequal in length to other articles together. Ischium short. Merus expanded dorso-distally over articulation with carpus. Carpus longer than merus, with row of simple setae on inner margin. Propodus with single setae on inner margin. Dactylus with three terminal setae and two subterminal setae, longest seta longer than article, and one seta at mid-point of inner margin (Fig. 39B).

Peraeopod 2 uniramous. Basis shorter than distal half of appendage, slightly projected over merus with plumose setae on outer distal margin, and with one specialized sensory seta on inner margin. Ischium absent. Merus and carpus subequal in length. Distal outer margin of carpus and inner margin with setae longer than propodus. Propodus shorter than dactylus. Dactylus and carpus subequal in length. Dactylus with two long terminal setae, longer than article, and two shorter terminal setae (Fig. 39C).

Peraeopod 3 uniramous. Basis shorter than remaining articles together, with two specialized sensory setae on inner margin, outer margin with distal setae longer than ischium. Ischium short with two setae on distal edge. Merus and carpus subequal in length. Distal outer edge of merus with setae longer than carpus. Carpus with three long setae on distal margin, setae longer than propodus and dactylus together. Propodus longer than dactylus, with setae longer than dactylus on distal inner edge. Dactylus armed with two terminal setae (Fig. 39D).

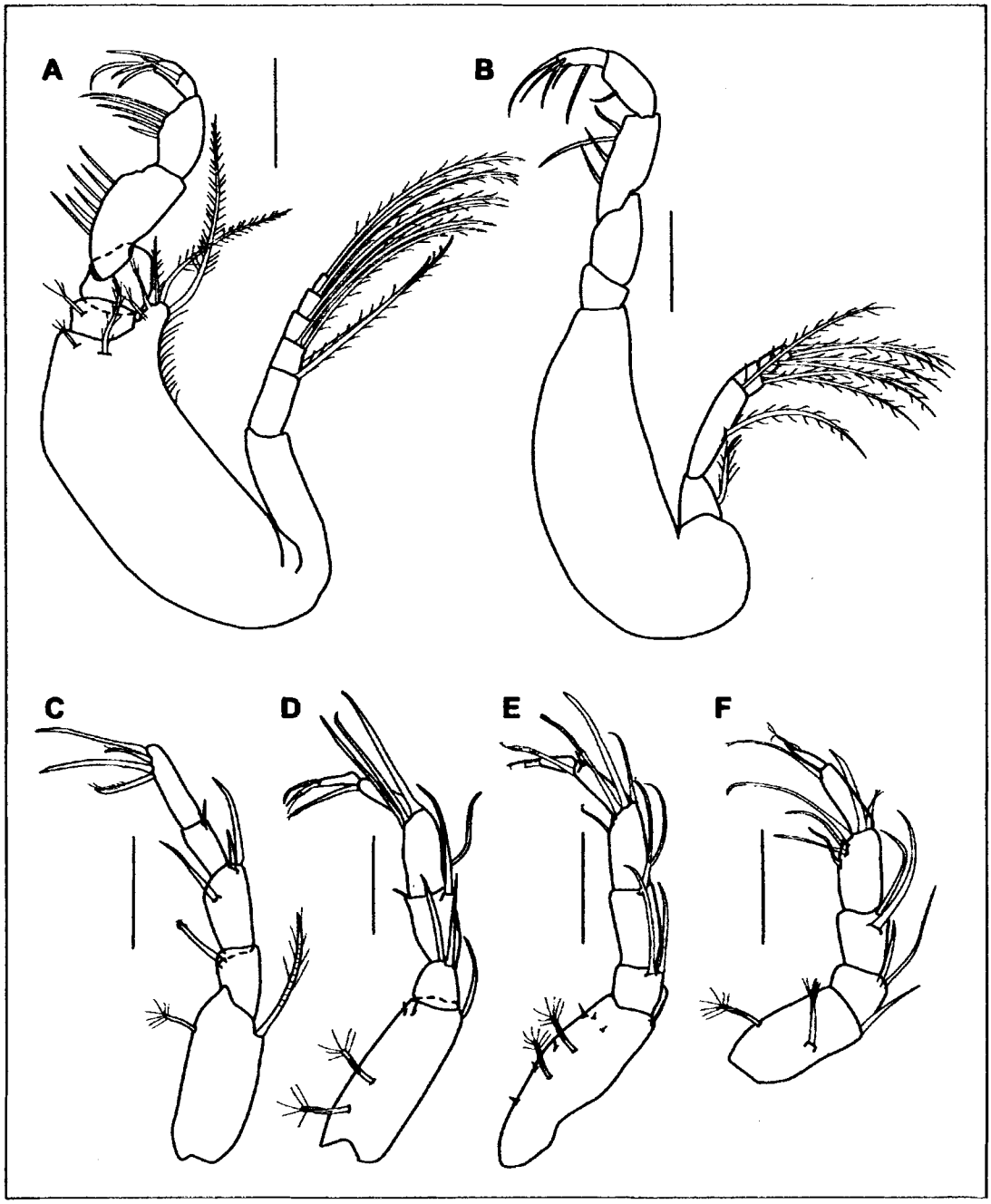


Figure 39. *Austrocuma* sp. ovigerous female, peraeopods. A. Maxilliped 3. B-F. Peraeopods 1-5. Scale bars represent 0.1 mm.

Peraeopod 4 uniramous. Basis shorter than remaining articles together. Proportions of length of articles similar to peraeopod 3. Setae location and shape also similar to peraeopod 3. Merus bears a bifurcated setae on distal portion close to inner edge (Fig. 39E).

Peraeopod 5 uniramous, with similar armoring similar to peraeopod 3. Basis shorter than rest of articles together. Merus shorter than carpus. Carpus and propodus subequal in length.

Uropods with unarmed peduncle; peduncle approximately 2.5 times longer than pleonite six, and approximately 1.6 times longer than rami (Fig. 37C). Uropod rami subequal in length, endopod uniarticulate; exopod 2-articulate with distal article approximately 3 times longer than proximal (Fig. 37C); endopod and exopod bear terminal setae.

Adult male (only the characters that differ from female will be described). Length ranges between 1.45 and 1.55 mm. Carapace longer than wide.

Pseudorostral lobes not meeting in mid-line anteriorly to frontal lobe. Antennal notch as a shallow concavity, anterolareal corner bluntly rounded.

First peraeonite not visible. Peraeonite 2 narrower than in female.

Antenna 1, first peduncular article shorter than other two articles together. Accessory flagellum uni-articulate, wider than long, with a group of sensory setae (Fig. 40D).

Antenna 2 short, not extending beyond the carapace, flagellum highly modified for grasping, with pad-like sensory setae (Fig. 39B-C).

Maxilliped 3 basis less arcuate than in female (Fig. 40E).

Peraeopod 1, basis of endopod stout, outer margin straight (Fig. 40F).

Pleopods present on pleonites 1-4. Endopod with internal process; distally armed with three simple setae (Fig. 40G). Last pair of pleopods with endopod reduced to half length of the exopod. Rami of all four pleopods with long setae.

Uropods with peduncle approximately 1.5 times longer than rami (Fig. 40A-B).

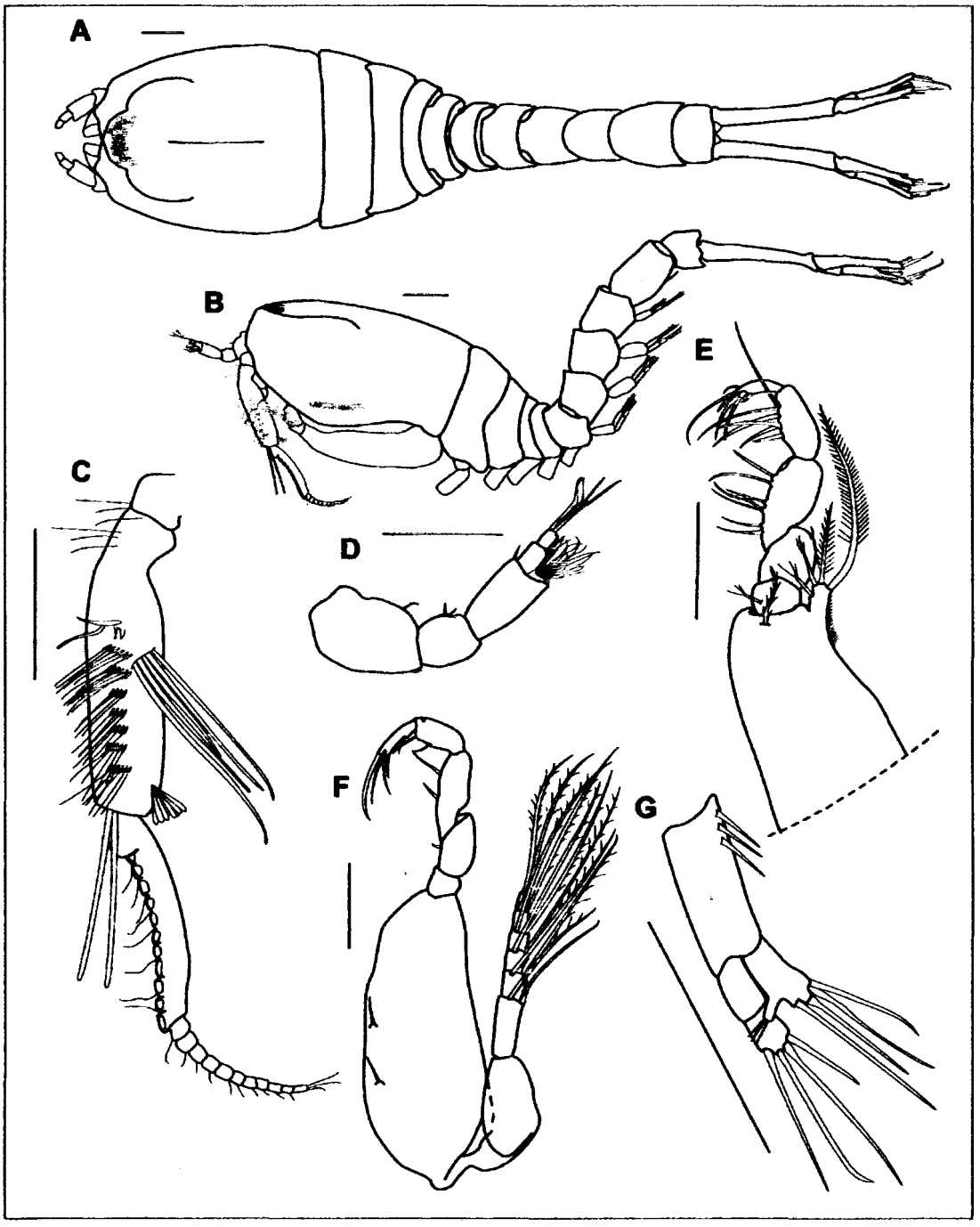


Figure 40. *Austrocuma* sp. mature male. A. Dorsal view of whole body. B. Lateral view of whole body. C. Antenna 2. D. Antenna 1. E. Maxilliped 3. F. Peraeopod 1. G. Pleopod 1. Scale bars represent 0.1 mm.

Remarks

Austrocuma sp. is closely related to *Austrocuma platyceps* by its carapace shape, pigmentation of the eyelobe, exposure of peraeonite 1, width of peraeonite 2 on females, males with short antenna 2, dorso-distal expansion of maxilliped 3 armed with plumose setae, presence of less than five pairs of pleopods, peraeopod 2 with ischium missing and the length ratio of pleonite 6 and peduncle of uropods. The carapace of *Austrocuma* sp. lacks the strong lateral ridges characteristic of the carapace of *Austrocuma platyceps*. The frontal lobe of *Austrocuma* sp. is more extended anteriorly than on *Austrocuma platyceps*, and the armoring of the peduncle of the uropods is absent in *Austrocuma* sp. In addition, while males of *Austrocuma platyceps* have three pairs of pleopods, those of *Austrocuma* sp. have four pairs.

The definition of the genus *Austrocuma* has to change only slightly to accommodate *Austrocuma* sp. since males of this new species have a different number of pleopods, yet both species of the genus have less than five pairs.

The placement of *Austrocuma* within the Family Bodotriidae is supported by the shape of the hepatic diverticula (Fig. 38G), the naviculoid shape of the mandible (Fig. 38 B), the absence of gill plates and supports (Fig. 38E) , the presence of a process on the endopod of the pleopod (Fig. 40G), and the lack of an articulated telson among other features. In addition, the genus *Austrocuma* belongs to the subfamily Bodotriinae since it lacks exopods beyond the first pair of peraeopods and females have a bi-articulated antenna 2.

The genus *Austrocuma* is closely related to the genus *Coricuma* (see Chapter 3). These two genera are distinguished from all other members of the Bodotriinae in that males have an antenna 2 highly modified for grasping and fewer than five pairs of pleopods.

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Appendix A

MORPHOLOGICAL CHARACTERS, CHARACTER STATES, AND DATA MATRICES FOR THE ORDER CUMACEA

Morphological Characters and Character States

1. Antenna 2, main flagellum, male: size of articles (1= short; 2= short to medium; 3= long)
2. Antenna 2, main flagellum, male: fusion of articles 4 and 5 (1=present; 2= absent)
3. Antenna 2, main flagellum, male: sensory setae on anterior margin of article 4 (1= present; 2= absent)
4. Antenna 2, female: maximum number of articles present (character states denoted by number 0-5)
5. Maxilla 1: palp number of bristles (1= none; 2= one; 3= two)
6. Mandible: fusion part (dorsal to pars molaris) (1= extended, naviculoid; 2= not extended, triangular)
7. Maxilliped 1: gill plates (1= present; 2= absent)
8. Maxilliped 2: length of basis relative to distal articles (1= equal or longer; 2= shorter)
9. Maxilliped 3, female: exopod (1= present; 2= absent)
10. Peraeopod 2: ischium (1=present; 2=absent)
11. Peraeopod 1 (P1), female: exopod (1= present; 2= absent)
12. P2 female: exopod (1= present; 2= rudimentary; 3= absent)
13. P3 female: exopod (1= present; 2= rudimentary; 3= absent)
14. P4 female: exopod (1= present; 2= rudimentary; 3= absent)
15. P2 male: exopod (1= present; 2= rudimentary; 3= absent)
16. P3 male: exopod (1= present; 2= rudimentary; 3= absent)
17. P4 male: exopod (1= present; 2= rudimentary; 3= absent)
18. Pleopods, male: maximum number of pairs present (character states denoted by number 0-5)

19. Pleopods, male: process on the endopod (1=present; 2=absent)
20. Pleon: terminal segment (1= telson; 2=pleotelson)
21. Uropod: number of articles on the endopod (number present 1, 2, or 3)
22. Hepatic diverticula: number and shape(1= 4 lobes; 2= 3 lobes; 3= 2 lobes; 4= 1 bifurcated lobe; 5= 1 lobe; 6=none

Table A1. Character states present in eight cumacean families

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Bodotriidae	1/3	1	1/2	4	2/3	1	2	1	1	1/2	1	1/2/3	1/2/3	2/3	1/2/3	1/2/3	1/2/3	5	1/2	2	1/2	4
Ceratocumatidae	1	1	2	5	3	1	2	1	1	1/2	1	1/3	1/3	3	1	1/3	1/3	5	1	1	1	2
Diastylidae	3	1	2	4	3	1/2	1	1/2	1/2	1/2	1/2	1/3	2/3	2/3	1	1/3	1/3	2	2	1	1/2/3	2
Gynodiastylidae	1	2	N/A	3	3	1	2	1	2	1	1/2	1/3	2/3	2/3	1	1/3	1/3	0	N/A	1	1/2/3	2
Lampropidae	1	1	1	5	1/3	1	1	1	1	1	1	1/2/3	2/3	2/3	1	1	1	3	1	1	3	1
Leuconidae	2	1	1/2	3	2	2	2	2	1	1/2	1	1	1/3	3	1	1/3	1/3	2	2	2	1/2	1/4
Nannastacidae	3	1	1	3	2/3	1/2	1/2	2	1/2	1/2	1/2	1/3	1/3	3	1	1/3	1/3	0	N/A	2	1	5/6
Pseudocumatidae	1/2/3	1	2	3	3	1	1	1	1	1	1	1	2	2	1	1	1	2	2	1	1	3

N/A= non-applicable

Table A2. Character states present in the three subfamilies of the Family Bodotriidae

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	20
Bodotriininae	1	1	1	3	2/3	1	2	1	1	1/2	1	3	3	3	3	3	3	5	1/2	2	1/2	4
Mancocuminae	1	1	1/2	4	3	1	2	1	1	1	1	1	2	3	1	1	2	3	1/2	2	2	4
Vaunthompsoniinae	1/3	1	1	3	2/3	1	2	1	1	1/2	1	1/2	1/2/3	2/3	1/2	1/2/3	1/2/3	5	1/2	2	2	4

Appendix B

CHARACTERS AND CHARACTER STATES USED FOR PHYLOGENETIC ANALYSIS OF THE FAMILY BODOTRIIDAE

Coding of characters as unordered or ordered is stated after each character number (U=unordered; O=ordered).

1. (U) Carapace versus pleon length:
    1. equal
    2. shorter
    3. longer
2. (U) Carapace and peraeon versus pleon length:
    1. equal
    2. shorter
    3. longer
3. (U) Carapace versus peraeon length:
    1. equal
    2. shorter
    3. longer
4. (U) Carapace viewed from dorsal:
    1. laterally compressed anteriorly
    2. laterally compressed posteriorly
    3. laterally compressed in the medial portion
    4. not compressed

5. (U) When carapace is laterally compressed anteriorly:
    1. oviform posteriorly
    2. not oviform
6. (U) Carapace shape in dorsal view:
    1. longer than wide
    2. wider than long
    3. as wide as long
7. (U) Median dorsal ridge on carapace:
    1. present
    2. absent
    3. as a dorsal serration
8. (O; absence assumed as plesiomorphic state) Dorso-lateral ridges on carapace:
    1. present
    2. absent
9. (O; absence assumed as plesiomorphic state) Lateral ridges on carapace:
    1. present
    2. absent
10. (O; absence assumed as plesiomorphic state) Anterior transverse ridge on carapace:
    1. present
    2. absent
11. (O; absence assumed as plesiomorphic state) Posterior transverse ridge on carapace:
    1. present
    2. absent
12. (O; absence assumed as plesiomorphic state) Lateral horns on carapace:
    1. present
    2. absent

13. (U) Pseudorostral lappets:

    1. extend beyond frontal lobe

    2. do not extend beyond the frontal lobe

14. (U) When pseudorostral lobes extend beyond frontal lobe they:

    1. meet in midline

    2. extend towards midline but do not meet (or partially meet leaving suture between them)

    3. widely separated

15. (O; not distinct assumed as plesiomorphic) Antennal notch:

    1. not distinct

    2. depression

    3. subacute incision

    4. acute incision

16. (O; not distinct assumed as plesiomorphic) Anterolateral corner of carapace:

    1. bluntly rounded (poorly defined, obtuse greater than 90 degrees)

    2. subacute tooth

    3. acute tooth

17. (U) Branchial siphons:

    1. extend just beyond pseudorostrum

    2. long, extending much beyond pseudorostrum

18. (O; presence assumed as plesiomorphic) Eyelobe:

    1. Present

    2. Absent

19. (O) Frontal lobe size:

    1. 1/5 or less of the carapace length

    2. 1/4 of carapace length

    3. 1/3 of carapace length

    4. half of carapace length

    5. more than half of the carapace length

20. (U) Frontal lobe shape:

    1. as wide as long

    2. wider than long

    3. longer than wide

21. (U) Frontal lobe:

    1. anteriorly linguiform (extended)

    2. somewhat extended

    3. notched anteriorly

    4. not extended

22. (O; presence assumed plesiomorphic) Ocular pigment:

    1. present

    2. absent

23. (O; presence assumed plesiomorphic) Eye lenses:

    1. present

    2. absent

24. (O) Antenna 1, basal article of the peduncle:

    1. geniculated

    2. arcuate

    3. straight

25. (U) Antenna 1, length of basal article of peduncle:

    1. longer than the other two articles together

    2. same length than the other two articles together

    3. shorter than the other two articles together

26. (U) Antenna 1, males with a group of aesthetasc on distal margin of peduncle:

    1. present

    2. absent

27. (O; reductions are assumed to be apomorphic) Antenna1, main flagellum:

    1. uni-articulated

    2. bi-articulated

    3. tri-articulated

    4. with 4 articles

    5. with 5 articles

28. (U) Antenna1, when main flagellum has three or more articles:

    1. third article longer than second

    2. second and third articles same length

    3. second article longer than third

29. (O) Antenna 1, number of aesthetasc in last article of main flagellum (sometimes only males):

    1. three or more

    2. two

    3. one

    4. none

30. (O) Antenna 1, number of aesthetasc on proximal article of main flagellum (sometimes only males):

    1. three or more

    2. two

    3. none

31. (O; reductions are assumed to be apomorphic) Antenna 1, accessory flagellum:

    1. not reduced

    2. reduced

    3. absent

32. (O; reductions are assumed to be apomorphic) Antenna 1, accesory flagellum:

    1. uni-articulated

    2. bi-articulated

33. (O) Antenna 1, brush of at least three setae on accessory flagellum:

    1. present

    2. absent

34. (O) Antenna1, aesthetasc on accessory flagellum:

    1. present

    2. absent

35. (O) Antenna 2 in males:

    1. not reaching the end of the peraeon

    2. reaching to end of peraeon

    3. reaching approximately half length of pleon

    4. reaching almost the end of the pleon

    5. reaching the end of the pleon

36. (U) Antenna 2 in males, modifications for grasping:

    1. on anterior margin

    2. on posterior margin

    3. absent

37. (O; reductions are assumed to be apomorphic) Male antenna 2, sensory setae on anterior margin of article 4:

    1. present

    2. absent

38. (O; reductions are assumed to be apomorphic) Female antenna 2, number of articles:

    1. one

    2. two

    3. three

    4. four

    5. five

39. (U) Mandible, shape dorsal to the pars molaris:

    1. naviculoid

    2. truncated

40. (O) Maxilliped 3, basis shape:

    1. geniculated

    2. arcuate

    3. straight

41. (U) Maxilliped 3, specialization:

    1. not specialized, leg-like

    2. specialized

42. (O) Maxilliped 3, basis shape:

    1. normal

    2. very expanded (with opercular functions)

43. (U) Maxilliped 3, extension of basis:

    1. dorsally over ischium

    2. ventrally over ischium

    3. absent

44. (U) Maxilliped 3, when basis has dorsal extension:

    1. extends beyond the articulation of the ischium and merus

    2. slightly expanded dorsally

45. (U) Maxilliped 3, ischium length relative to merus (without considering extensions):

    1. longer

    2. equal

    3. shorter

46. (U) Maxilliped 3, merus:

    1. without dorsal extension

    2. extended dorsally over carpus

    3. laterally expanded

47. (U) Maxilliped 3, carpus shape:

    1. proximally widened

    2. distally widened

    3. oviform

    4. not widened

48. (O) Maxilliped 3, length of carpus relative to propodus plus dactylus:

    1. longer

    2. equal or shorter

49. (U) Maxilliped 3, propodus shape:

    1. distally widened

    2. proximally widened

    3. oviform

    4. not widened

50. (O) Maxilliped 3, brush setae on propodus:

    1. present

    2. absent

51. (O) Number of peraeonites covered by carapace:

    1. One

    2. Three

52. (O) Visibility of first peraeonite:

    1. well exposed

    2. visible only above lateral midline

    3. not visible

53. (O) Peraeonite 2 and 3:

    1. fused

    2. not fused

54. (U) Peraeonite 2, length:

    1. proportional to other peraeonites

    2. narrow (not wider than the third)

    3. wide

55. (U) Peraeonite 2, ventrolateral expansion:

    1. present

    2. absent

56. (U) Ventrolateral expansion of peraeonite 2:

    1. not overriding other somites

    2. overriding peraeonite 1 and/or carapace

    3. overriding peraeonite 3

    4. overriding peraeonite 1 and/or carapace, and peraeonite 3

57. (U) Peraeonite 3, ventrolateral expansion:

    1. absent

    2. overriding peraeonite 2

    3. overriding peraeonite 4

    4. overriding peraeonites 2 and 4

58. (U) Peraeonite 4, ventrolateral expansion:

    1. absent

    2. overriding peraeonite 3

    3. overriding peraeonite 5

    4. overriding peraeonite 3 and 5

59. (O; presence is assumed plesiomorphic) Peraeopod 1, exopod in females:

    1. present

    2. absent

60. (O; presence is assumed plesiomorphic) Peraeopod 1, exopod in males:

    1. present

    2. absent

61. (O) Peraeopod 1, basis-carpus expanded and ischium-merus rotated for opercularity:

    1. present

    2. absent

62. (O) Peraeopod 1, basis shape:

    1. geniculated

    2. arcuate

    3. straight

63. (O) Peraeopod 1, row of setae on basis:

    1. present

    2. absent

64. (U) Peraeopod 1, extension on the basis:

    1. with dorso-distal extension on totally or partially covering the ischium

    2. ventral opercular extension

    3. ventral slight extension

    4. absent

65. (U) Peraeopod 1, basis inner apical angle:

    1. extended to form a subtriangular tooth-like process

    2. extended to form a convex process

    3. process absent

66. (O) Peraeopod 1, ischium length:

    1. elongate, often longer than merus

    2. normal size (small)

67. (O) Pareaeopod 1, ischium shape:

    1. modified as a rounded lobe with exterior concavity (opercular)

    2. not modified

68. (U) Peraeopod 1, carpus shape:

    1. oviform

    2. not oviform

69. (O) Peraeopod 1, row of setae on carpus:

    1. present

    2. absent

70. (O) Peraeopod 1, length of carpus relative to basis:

    1. shorter

    2. equal

71. (O) Peraeopod 1, presence and number of setae on the propodus:

    1. with a brush (3 or more) of long setae on the propodus (setae longer than carpus)

    2. at least three setae in a linear arrangement along propodus

    3. setae absent

72. (O) Peraeopod 1, length of basis relative to propodus:

    1. longer

    2. equal

73. (O) Peraeopod 1, length of carpus relative to propodus:

    1. longer

    2. equal

    3. shorter

74. (O) Peraeopod 1, at least three terminal setae on dactyl:

    1. present

    2. absent

75. (O; presence is assumed plesiomorphic) Peraeopod 2, exopod in females:

    1. fully developed

    2. reduced

    3. absent

76. (O; presence is assumed plesiomorphic) Peraeopod 2, exopod in males:

    1. fully developed

    2. reduced

    3. absent

77. (O; presence is assumed plesiomorphic) Peraeopod 2, ischium:

    1. present

    2. absent

78. (O) Peraeopod 2, length of dactyl relative to propodus:

    1. shorter

    2. equal

    3. longer

79. (O; presence is assumed plesiomorphic) Peraeopod 3, exopod in females:

    1. fully developed

    2. reduced

    3. absent

80. (O; presence is assumed plesiomorphic) Peraeopod 3, exopod in males:

    1. fully developed

    2. reduced

    3. absent

81. (O; presence is assumed plesiomorphic) Peraeopod 3, ischium:

    1. present

    2. absent

82. (O) Peraeopod 3, merus length:

    1. normal (much smaller than basis)

    2. enlarged (almost as large as basis)

83. (O) Peraeopod 3, modification of articulation of carpus and propodus:

    1. normal, articulated at the distal end of the carpus

    2. articulated on side wall of carpus

84. (O; presence is assumed plesiomorphic) Peraeopod 4, exopod in females:

    1. fully developed

    2. reduced

    3. absent

85. (O; presence is assumed plesiomorphic) Peraeopod 4, exopod in males:

    1. fully developed

    2. reduced

    3. absent

86. (O; presence is assumed plesiomorphic) Peraeopod 4, ischium:

    1. present

    2. absent

87. (O; presence is assumed plesiomorphic) Peraeopod 5, ischium:

    1. present

    2. absent

88. (O; absence is assumed plesiomorphic) Articular pegs on pleon:

    1. present

    2. absent

89. (U) Size of pleonite 5 relative to pleonite 6:

    1. longer

    2. as long as or shorter

90. (U) Pleonite 6, shape:

    1. longer than wide

    2. as wide as long

    3. wider than long

91. (O) Length of pleonite 6 relative to peduncle of uropods:

    1. longer

    2. equal

    3. shorter

92. (O) Setae on posterior edge of pleonite 6:

    1. present

    2. absent

93. (U) Pleonite 6, when setae present on posterior edge:

    1. two setae close to midline

    2. more than two setae at posterior end

94. (U) Pleonite 6:

    1. not extended past the insertion of the uropods

    2. extended past the insertion of the uropods

95. (U) Pleonite 6, amount extended between uropods:

    1. slightly extended

    2. well extended

    3. strongly extended

96. (U) Pleonite 6, amount extended between uropods:

    1. whole width of terminal end

    2. middle portion of distal end

97. (U) Pleonite 6, when whole terminal end extended:

    1. ends in a point

    2. ends in a line

    3. ends concave

    4. ends in a rounded apex

98. (U) Pleonite 6, width of the extension when only middle portion of terminal end extended:

    1. wide

    2. narrow

99. (U) Pleonite 6, when only middle portion of terminal end extended:

    1. ends in a point

    2. ends in a line

    3. ends concave

    4. ends rounded apex

100. (U) Anal plates, extension beyond posterior margin of pleonite 6:

    1. present

    2. absent

101. (U) Anal plates, setae on posterior edge:

    1. present

    2. absent

102. (O; reductions are assumed apomorphic) Number of articles of uropod endopod:

    1. one

    2. two

    3. three

103. (U) Length of articles of uropod endopod:

1. articles approximately equal
2. proximal article longer
3. proximal article shorter

104. (U) Length of articles of uropod exopod:

1. proximal article shorter
2. proximal article longer
3. articles approximately equal

105. (O) Uropods, length of peduncle relative to rami:

1. much longer than rami (more than 50% longer)
2. longer
3. equal
4. slightly shorter than exopods only
5. shorter

106. (U) Uropods,length of rami with respect to each other:

1. equal
2. endopod longer
3. endopod shorter

107. (O; presence is assumed plesiomorphic) Uropod, terminal setae on endopod:

1. present
2. absent

108. (O; presence is assumed plesiomorphic) Uropod, terminal setae on exopod:

1. present
2. absent

109. (O; presence is assumed plesiomorphic) Males, pleopods on pleonite 1:

1. present
2. absent

110. (O; presence is assumed plesiomorphic) Males, pleopods on pleonite 2:

1. present
2. reduced
3. absent

111. (O; presence is assumed plesiomorphic) Males, pleopods on pleonite 3:

1. present
2. reduced
3. absent

112. (O; presence is assumed plesiomorphic) Males, pleopods on pleonite 4:

1. present
2. absent

113. (O; presence is assumed plesiomorphic) Males, pleopods on pleonite 5:

1. present
2. reduced
3. absent

114. (O) Males, process on pleopodal endopod:

1. well developed
2. reduced
3. absent

Appendix C

FIGURES OF MORPHOLOGICAL CHARACETRS FOR THE FAMILY BODOTRIINAE

All characters used for phylogenetic analysis (Appendix 2) are illustrated here. Within boxes are figures of general anatomy useful for understanding the characaters and their states.

Figure C1. External anatomy of Cumacea

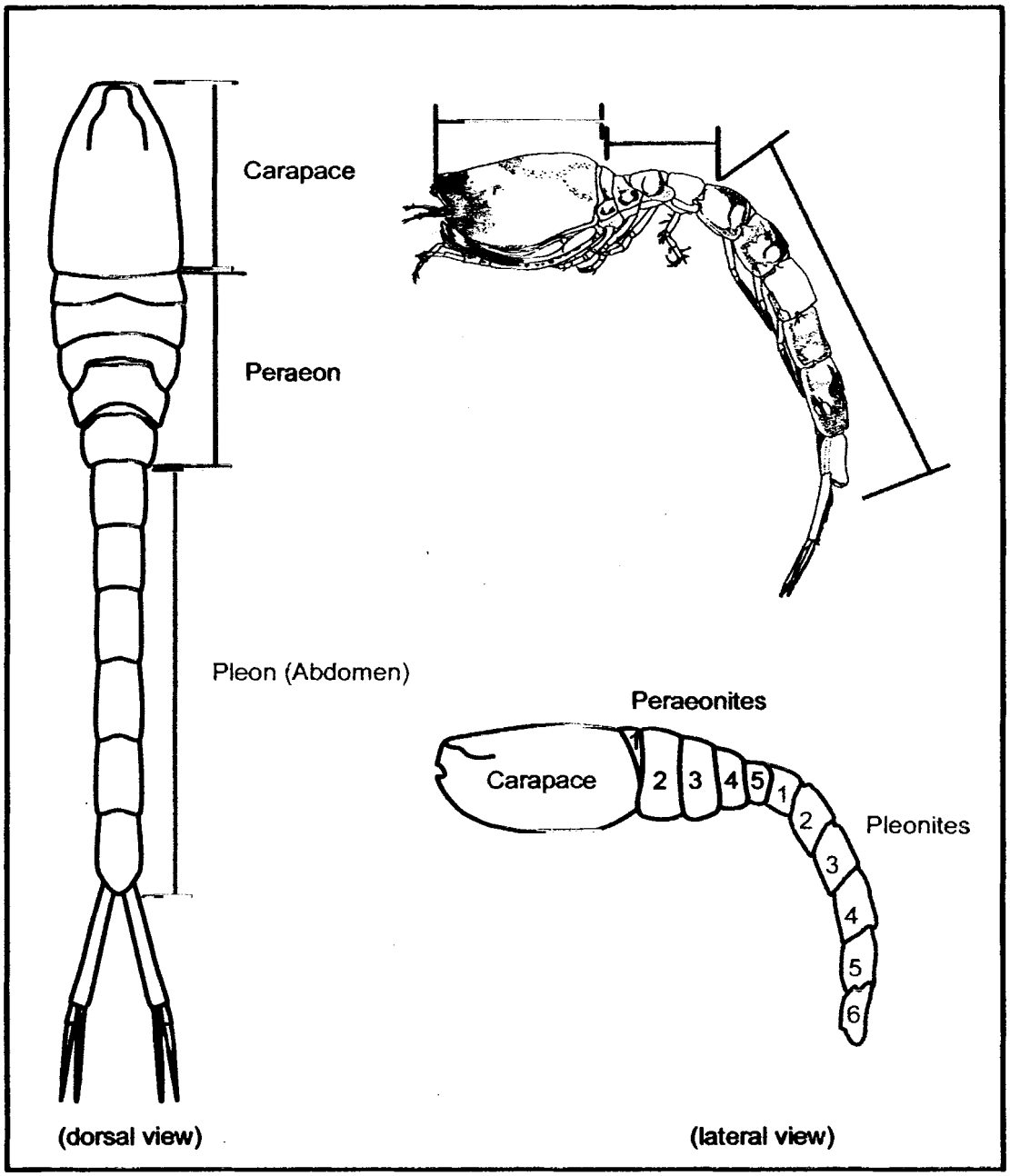


Figure C2. Body - carapace and pleon length

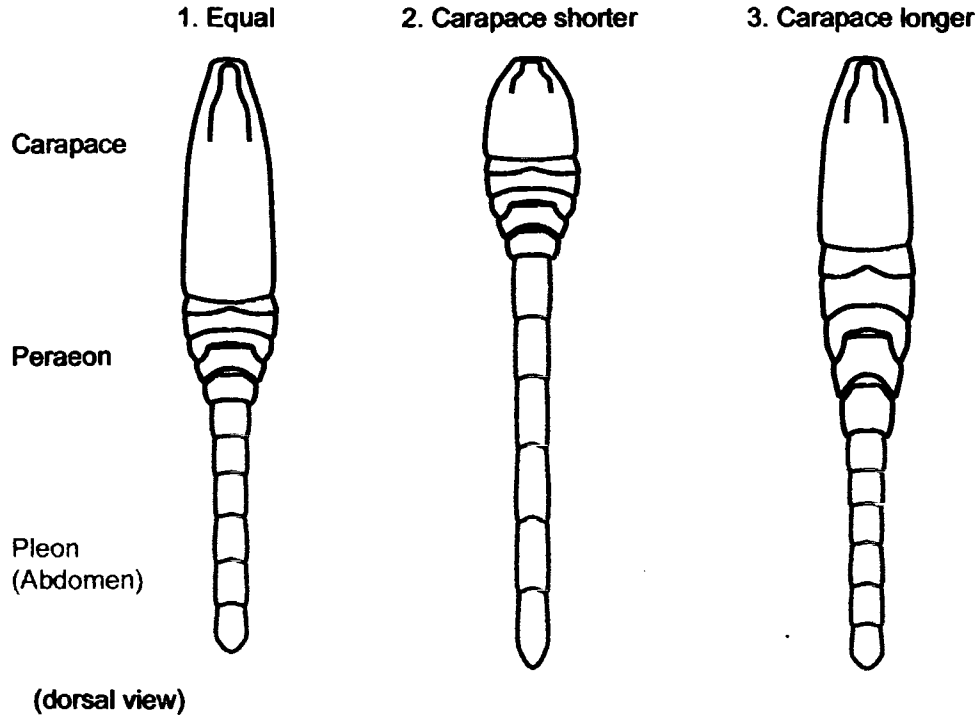


Figure C3. Body - carapace-peraeon versus pleon length

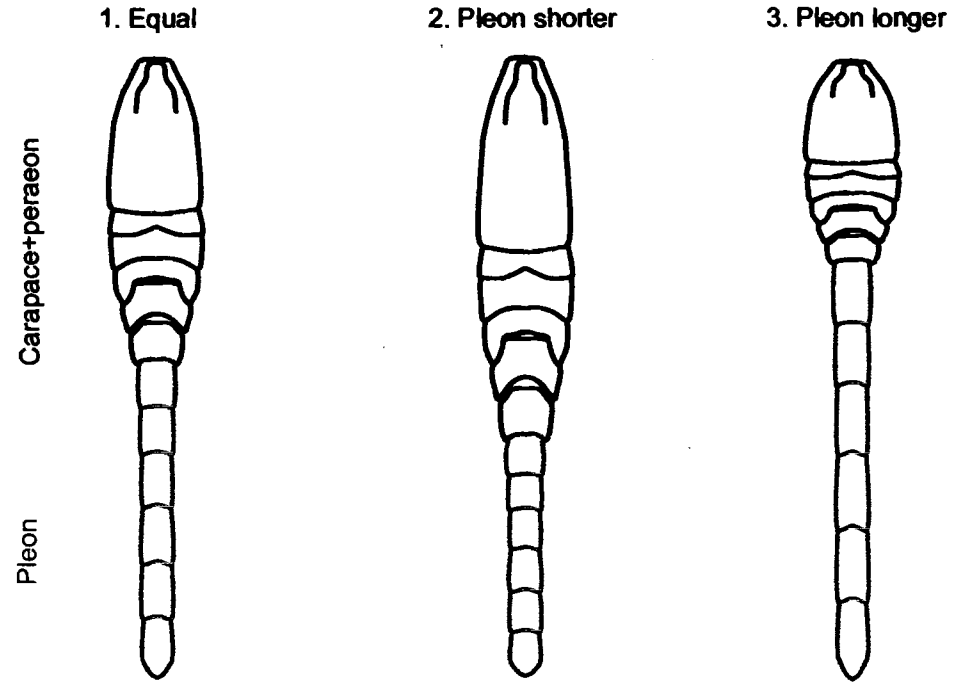


Figure C4. Body - carapace and peraeon length

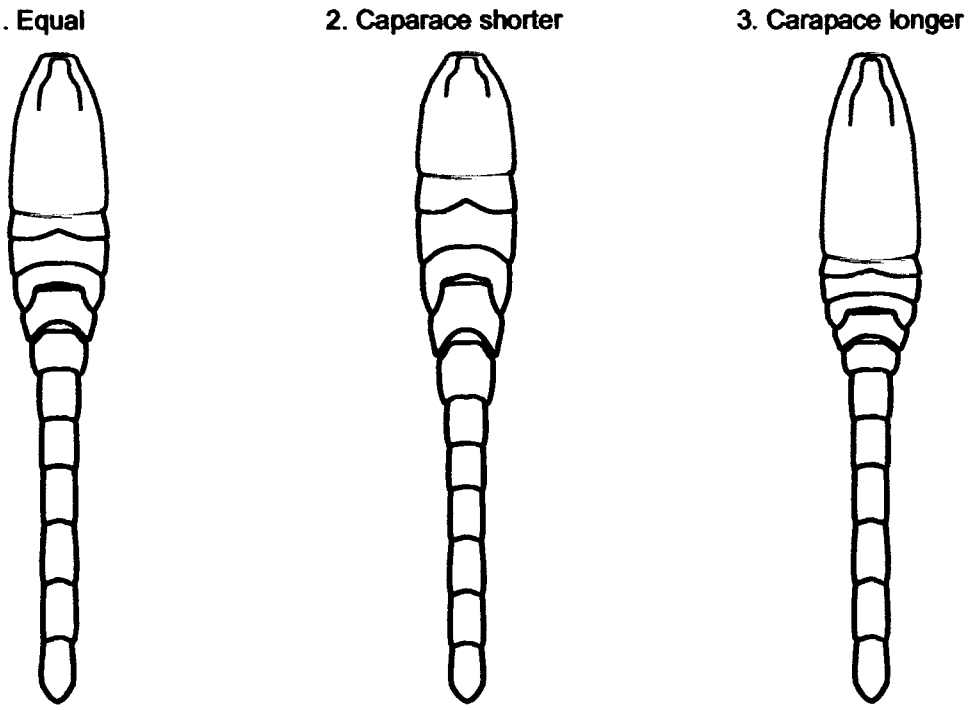


Figure C5. Carapace - lateral compression

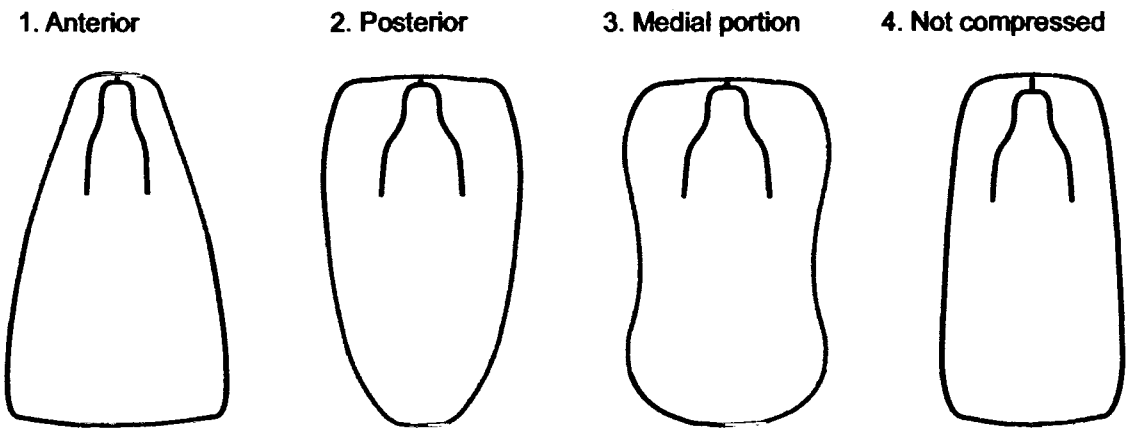


Figure C6. Carapace - shape when laterally compressed anteriorly

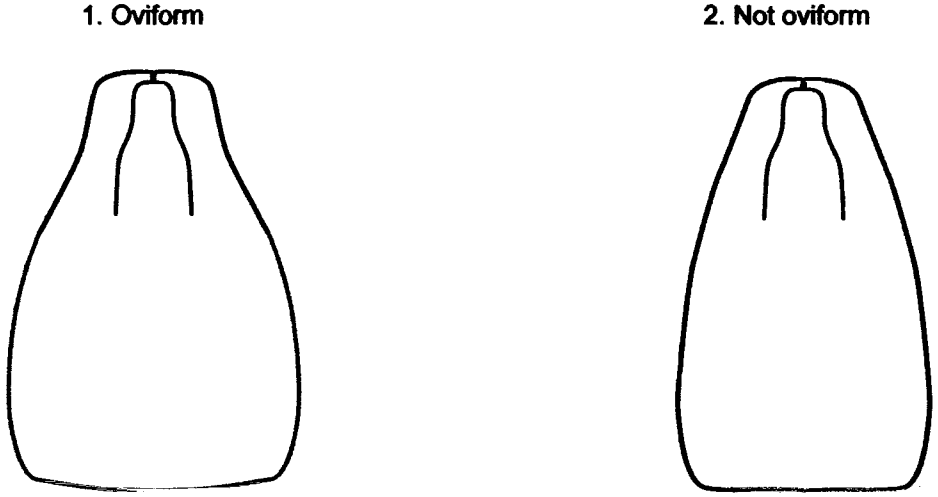


Figure C7. Carapace - shape

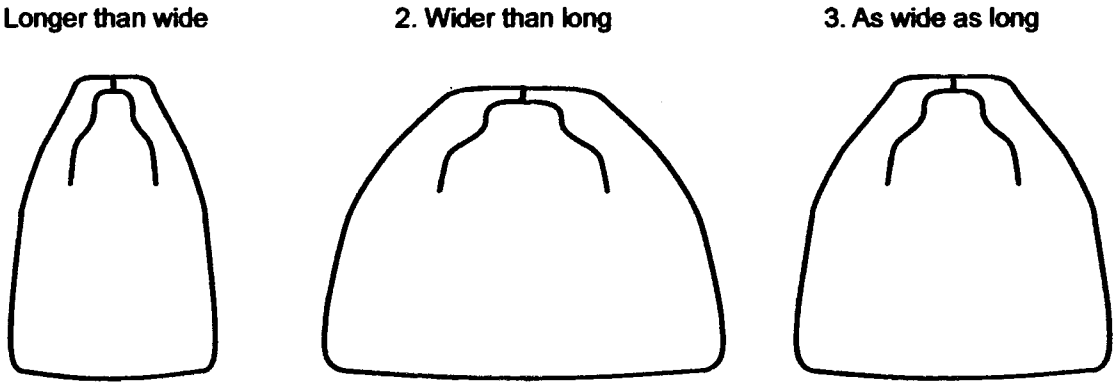


Figure C8. Carapace - Ridges

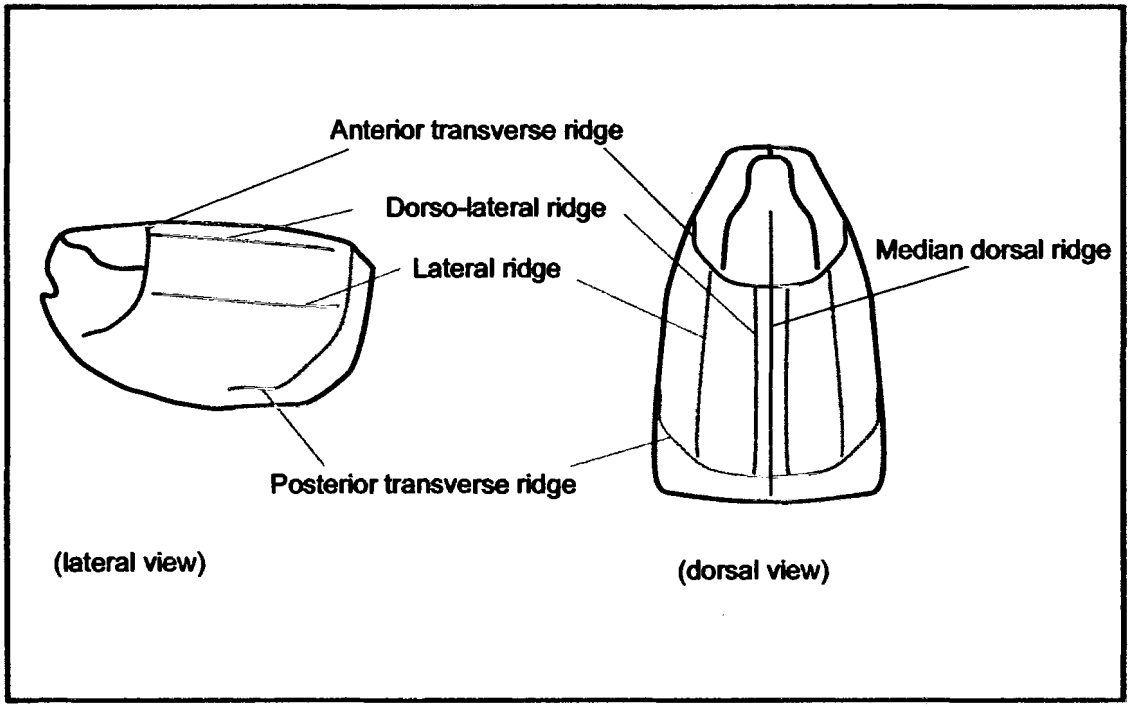


Figure C9. Carapace - median dorsal ridges

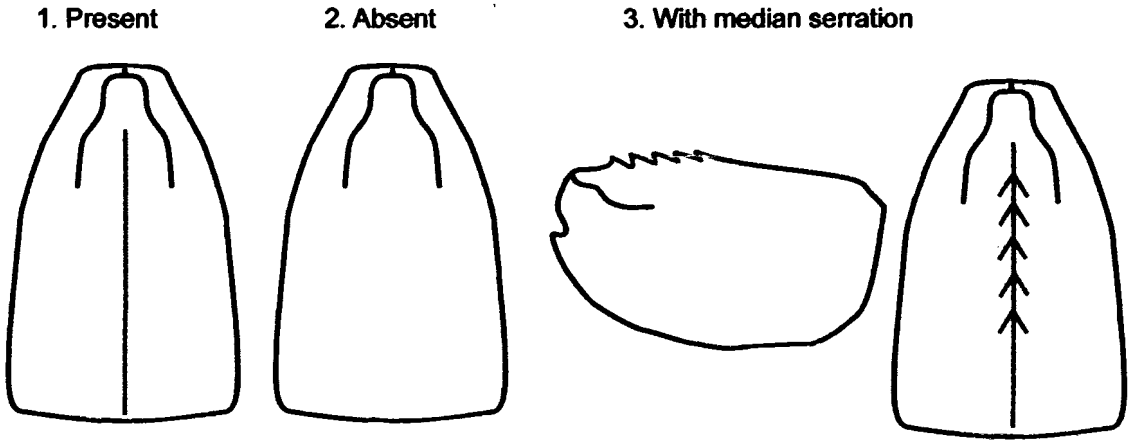
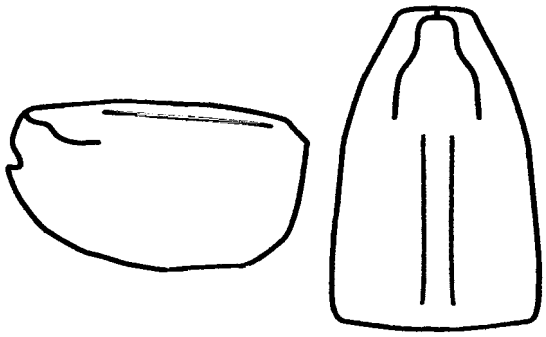


Figure C10. Carapace - dorso-lateral ridges

1. Present



2. Absent

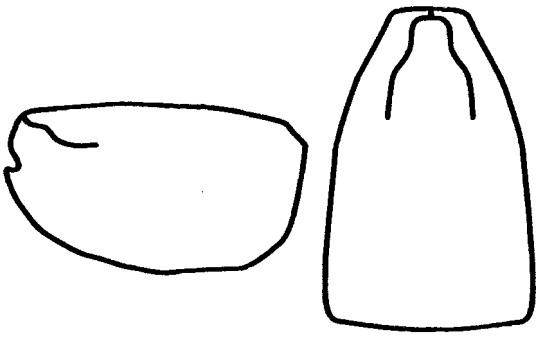
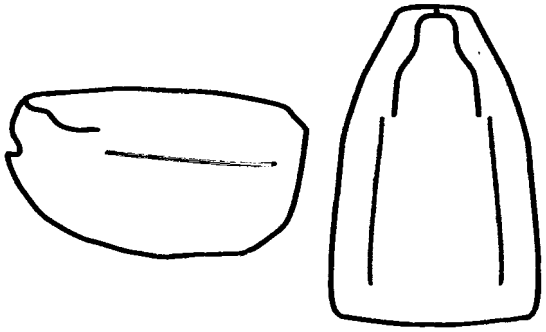


Figure C11. Carapace - lateral ridges

1. Present



2. Absent

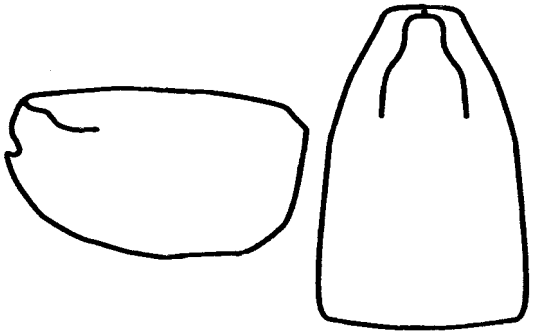


Figure C12. Carapace - anterior transverse ridge

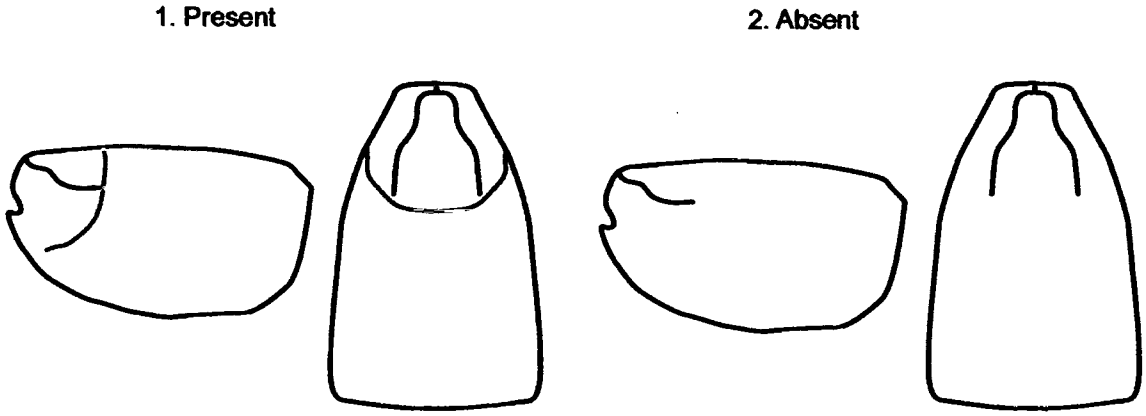


Figure C13. Carapace - posterior transverse ridge

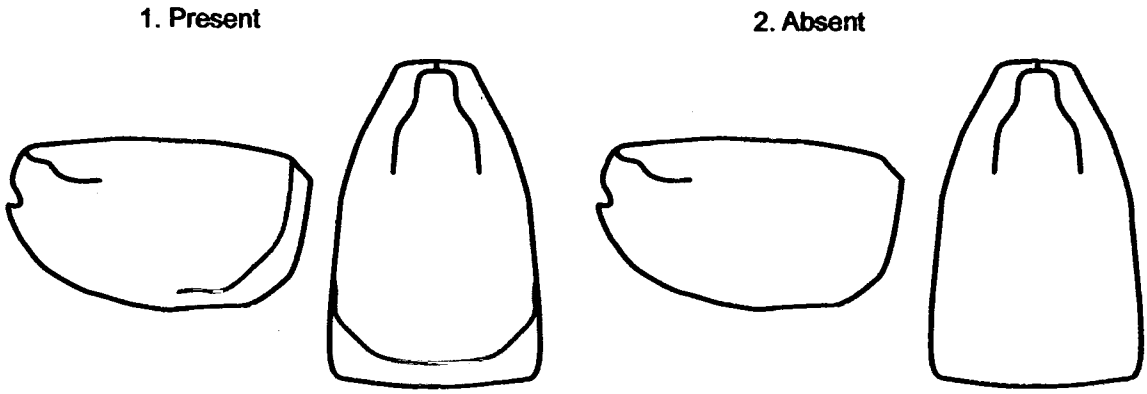


Figure C14. Carapace - lateral horns

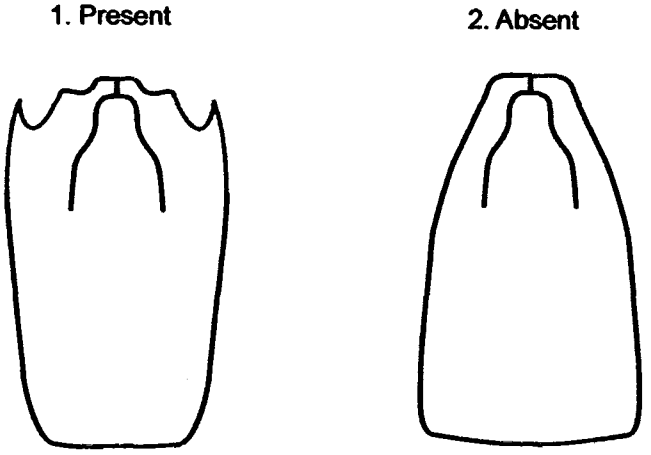


Figure C15. Carapace - extension of pseudorostral lappets with respect to ocular lobe

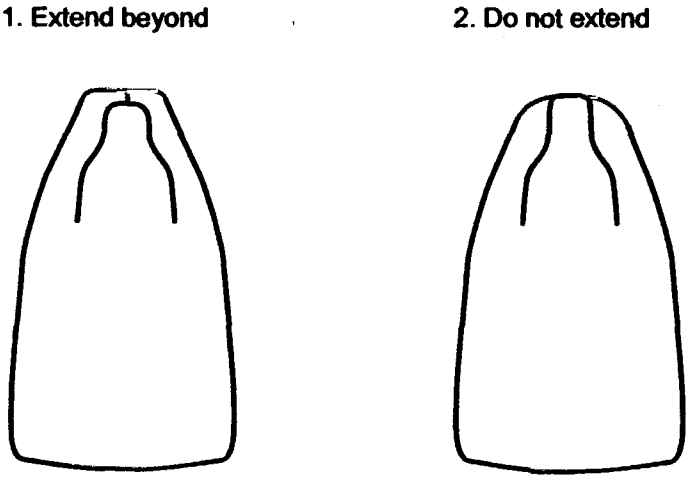


Figure C16. Carapace - projection of pseudorostral lappets beyond frontal lobe

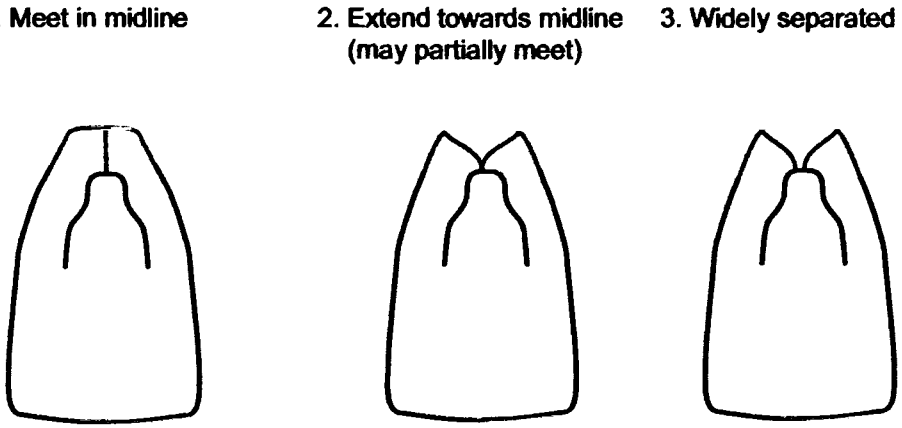


Figure C17. Carapace - antennal notch

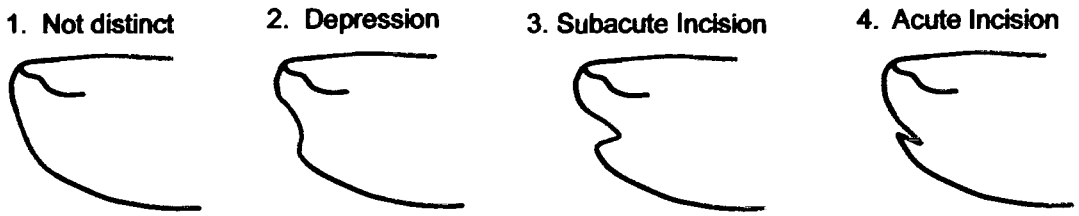


Figure C18. Carapace - anterolateral corner

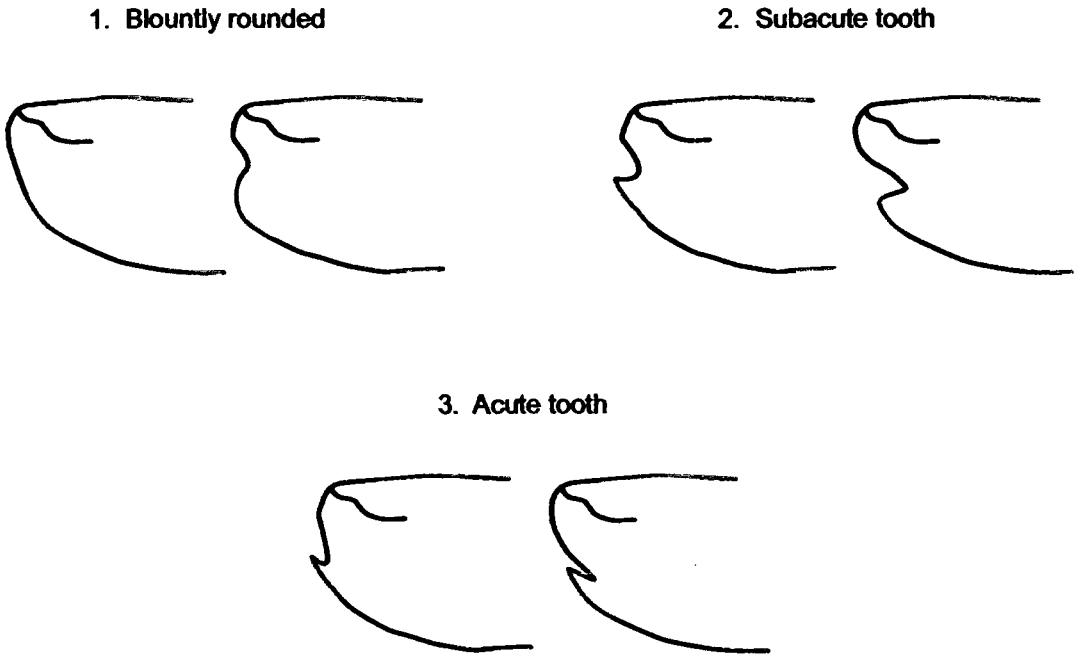


Figure C19. Carapace - branchial siphons

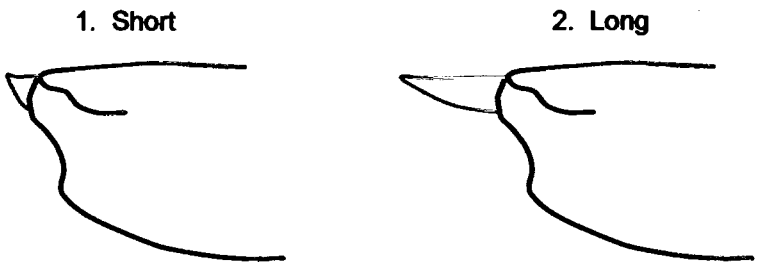


Figure C20. Carapace - eyelobe presence or absence

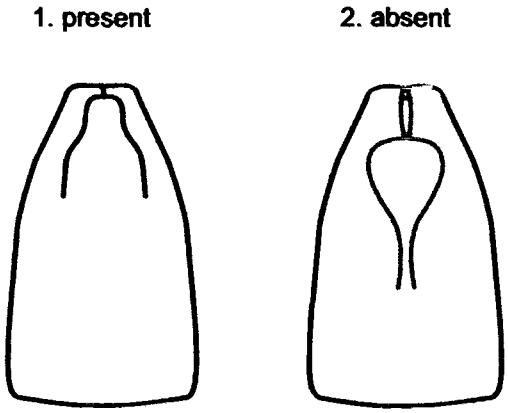


Figure C21. Carapace - frontal lobe length relative to carapace

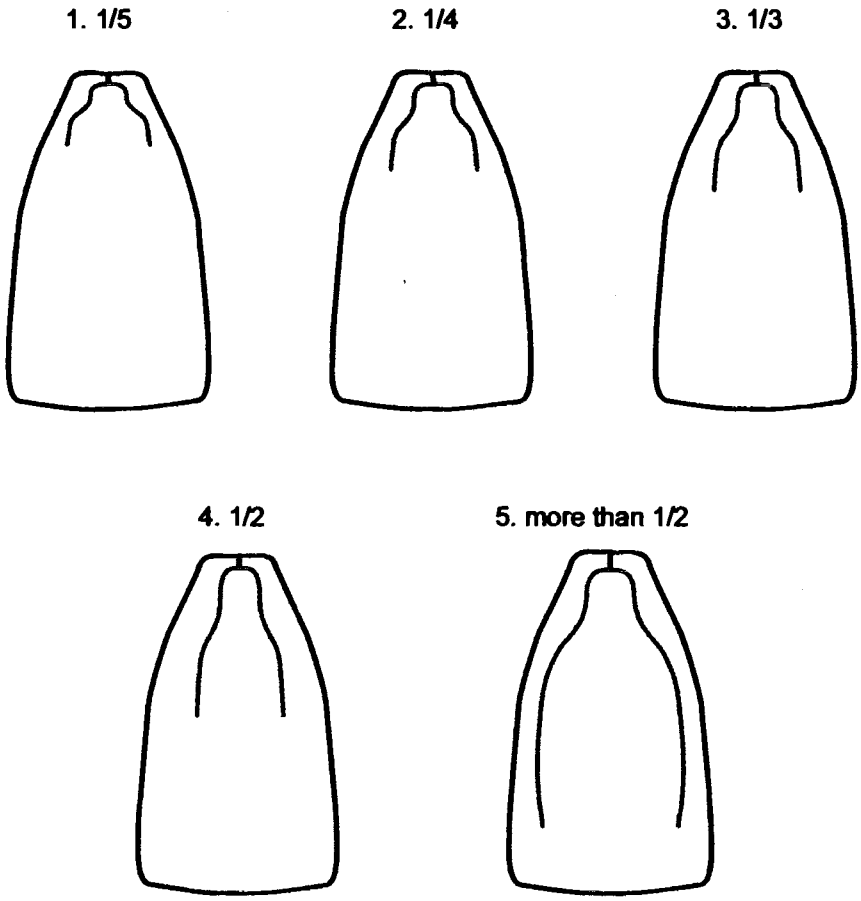


Figure C22. Carapace - frontal lobe shape

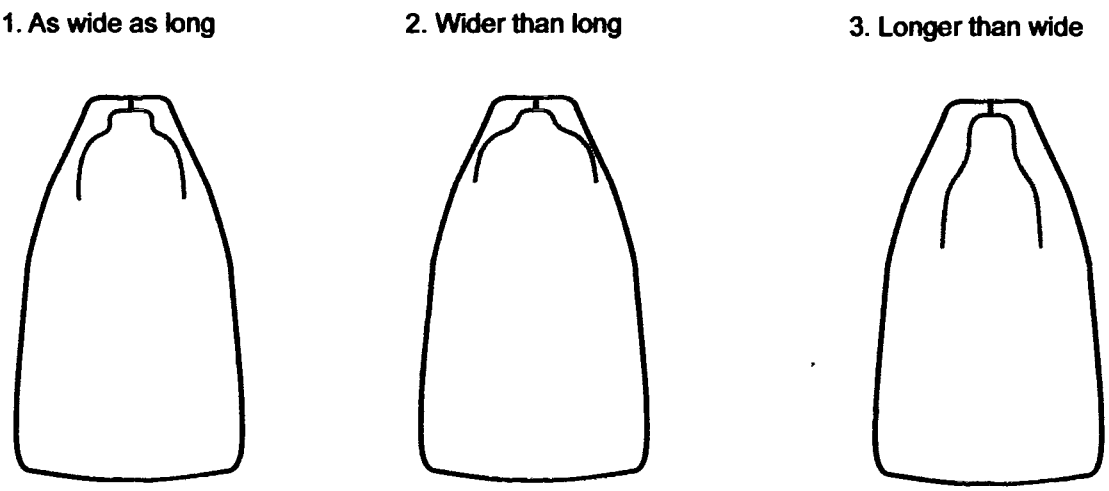


Figure C23. Carapace - frontal lobe extension

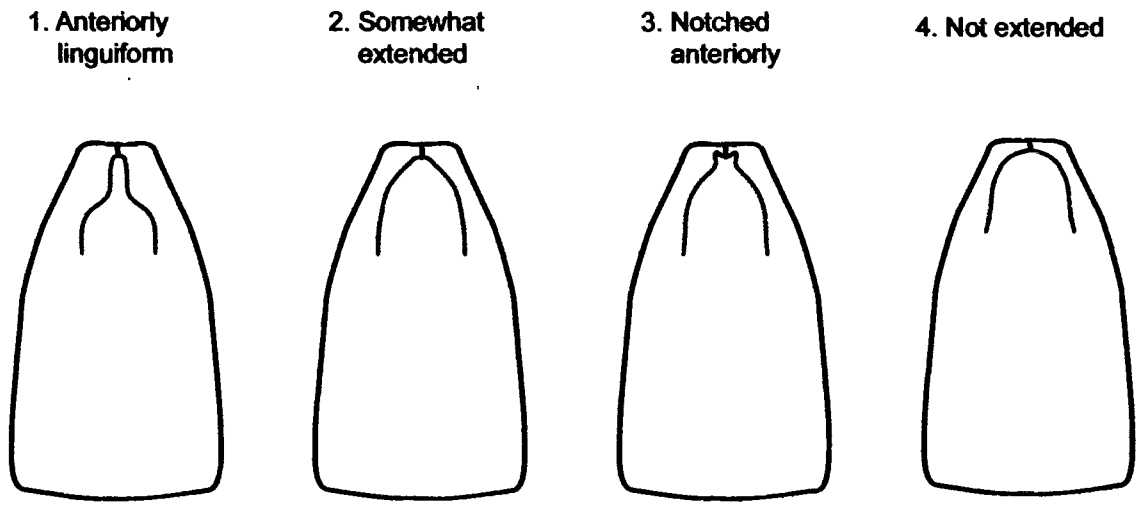
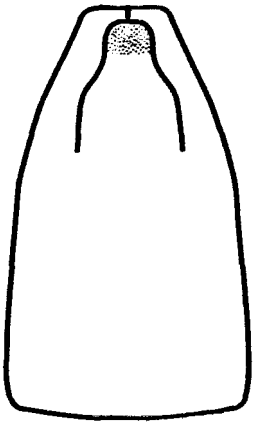


Figure C24. Carapace - frontal lobe: ocular pigment

1. Present
(distribution may vary)



2. Absent

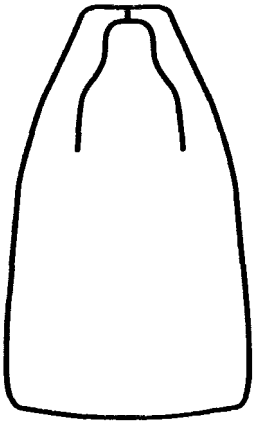
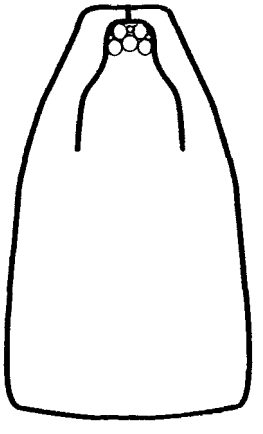


Figure C25. Carapace - frontal lobe: eye lenses

1. Present (one or more)
(distribution may vary)



2. Absent

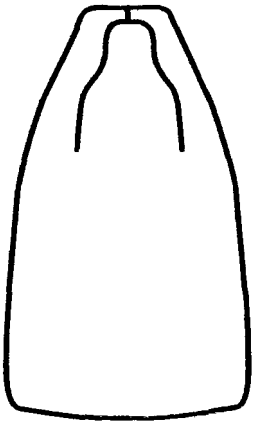


Figure C26. Structure of antenna 1

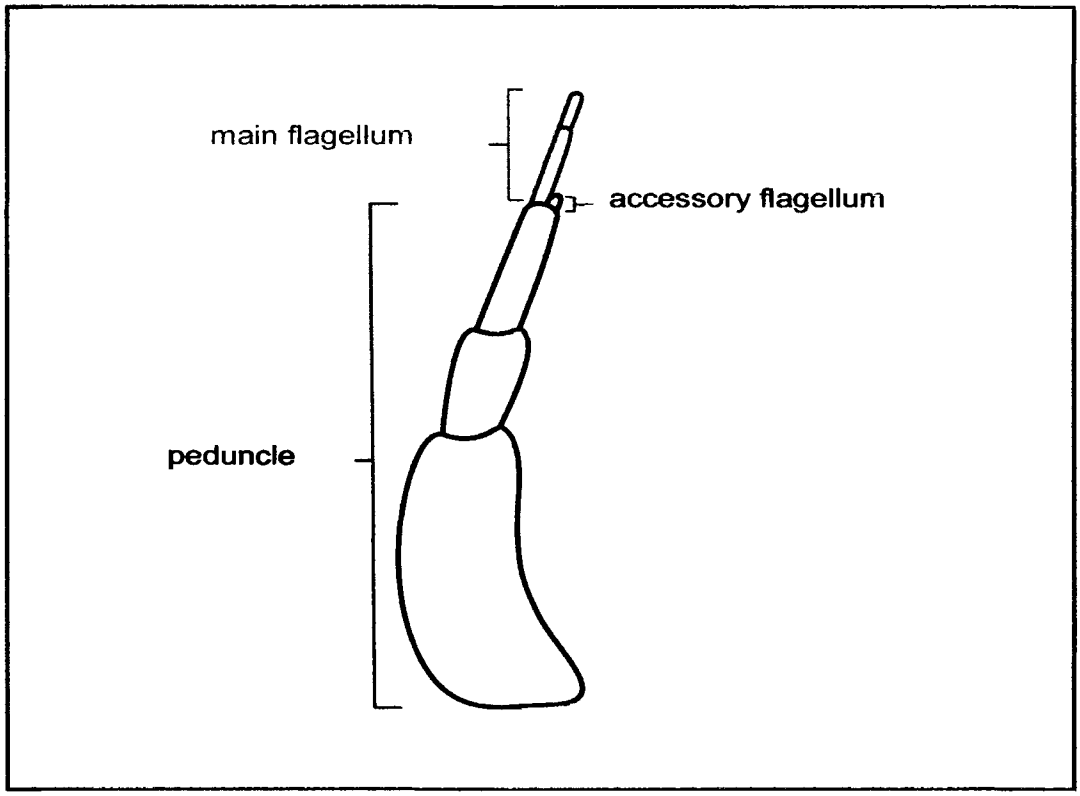
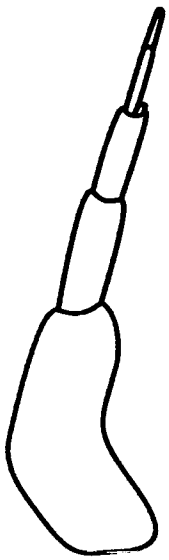


Figure C27. Antenna 1- peduncle geniculation

1. Geniculated



2. Arcuate

3. Straight

Figure C28. Antenna 1 - peduncle - length of basal article relative to other two articles

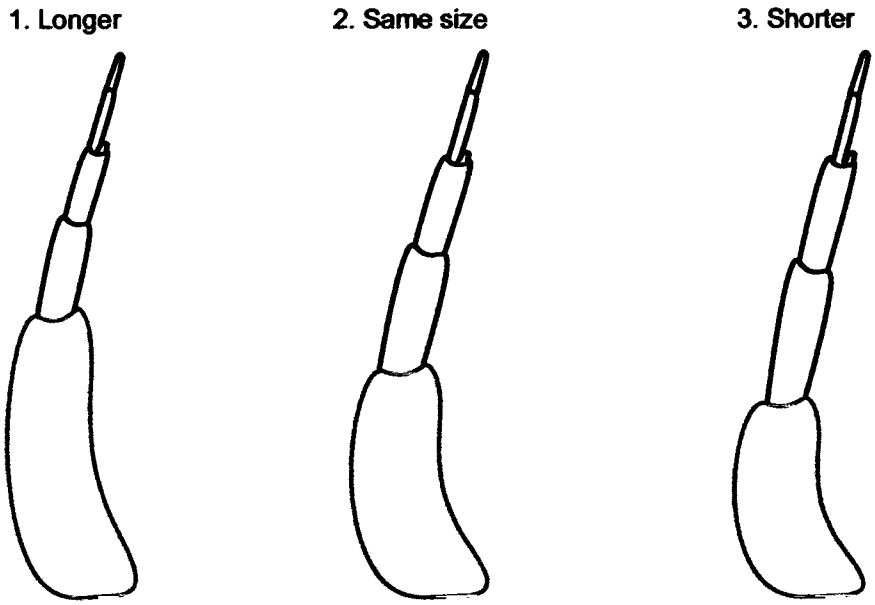


Figure C29. Antenna 1, male - peduncle - group of aesthetasc on distal article

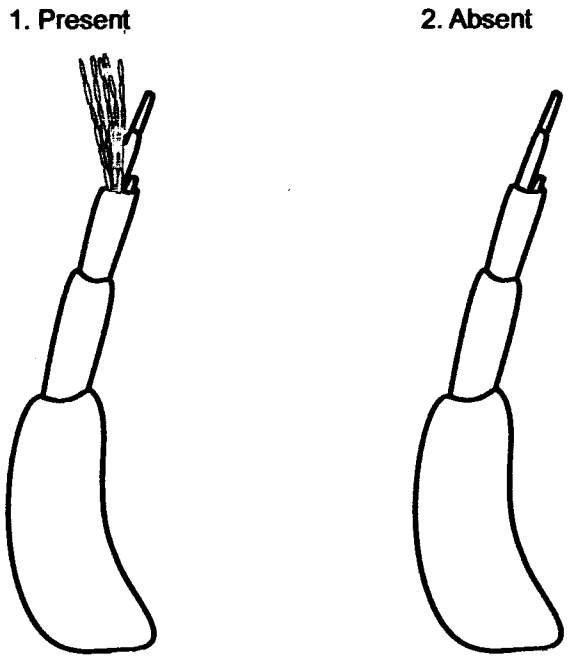


Figure C30. Antenna 1 - main flagellum

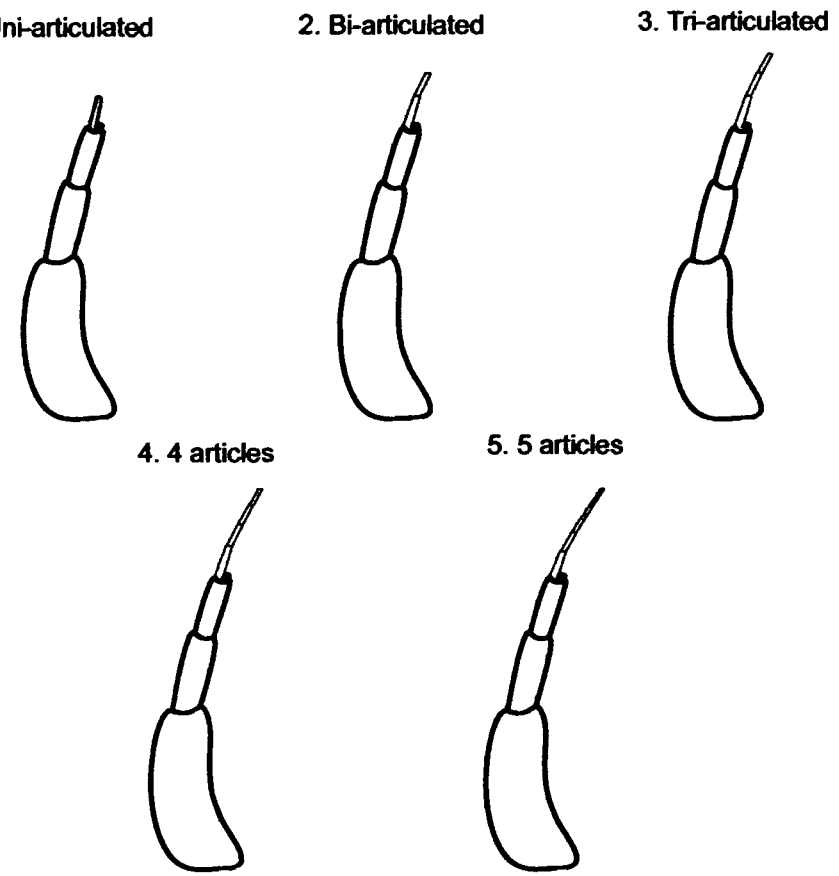


Figure C31. Antenna 1 - main flagellum - length of second and third articles

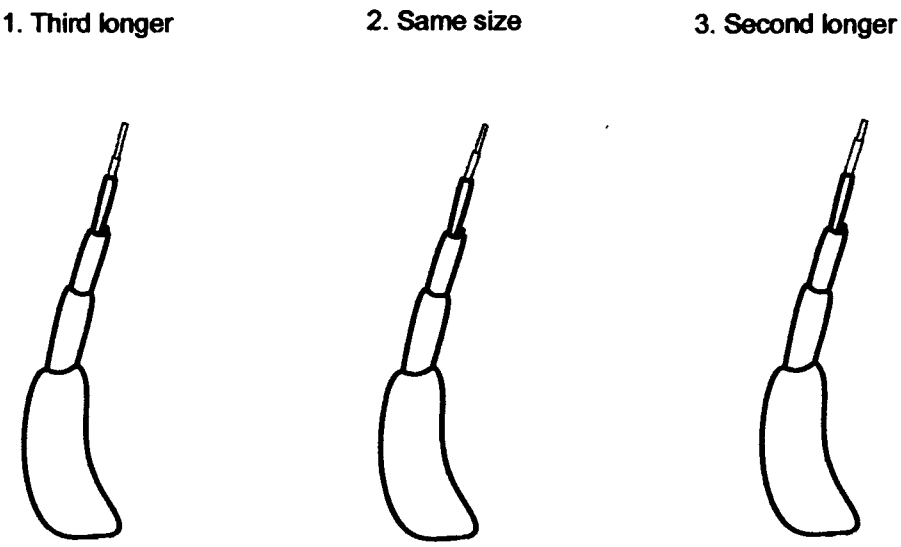


Figure C32. Antenna 1 - main flagellum - number of aesthetasc on last article

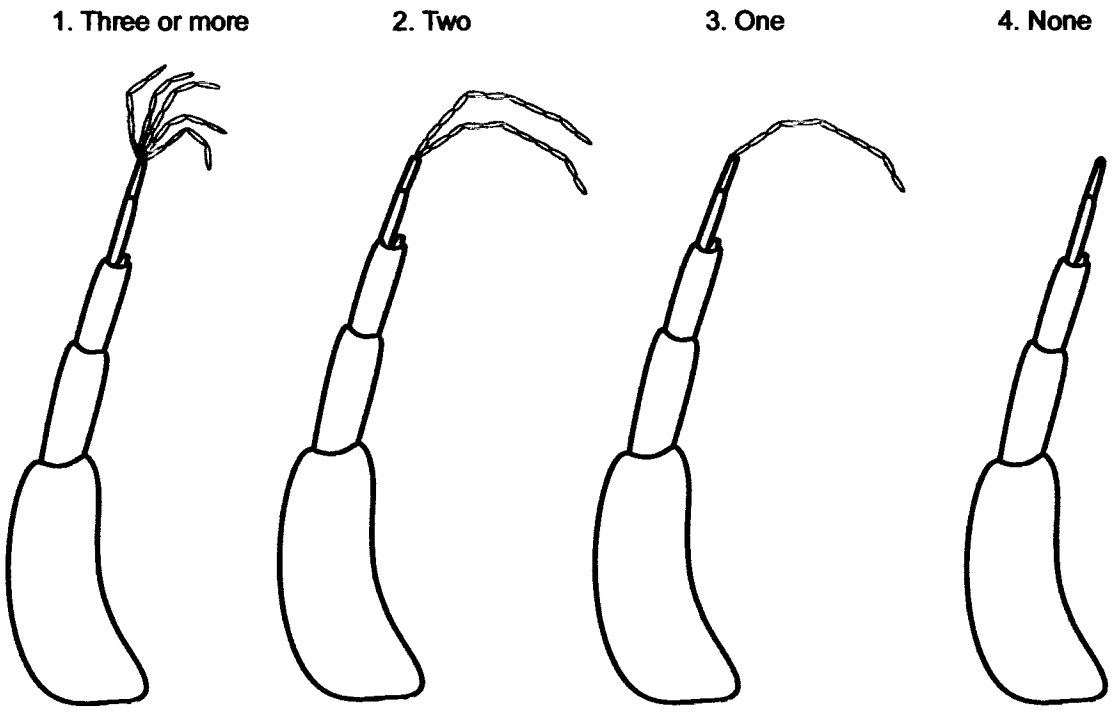


Figure C33. Antenna 1 - main flagellum - aesthetasc on proximal article.

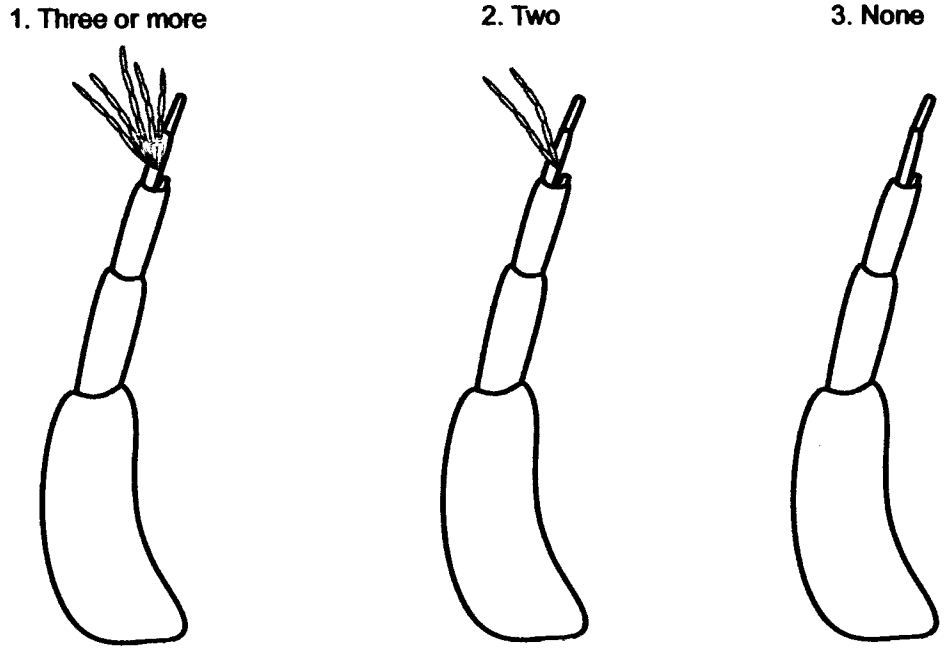


Figure C34. Antenna 1 - accessory flagellum - size

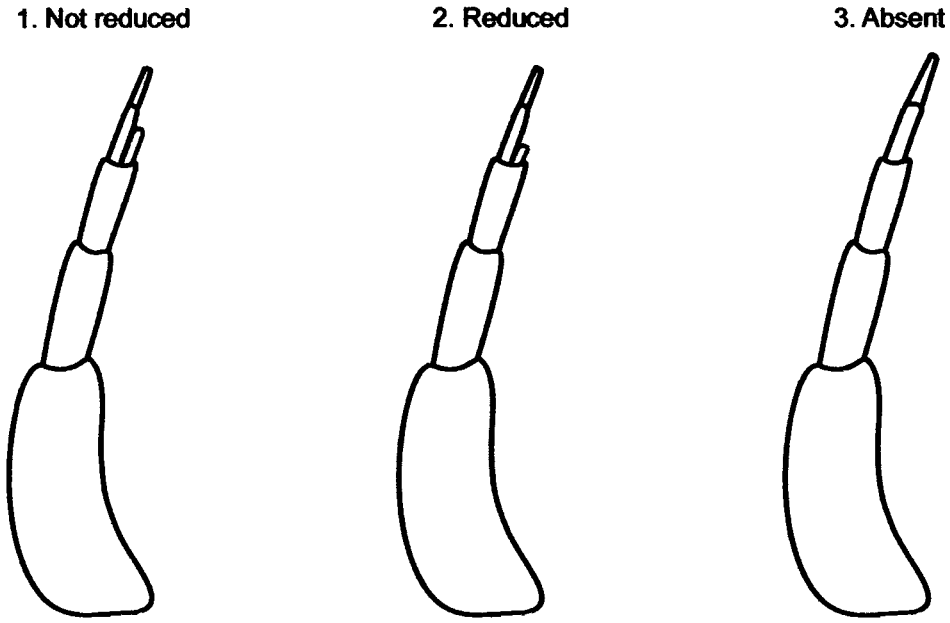


Figure C35. Antenna 1 - accessory flagellum - number of articles

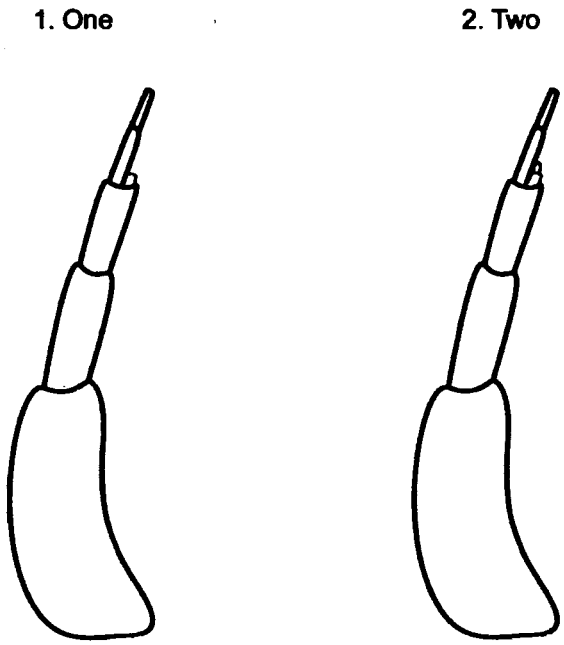
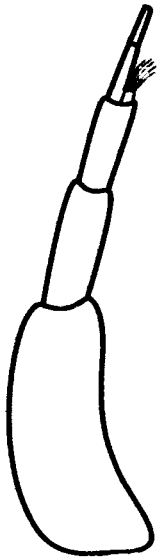


Figure C36. Antenna 1 - accessory flagellum - brush of setae

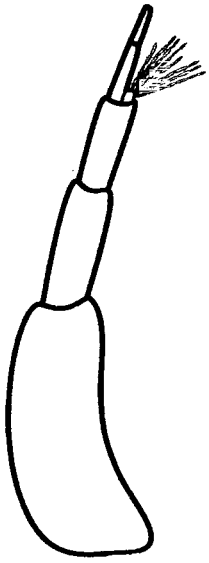
1. Present



2. Absent

Figure C37. Antenna 1 - accessory flagellum - aesthetasc

1. Present



2. Absent

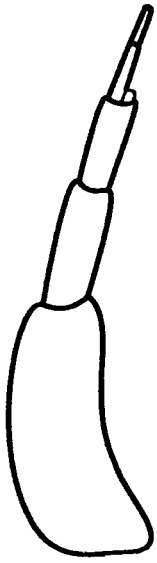


Figure C38. Male antenna 2

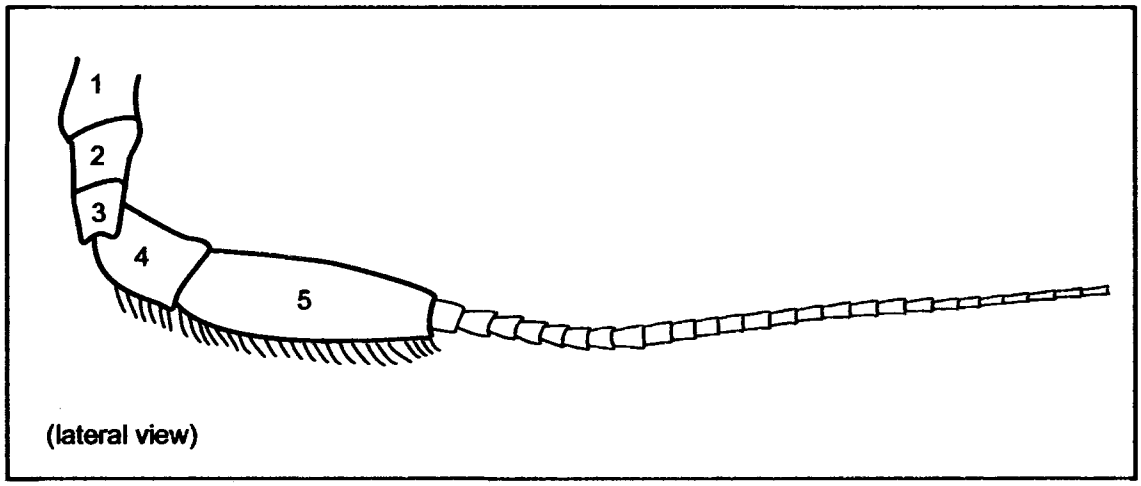


Figure C39. Antenna 2, males - length

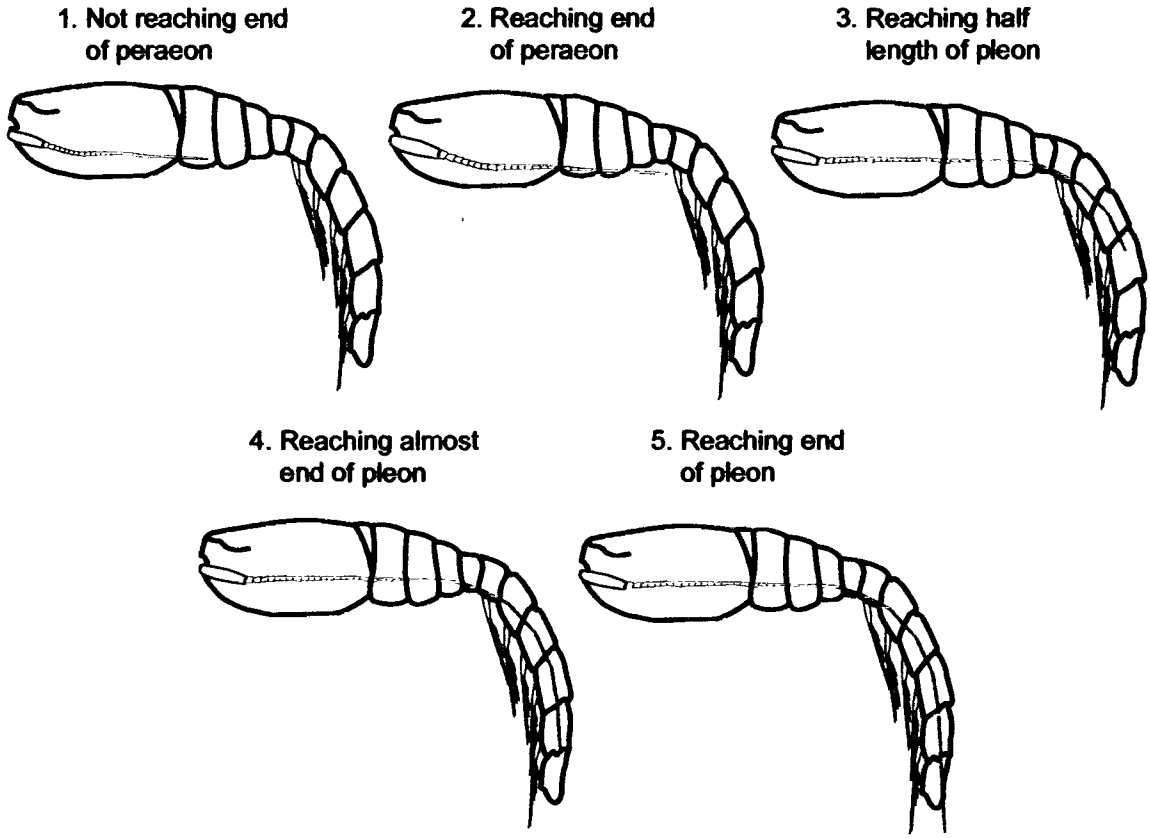


Figure C40. Antenna2, males - modifications

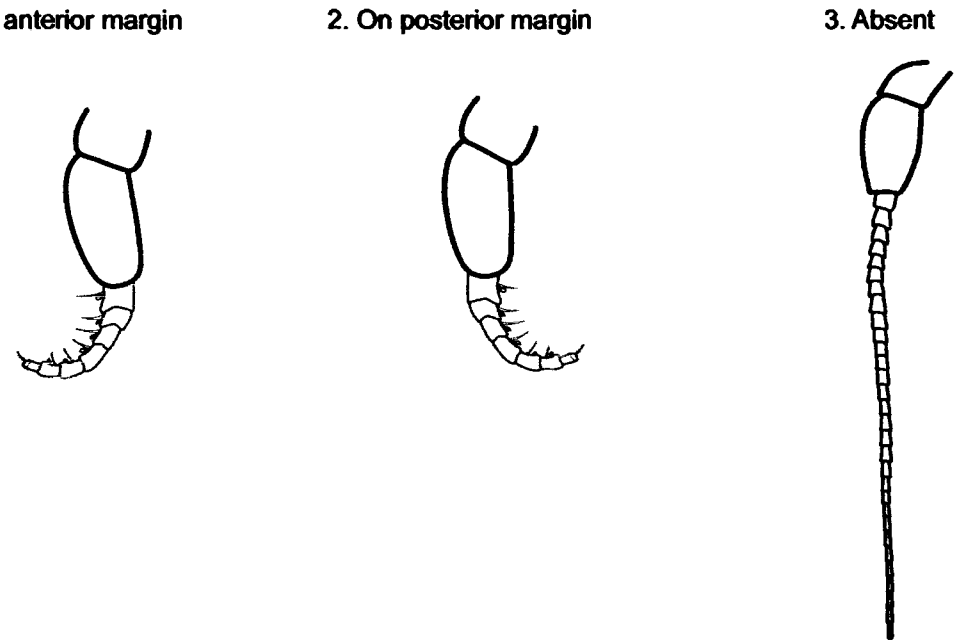


Figure C41. Antenna 2, males - sensory setae on anterior margin of article 4

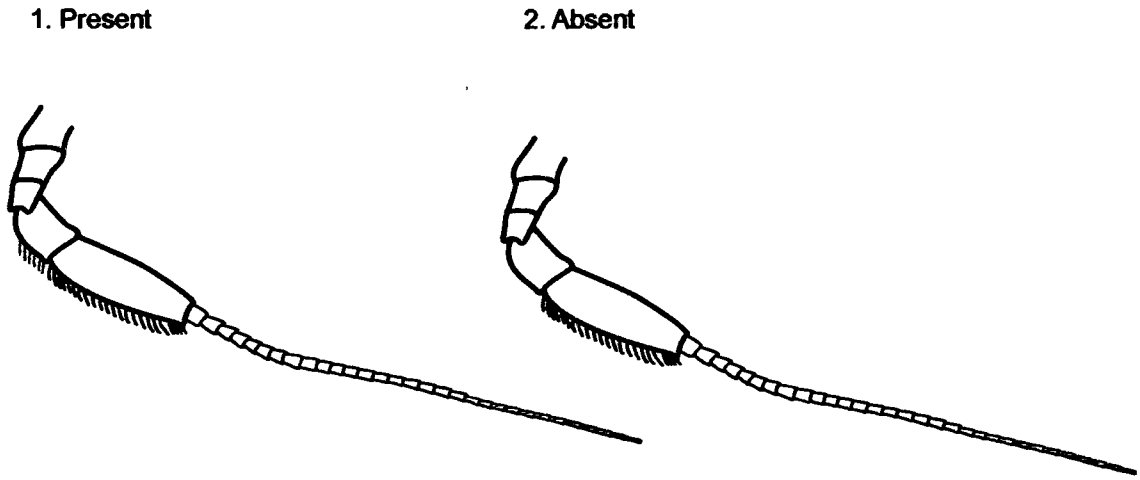


Figure C42. Antenna 2, females - number of articles

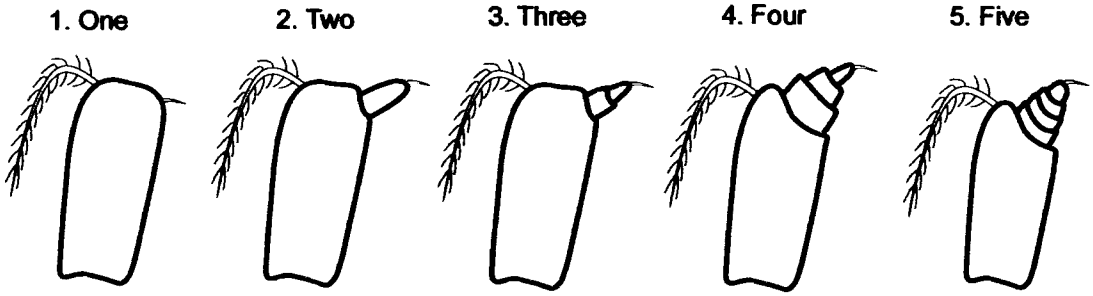


Figure C43. Mandible - shape dorsal to the pars molaris

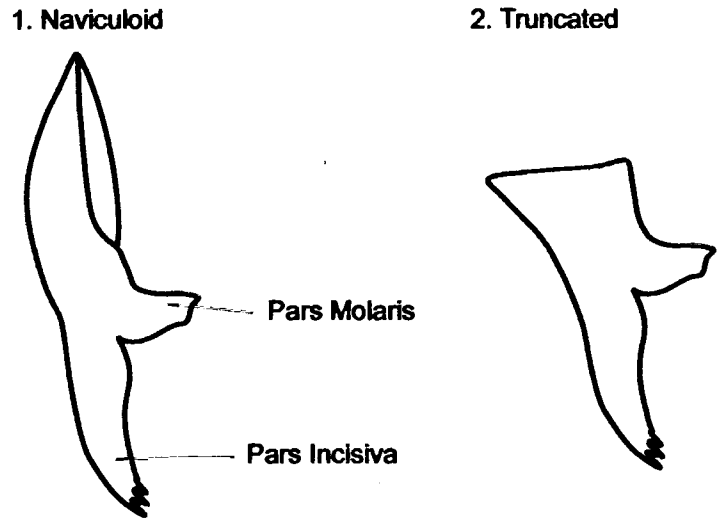


Figure C44. General structure of thoracopods

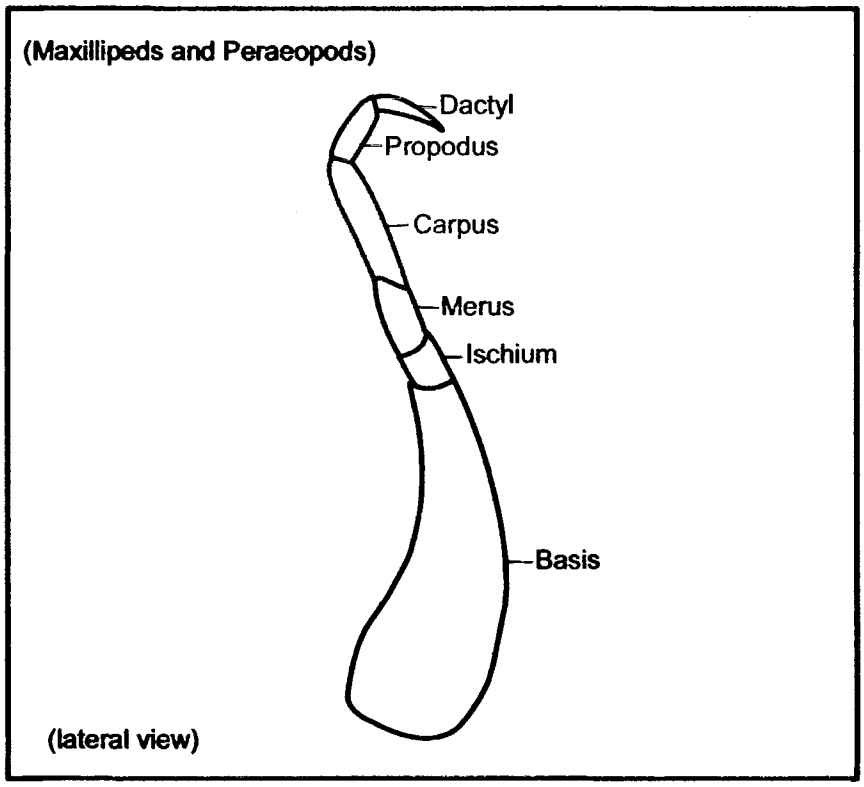


Figure C45. Maxilliped 3 - basis shape

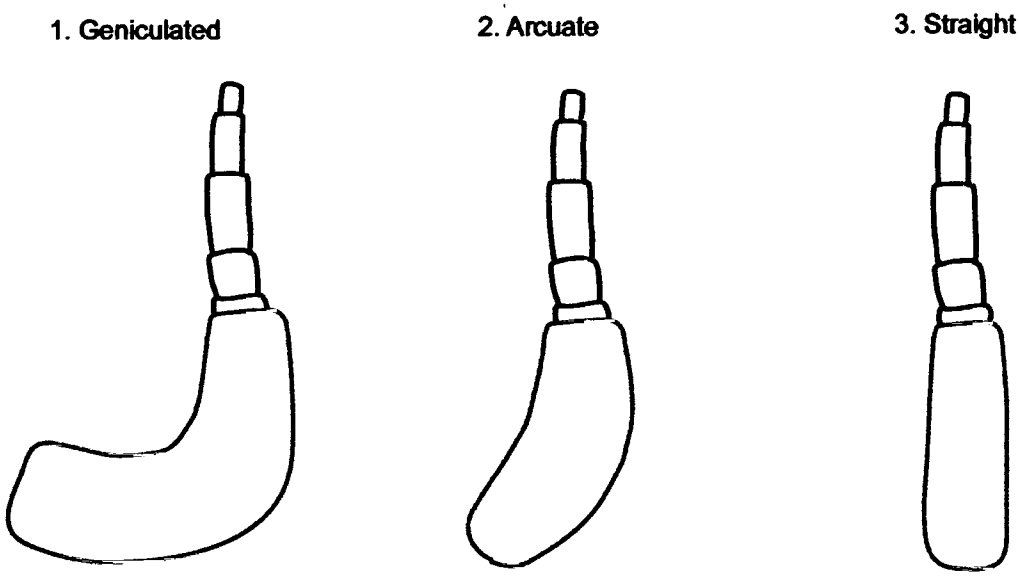


Figure C46. Maxilliped 3 - shape

1. Unspecialized
(looks like paraeopod 1)

2. Specialized
(depicted are three types of specializations)

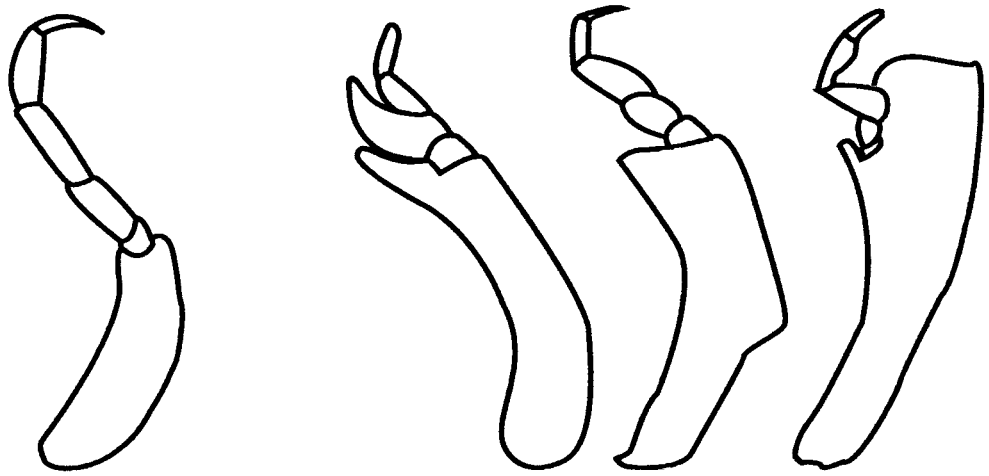


Figure C47. Maxilliped 3 - modification of basis

1. Normal

2. Opercular

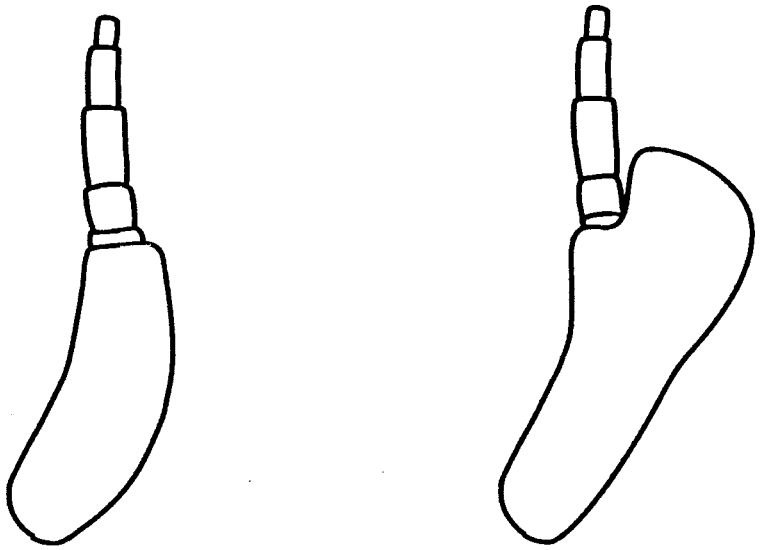


Figure C48. Maxilliped 3 - extension of basis

1. Dorsally

2. Ventrally

3. Absent

Figure C49. Maxilliped 3 - dorsal extension of basis

1. Extended beyond articulcation of ischium and merus

2. Slightly expanded

Figure C50. Maxilliped 3 - ischium length relative to merus

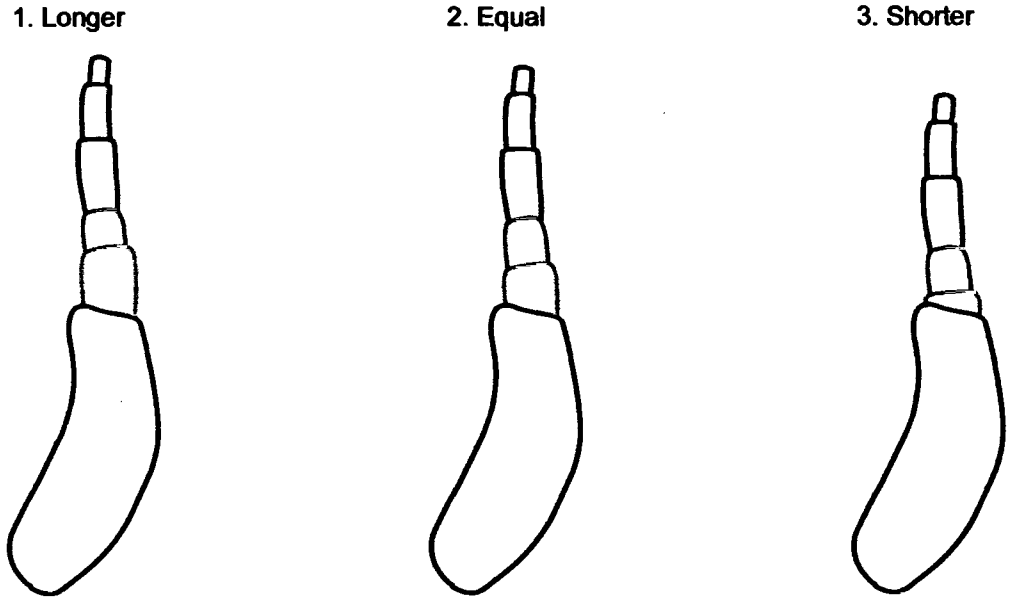


Figure C51. Maxilliped 3 - extension of merus

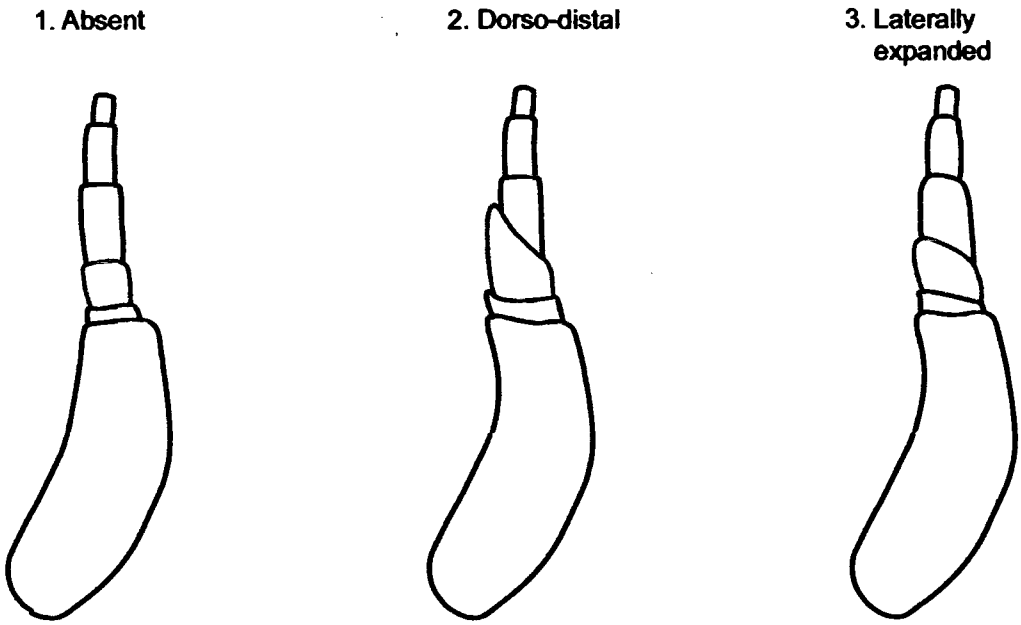


Figure C52. Maxilliped 3 - carpus expansion

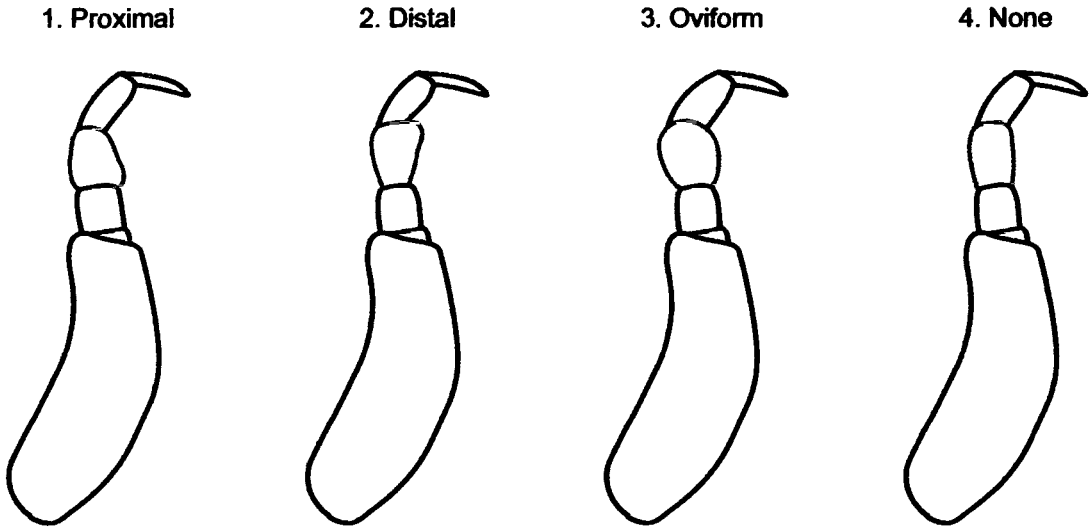


Figure C53. Maxilliped 3 - carpus length relative to length of propodus-dactylus

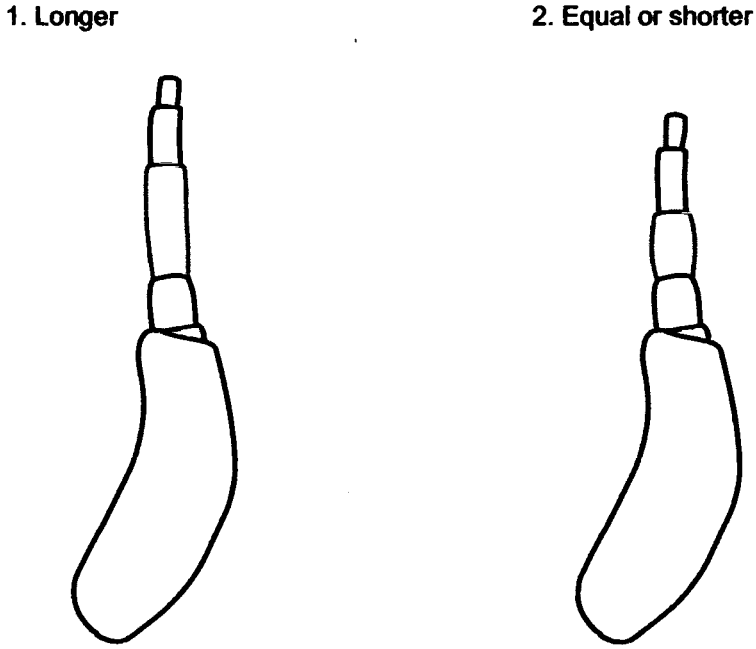


Figure C54. Maxilliped 3 - propodus expansion

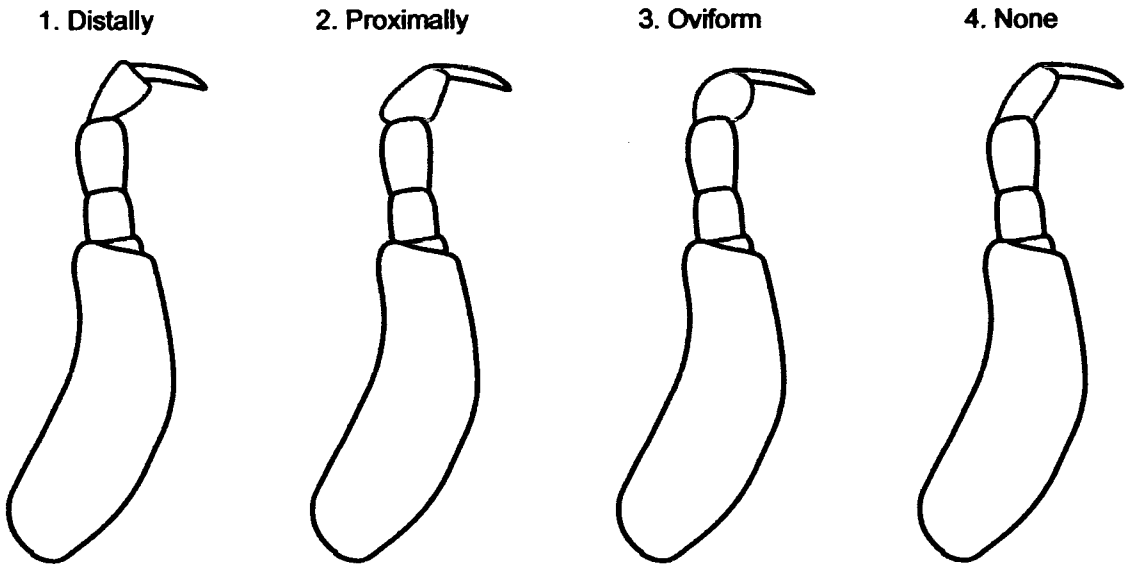


Figure C55. Maxilliped 3 - Brush of setae on propodus

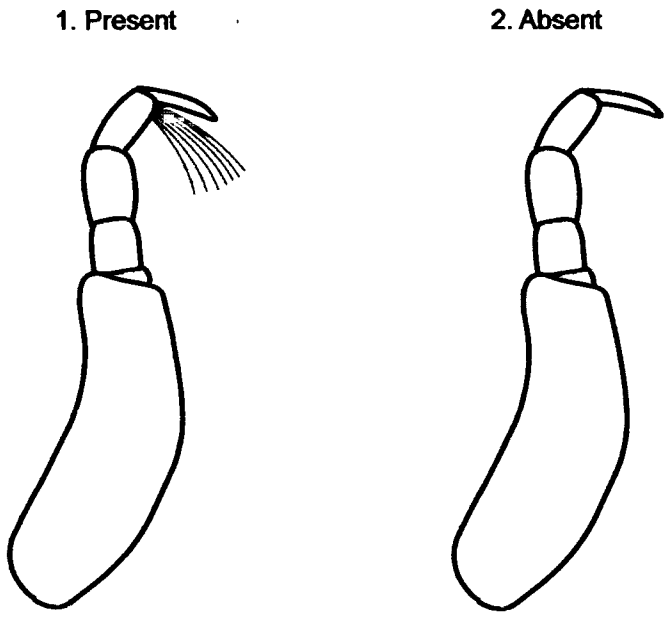
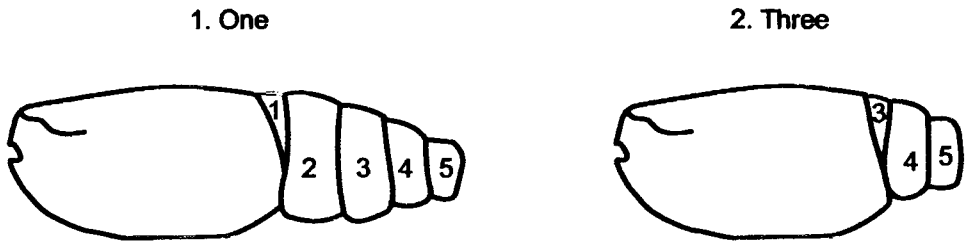


Figure C56. Peraeon - number of peraeonites covered by carapace



(lateral view)

Figure C57. Peraeon - first peraeonite

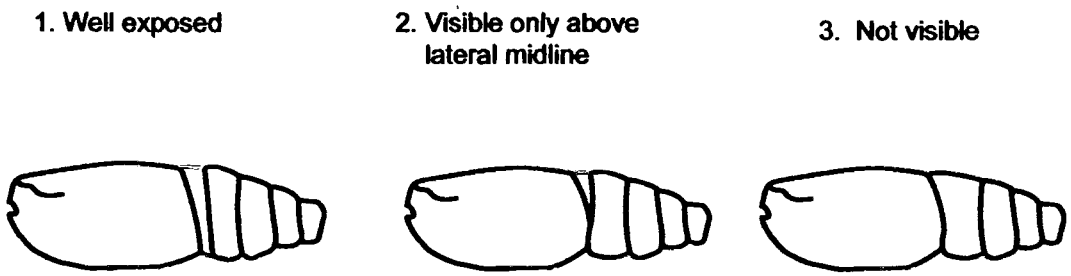


Figure C58. Paraeon - fusion of paraeonites 2 and 3

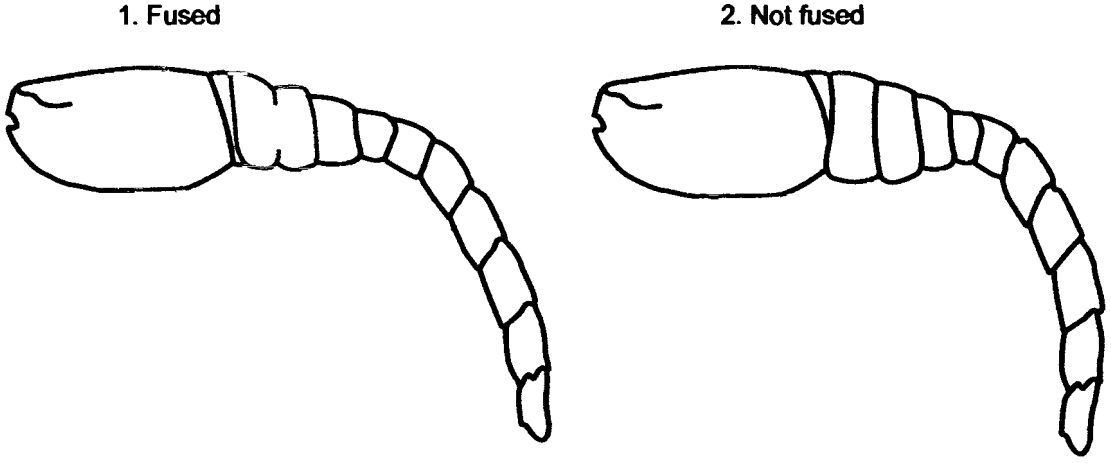


Figure C59. Paraeon - length of paraeonite 2

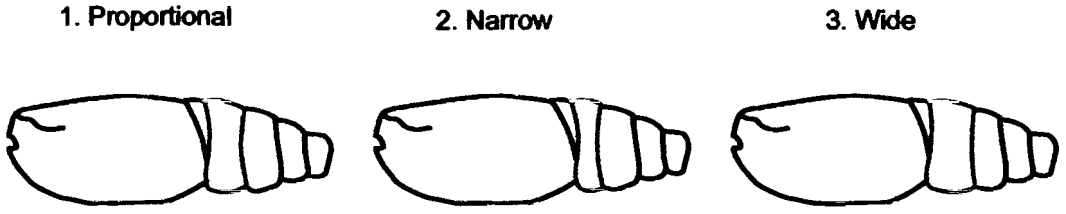
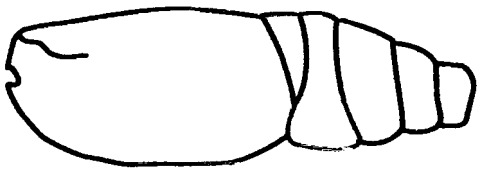


Figure C60. Paraeon - paraeonite 2 ventrolateral expansion

1. Present



2. Absent

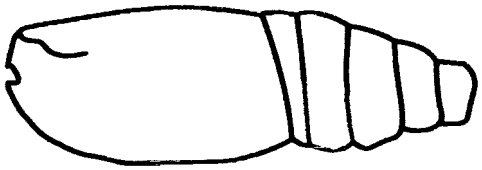
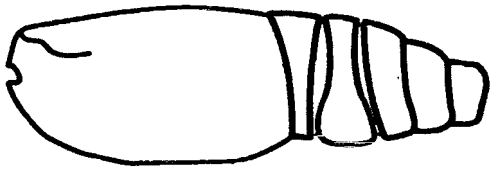
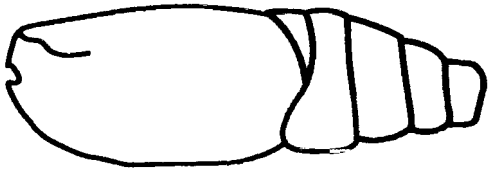


Figure C61. Paraeon - expansion of paraeonite 2

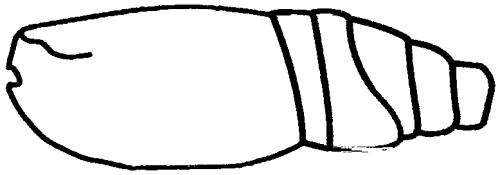
1. Does not overide other somites



2. Overides peraeonite 1 and/or carapace



3. Overides peraeonite 3



4. Overides peraeonite 3, and peraeonite1 and/or carapace

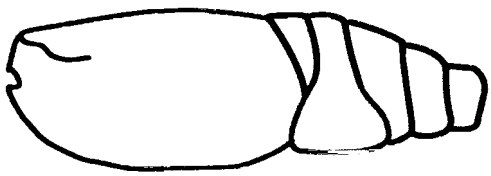
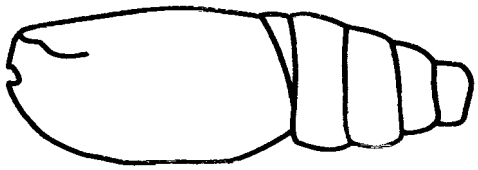
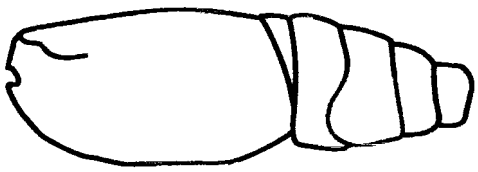


Figure C62. Paraeon - expansion of paraeonite 3

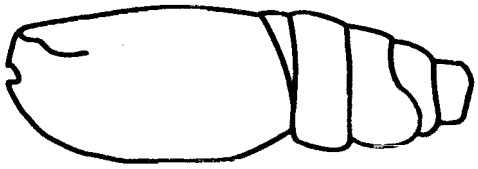
1. Absent



2. Overriding peraeonite 2



3. Overriding peraeopod 4



4. Overriding peraeonite 2 and 4

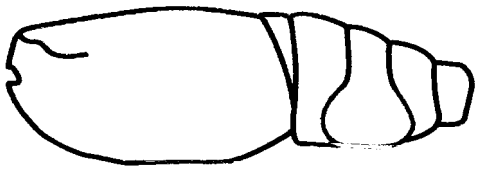
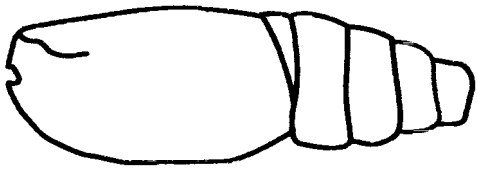
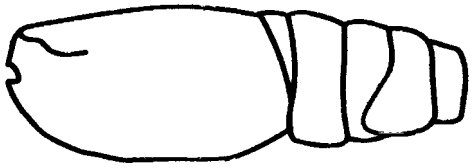


Figure C63. Paraeon - expansion of paraeonite 4

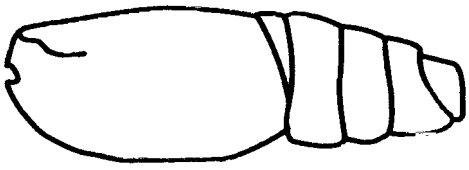
1. Absent



2. Overriding peraeonite 3



3. Overriding peraeonite 5



4. Overriding peraeonite 3 and 5

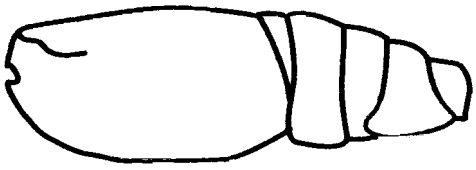
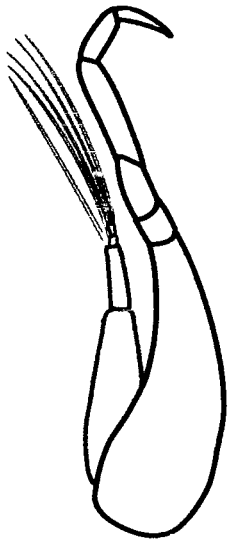


Figure C64. Peraeopod 1 - exopod

1. Present



2. Absent

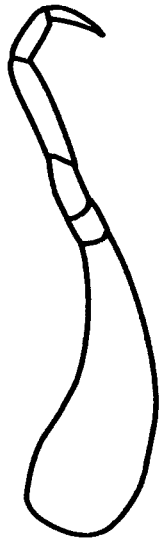
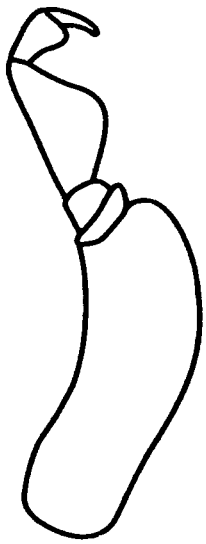


Figure C65. Paraeopod 1 - opercularity

1. Opercular



2. Non-opercular

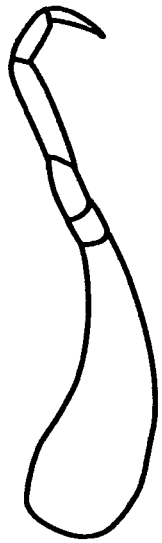


Figure C66. Peaeopod 1 - basis shape

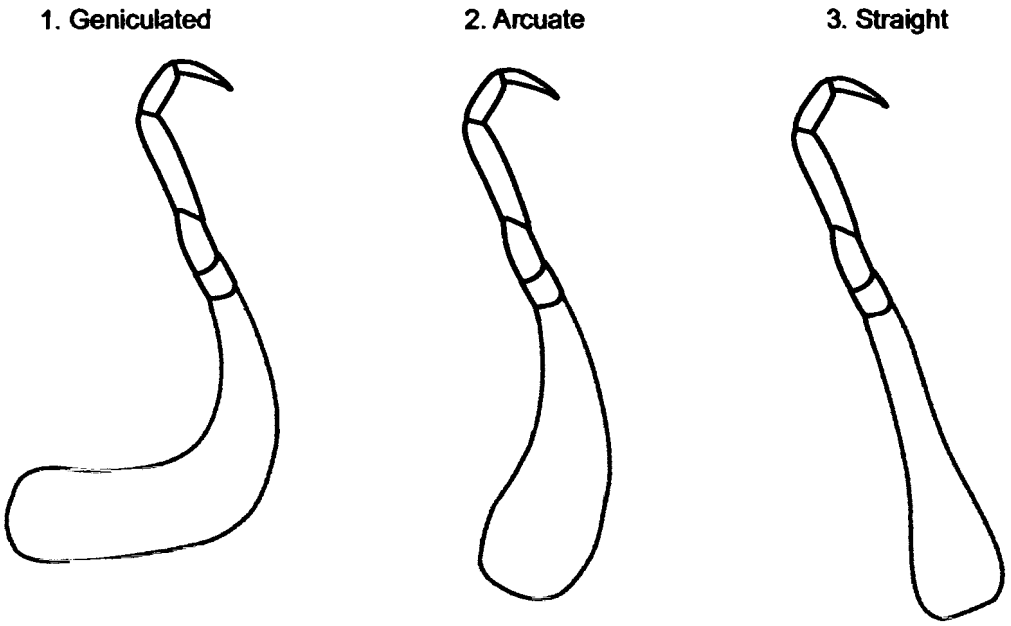


Figure C67. Peraeopod 1 - row of setae on basis

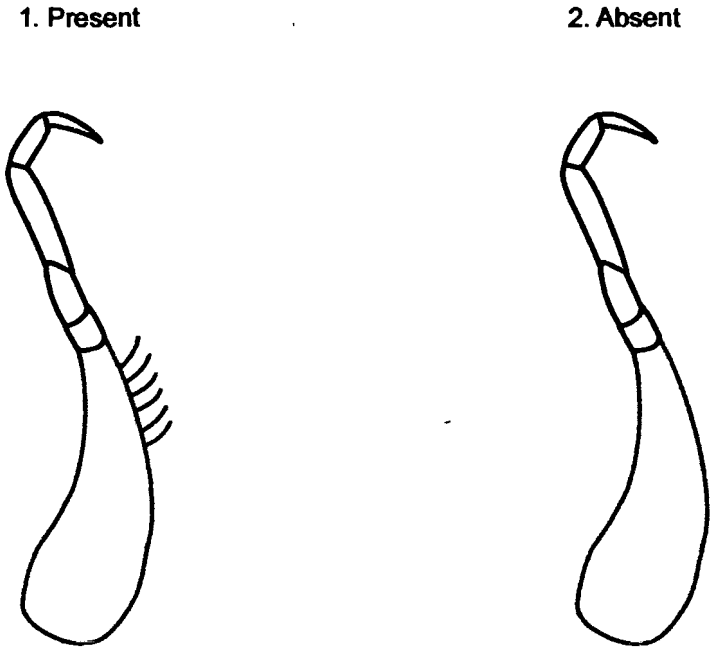


Figure C68. Paraeopod 1 - distal extension of basis

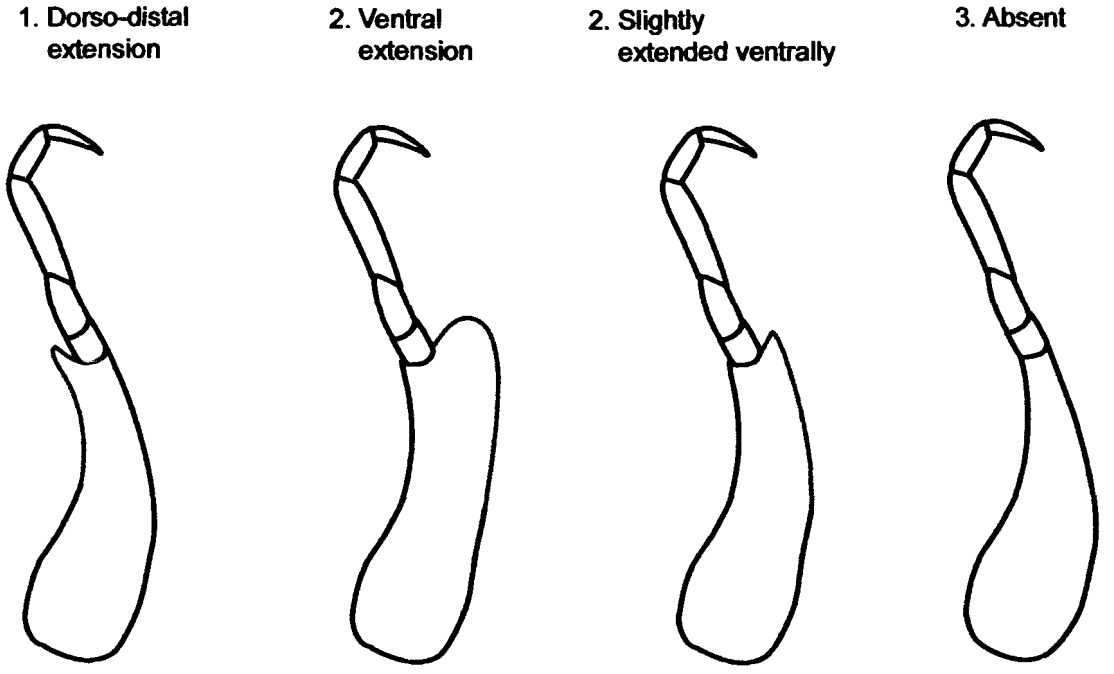


Figure C69. Paraeopod 1 - basis inner apical angle

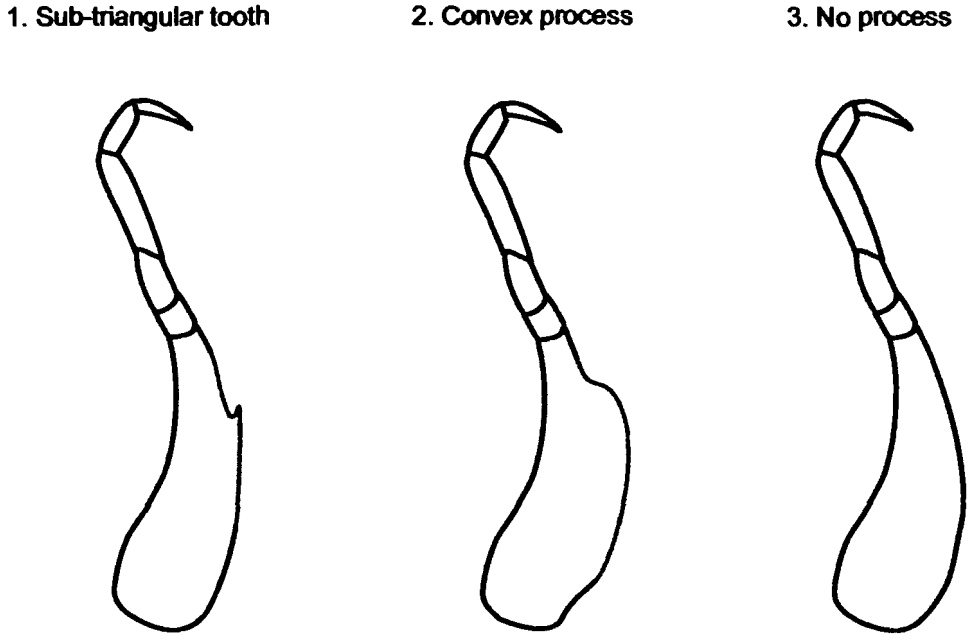
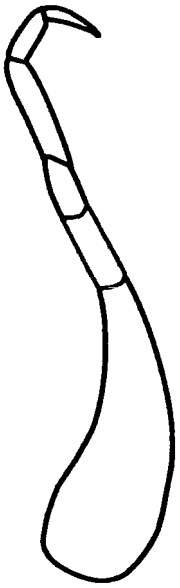


Figure C70. Paraeopod 1 - length of ischium

1. Elongated



2. Small

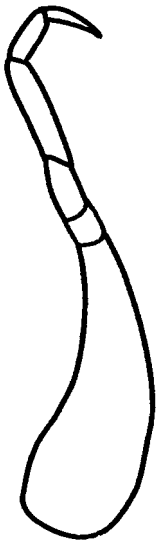


Figure C71. Peraeopod 1 - ischium modification

1. As round lobe with exterior concavity (opercular)

2. Not modified

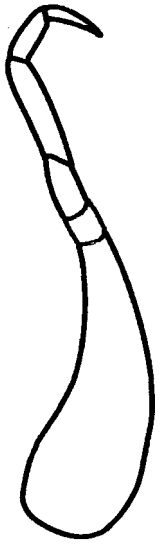
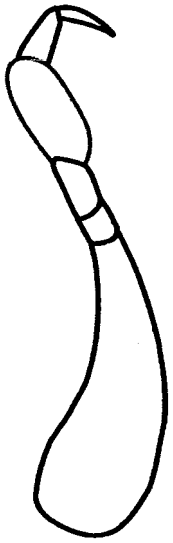


Figure C72. Paraeopod 1 - carpus shape

1. Oviform



2. Not oviform

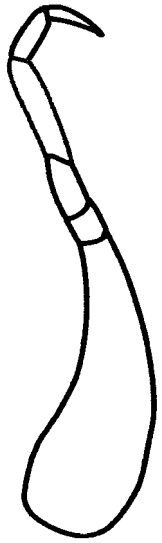
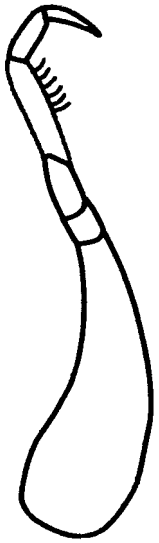


Figure C73. Peraeopod 1 - row of setae on carpus

1. Present



2. Absent

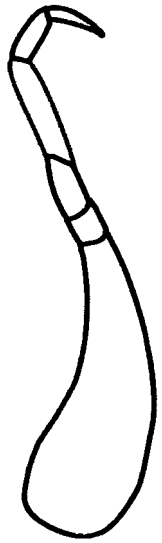
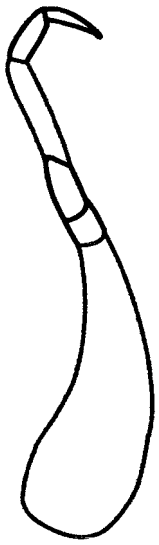


Figure C74. Paraeopod 1 - carpus length relative to basis

1. Shorter



2. Equal

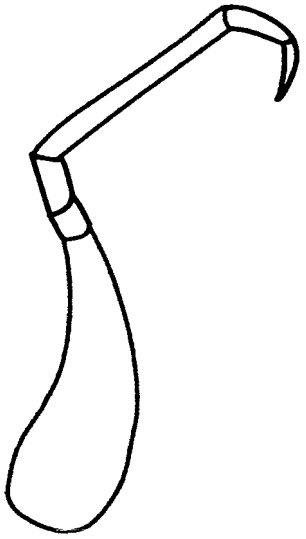
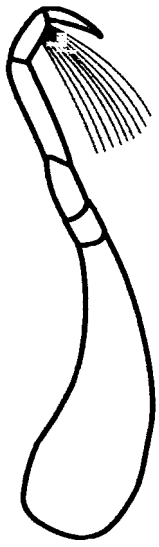
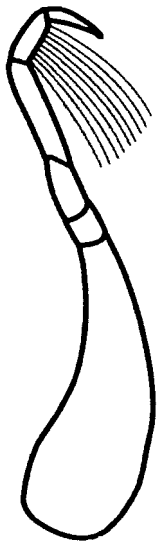


Figure C75. Paraeopod 1 - setae on propodus

1. Brush of long setae



2. Linear arrangement along propodus



3. absent

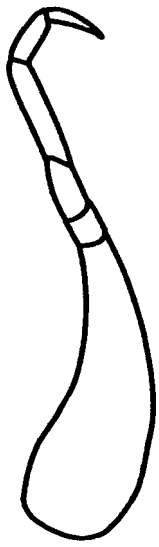
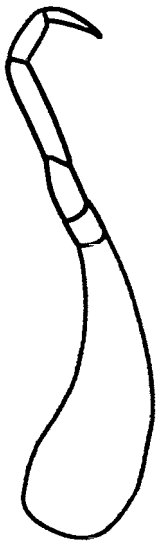


Figure C76. Paraeopod 1 - basis length relative to propodus

1. Longer



2. Equal

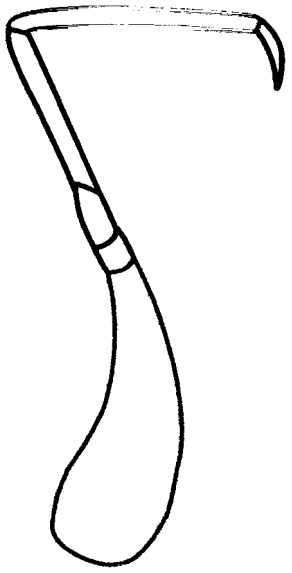
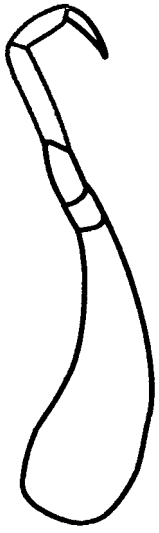
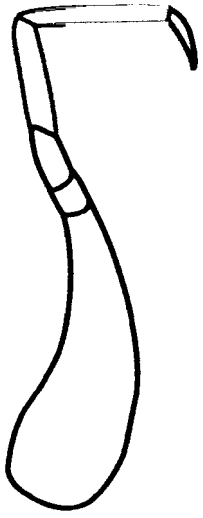


Figure C77. Paraeopod 1 - carpus length relative to propodus

1. Longer



2. Equal



3. Shorter

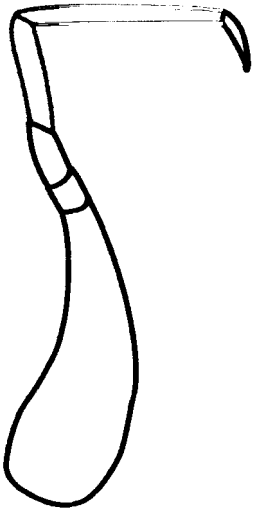


Figure C78. Paraeopod 1 - brush of setae on dactyl

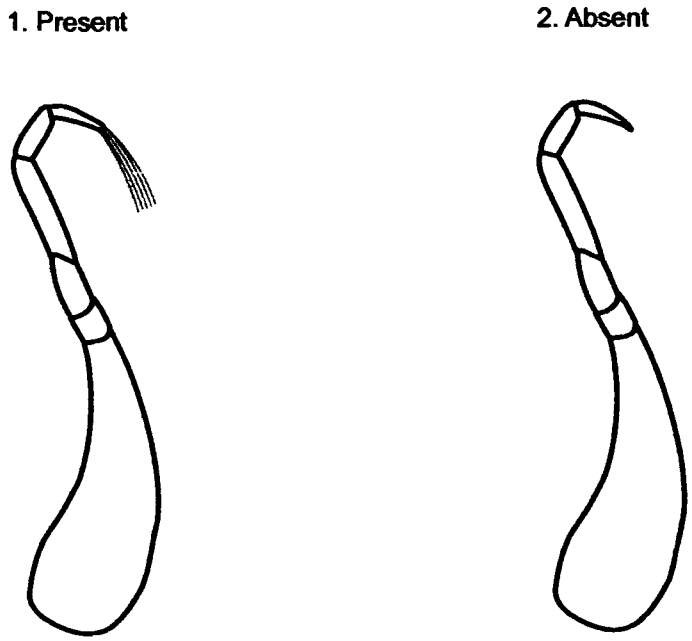


Figure C79. Peraeopod 2 - exopod

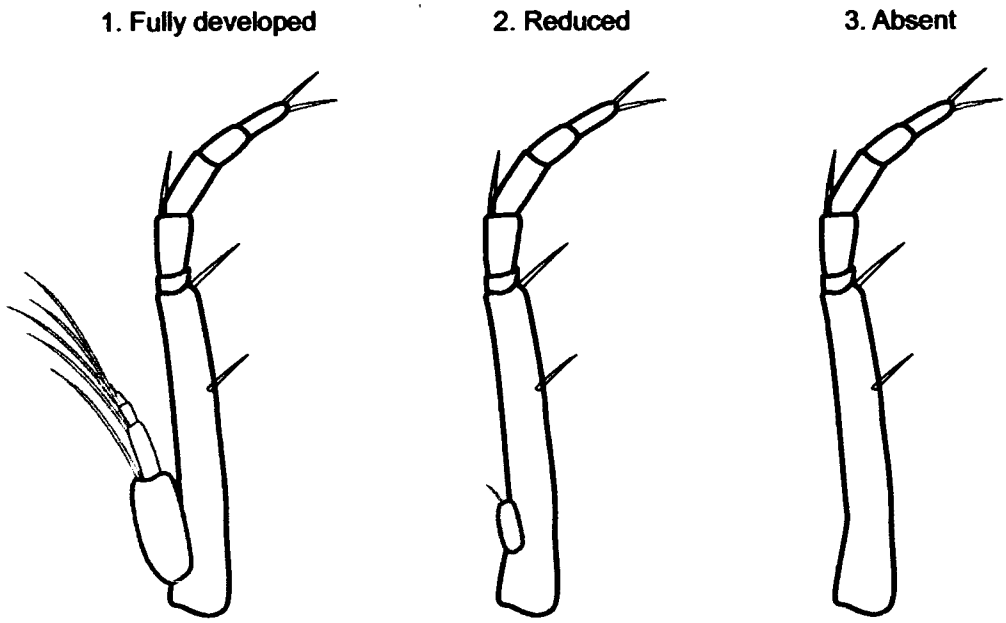


Figure C80. Peraeopod 2 - ischium

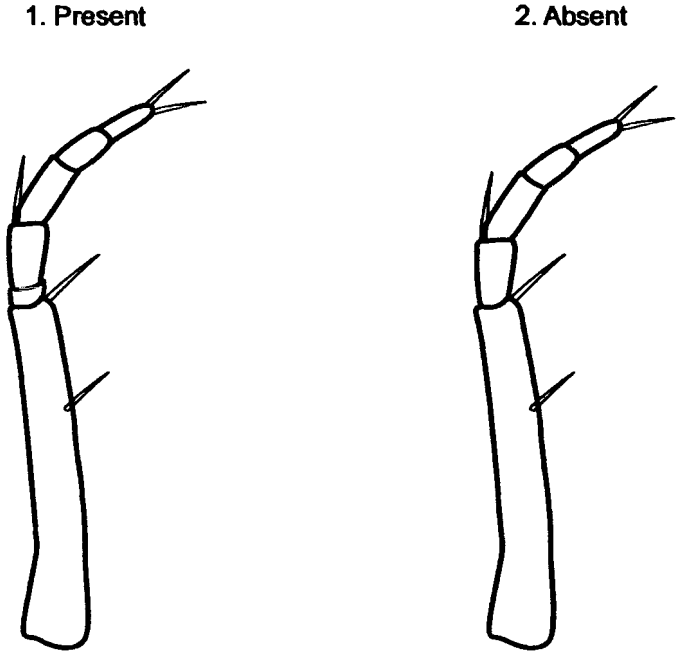


Figure C81. Peraeopod 2 - dactyl size relative to propodus

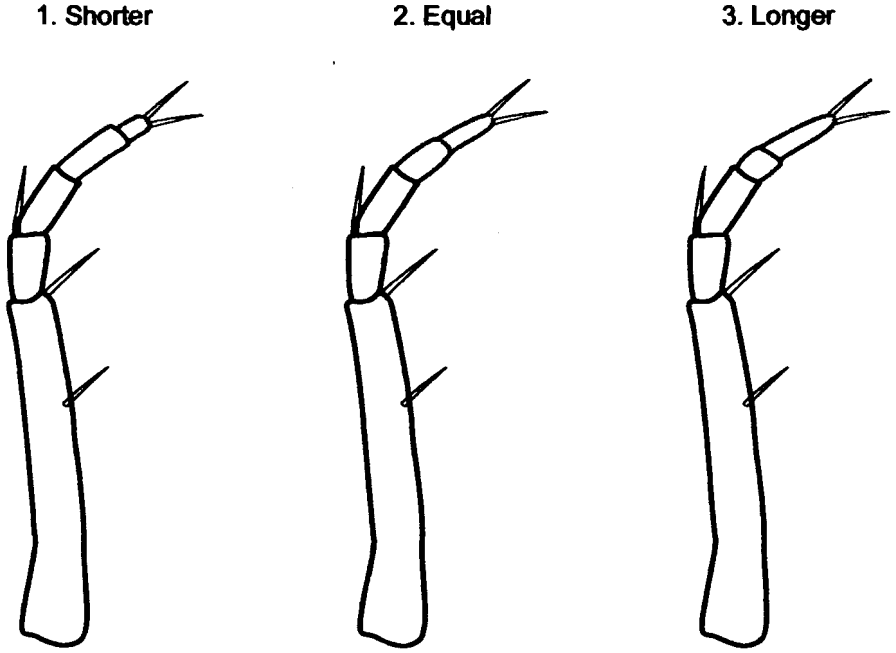


Figure C82. Peraeopod 3 - exopod

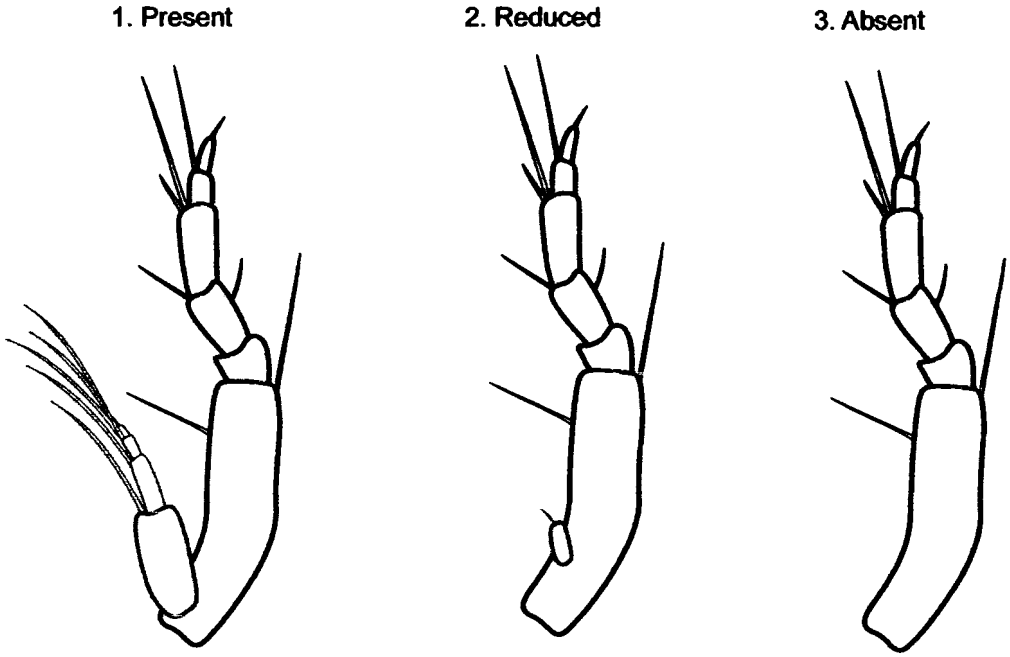


Figure C83. Peraeopod 3 - ischium

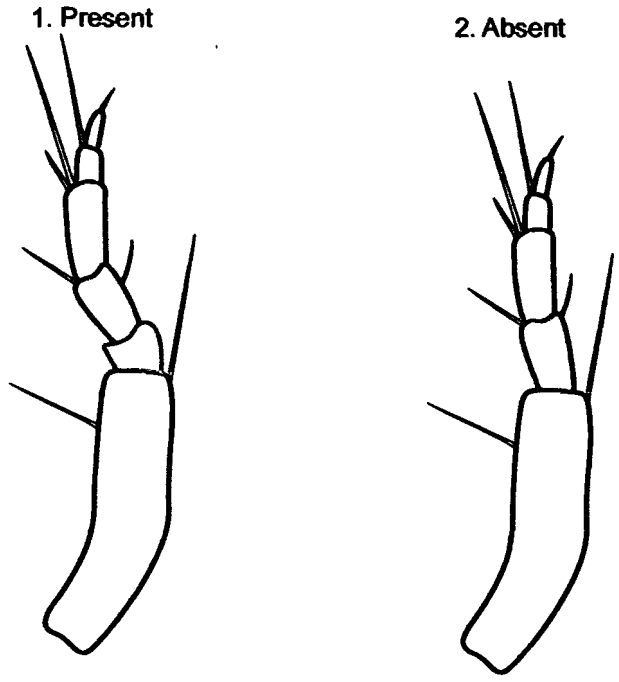
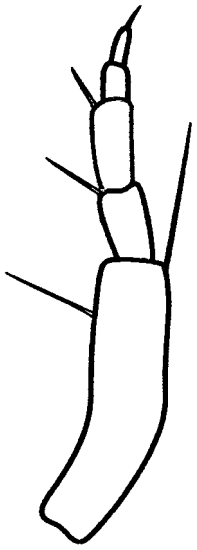


Figure C84. Peraeopod 3 - size of merus

1. Much smaller than basis (normal)



2. Almost as long as, or as long as basis

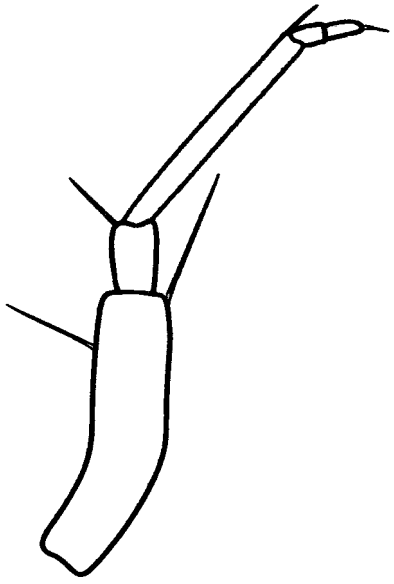
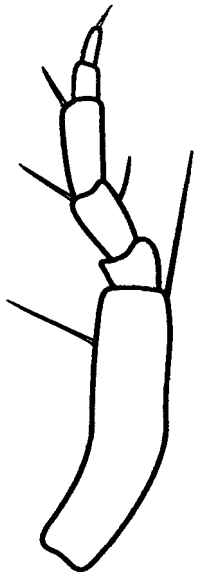


Figure C85. Peraeopod 3 - articulation of propodus

1. Not modified



2. Articulated at the side of the carpus

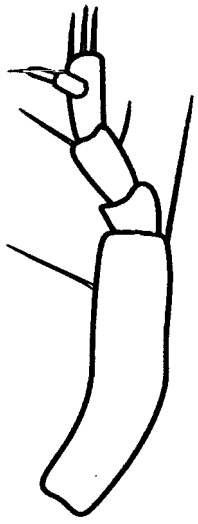


Figure C86. Peraeopod 4 - exopod

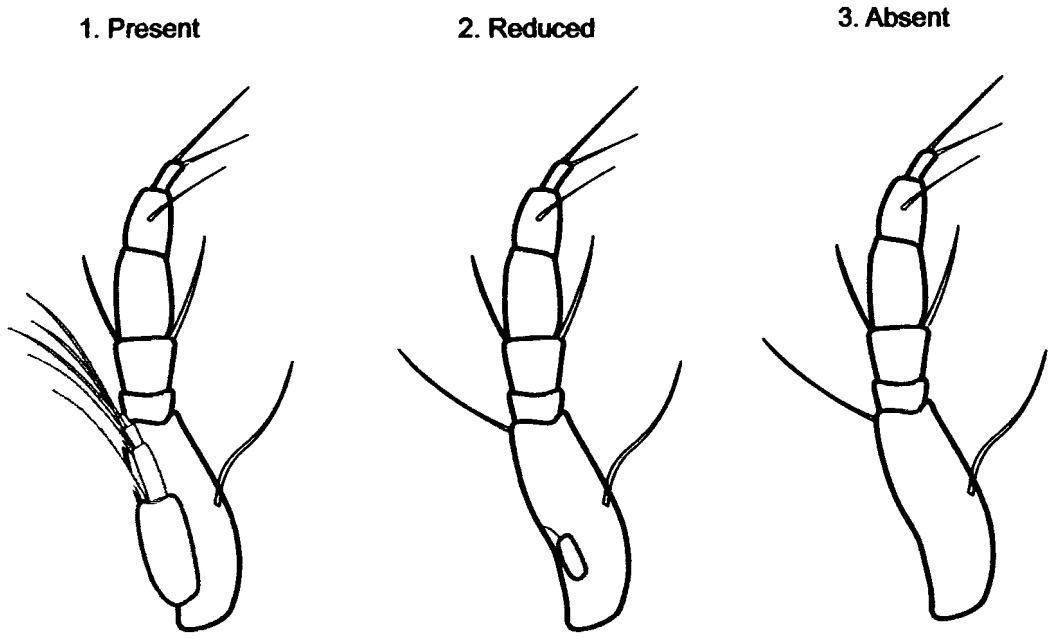


Figure C87. Peraeopod 4 - ischium

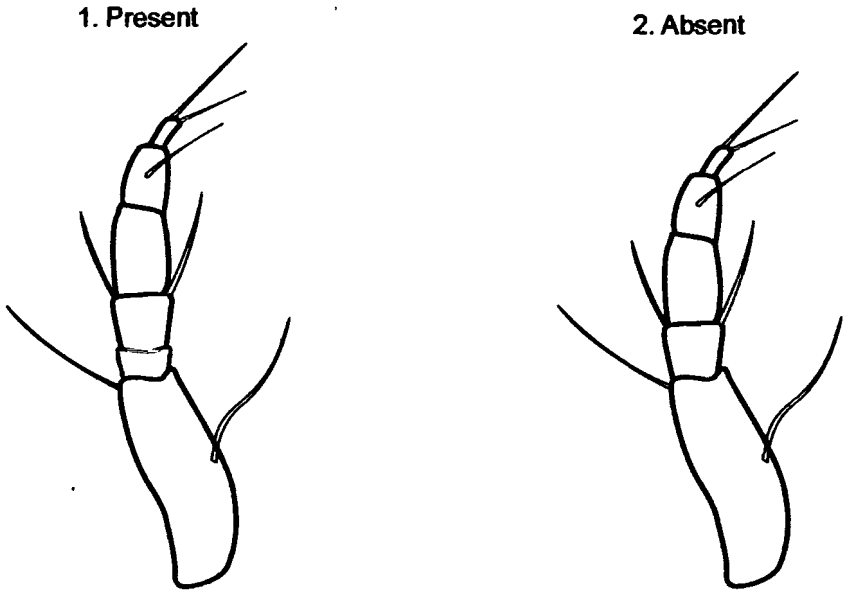
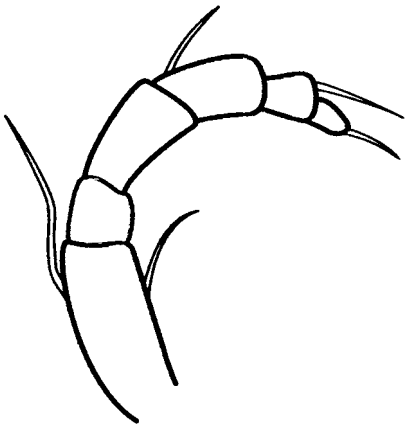


Figure C88. Peraeopod 5 - ischium

1. Present



2. Absent

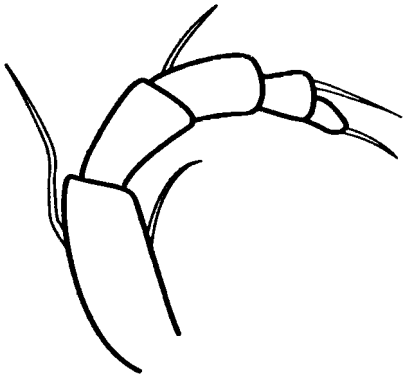
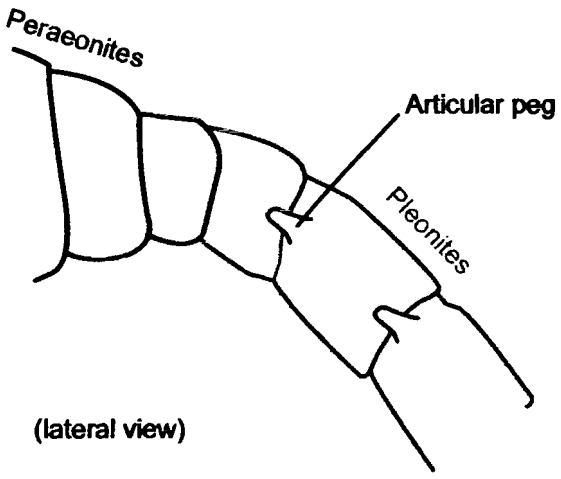


Figure C89. Pleon - articular pegs

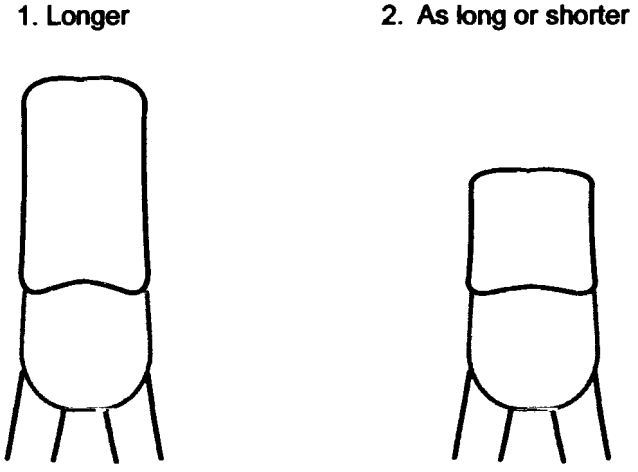
1. Present

2. Absent



(lateral view)

Figure C90. Pleonite 5 - length relative to pleonite 6



(dorsal view of pleonites 5 and 6)

Figure C91. Pleonite 6 - shape

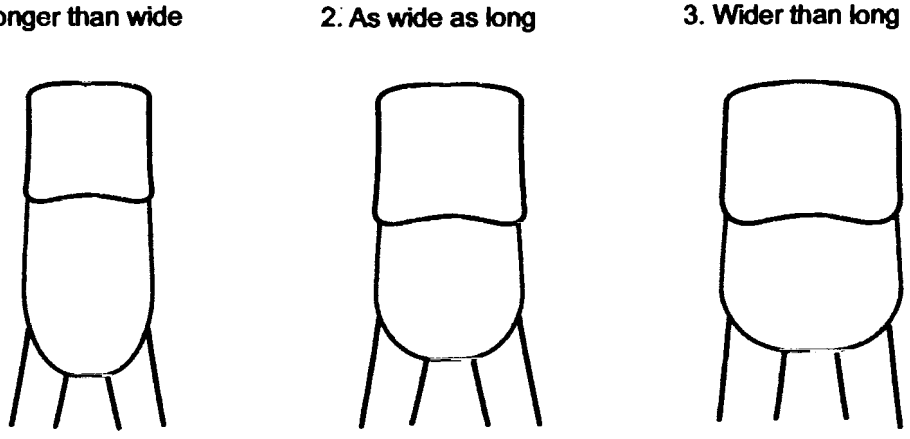


Figure C92. Pleonite 6 - length relative to peduncle of uropod

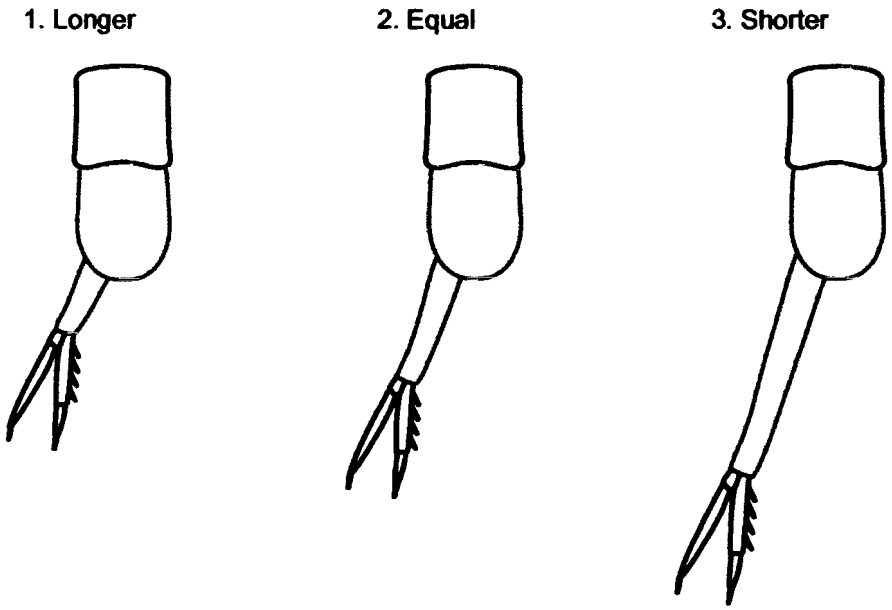


Figure C93. Pleonite 6 - setae on posterior edge

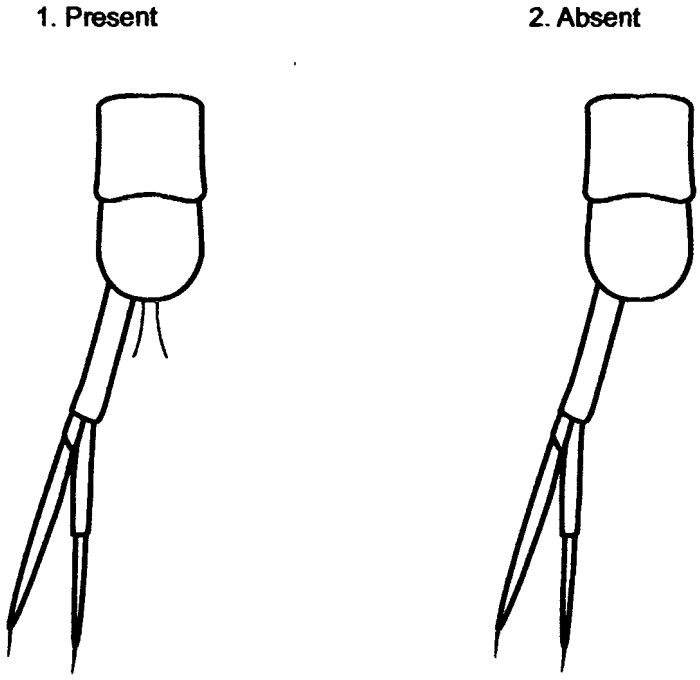
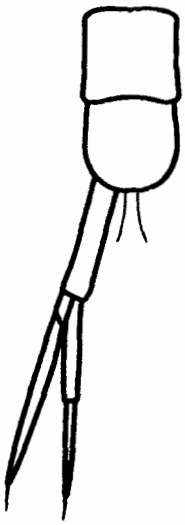


Figure C94. Pleonite 6 - conditions when setae present

1. Two setae close to midline



2. More than two setae at posterior end

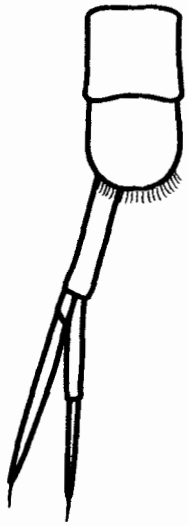
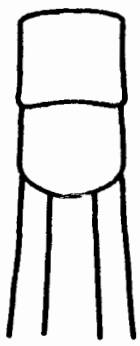


Figure C95. Pleonite 6 - extension past insertion of uropods

1. Absent



2. Present

Figure C96. Pleonite 6 - degree of extension past insertion of the uropods

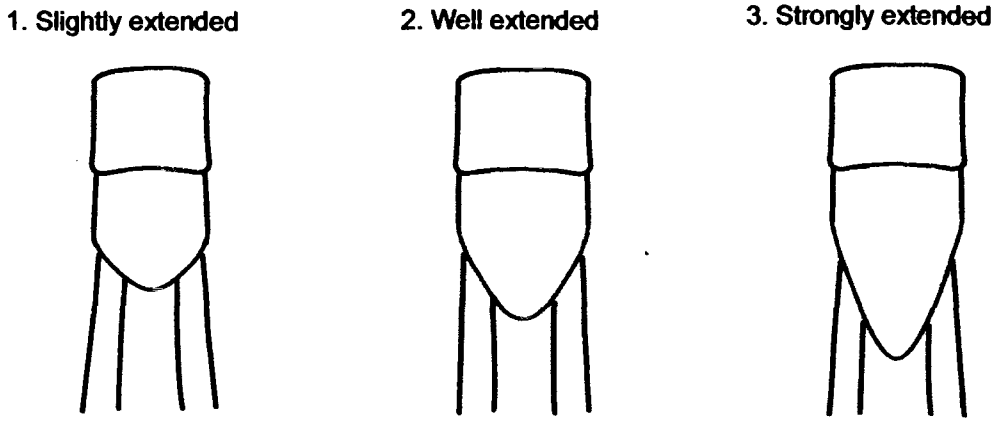


Figure C97. Pleonite 6 - type of extension

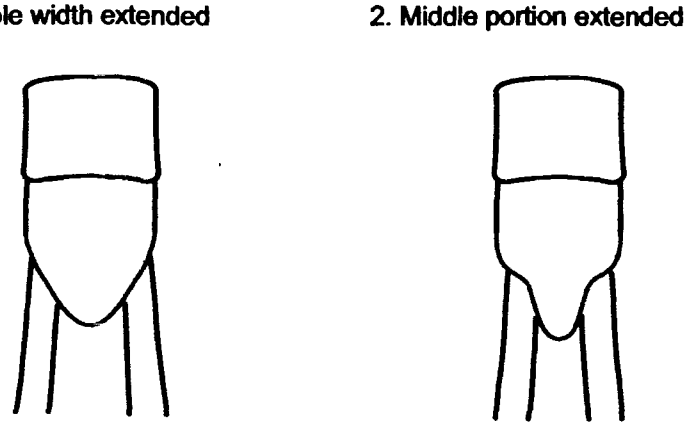


Figure C98. Pleonite 6 - terminal end shape of whole width extension

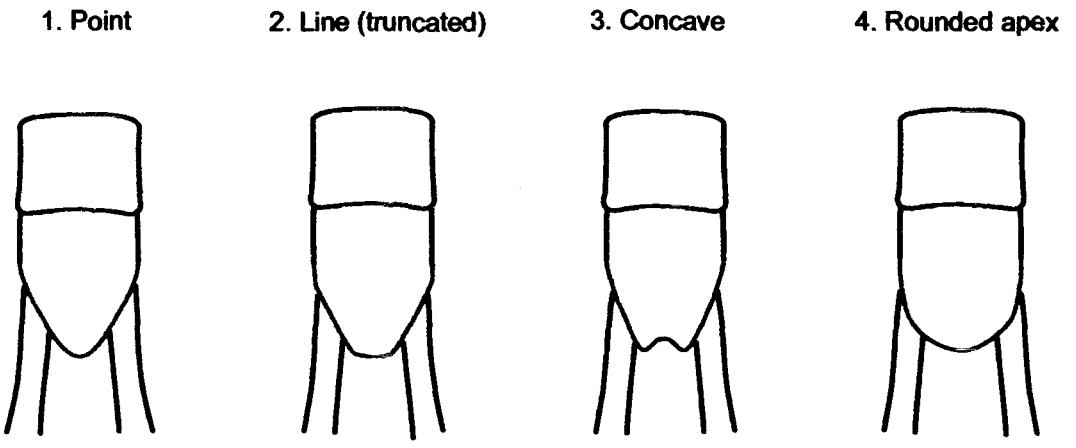


Figure C99. Pleonite 6 - width of middle portion extension

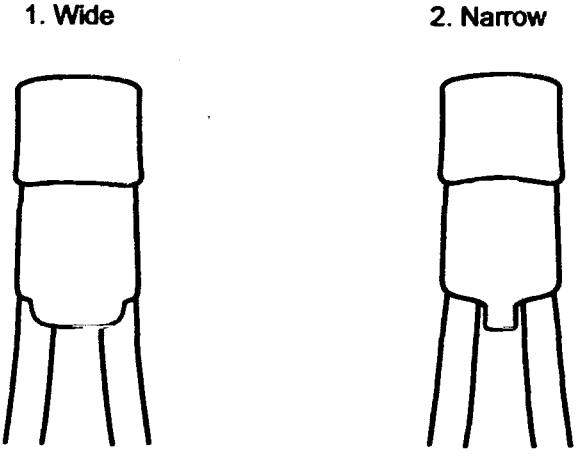


Figure C100. Pleonite 6 - terminal end shape of middle portion extensions

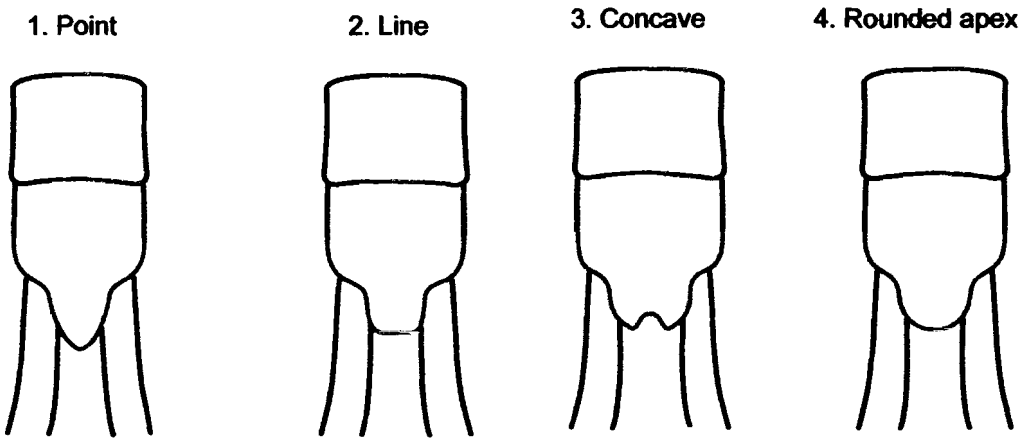


Figure C101. Anal Plates - extension

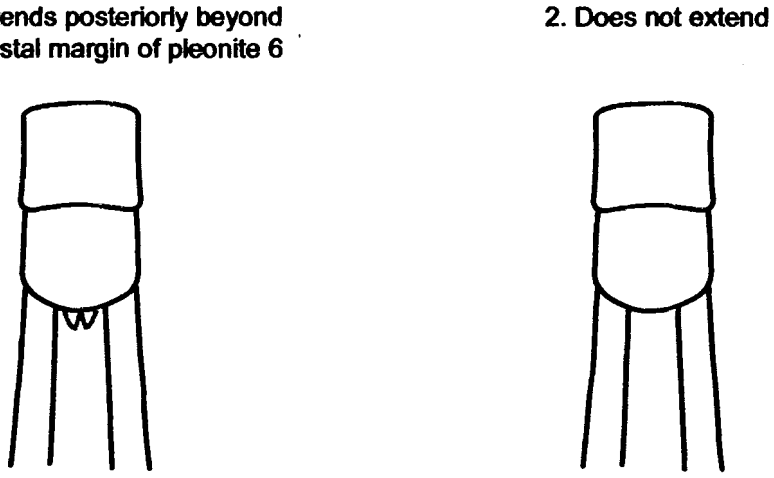


Figure C102. Anal Plates - setae

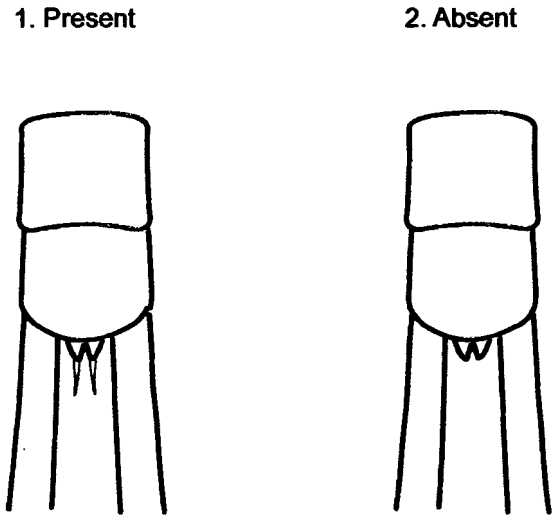


Figure C103. Pleon - uropod endopod - number of articles

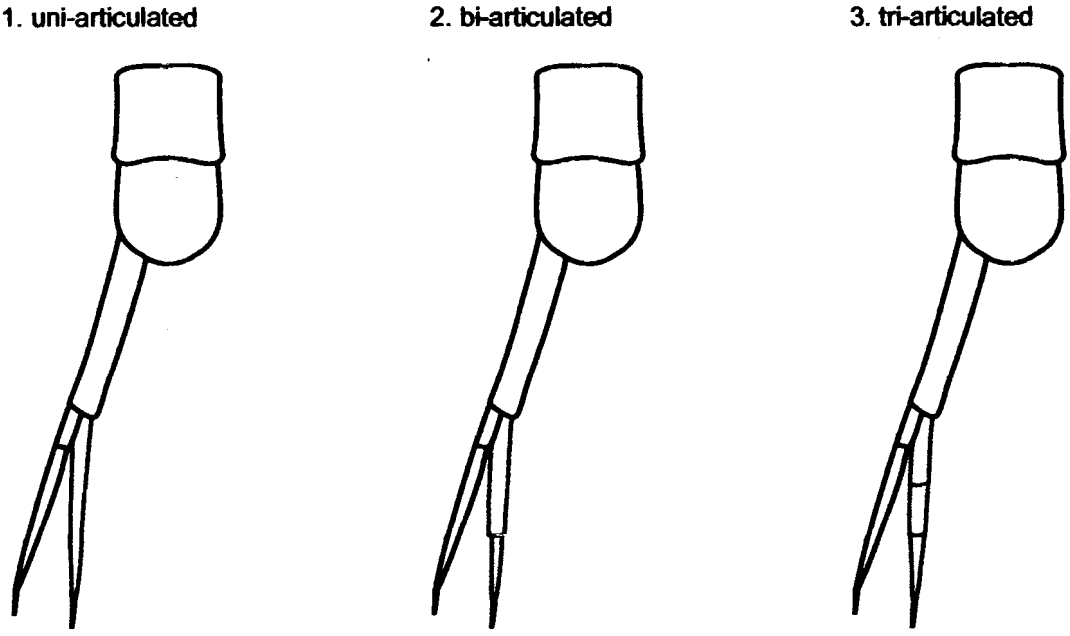


Figure C104. Pleon - uropod endopod - length of proximal and distal articles

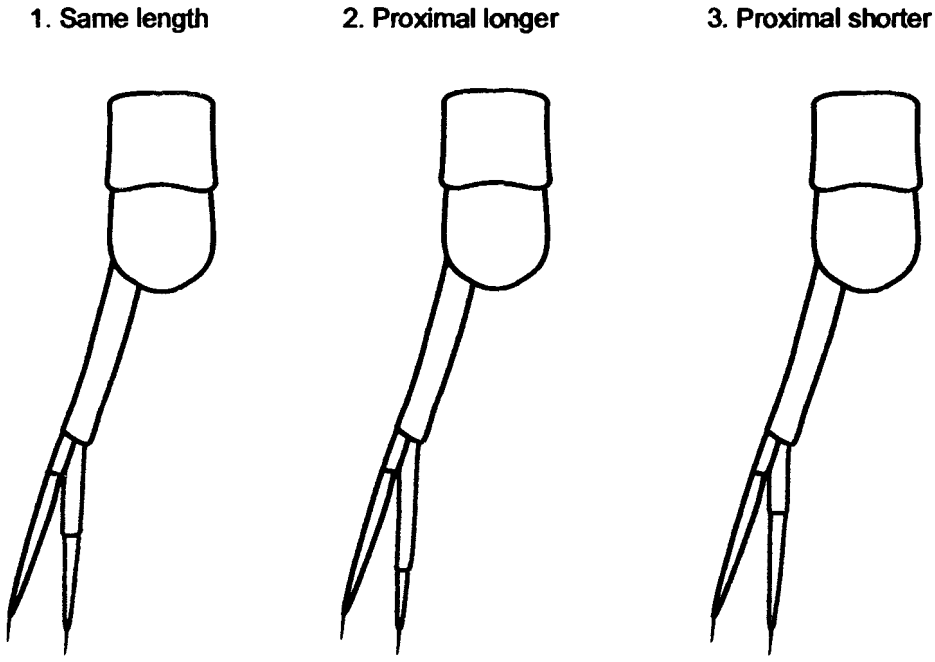


Figure C105. Pleon - uropod exopod - length of proximal and distal articles

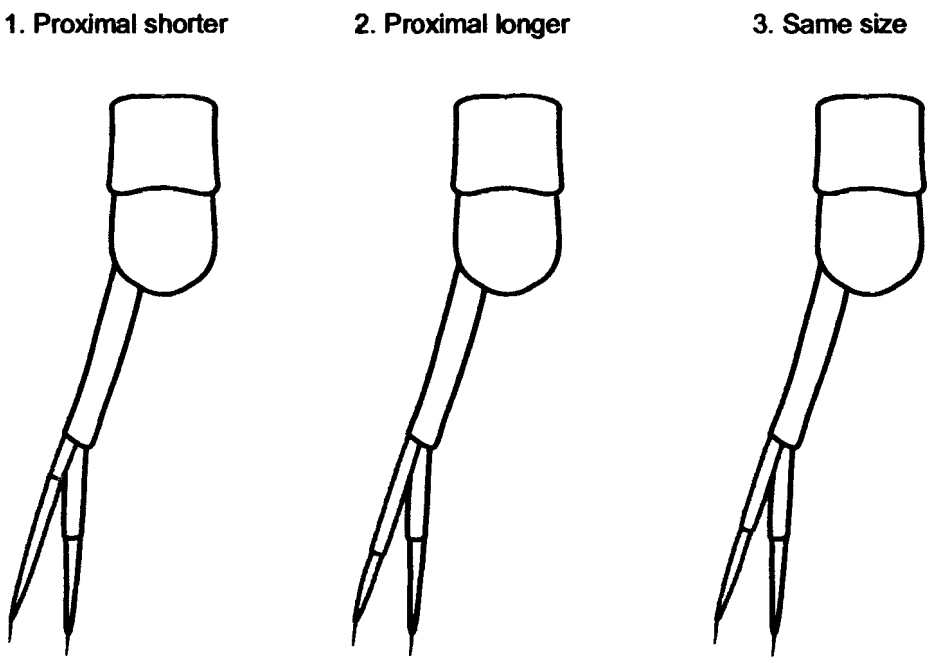


Figure C106. Pleon - uropods - peduncle length with respect to rami

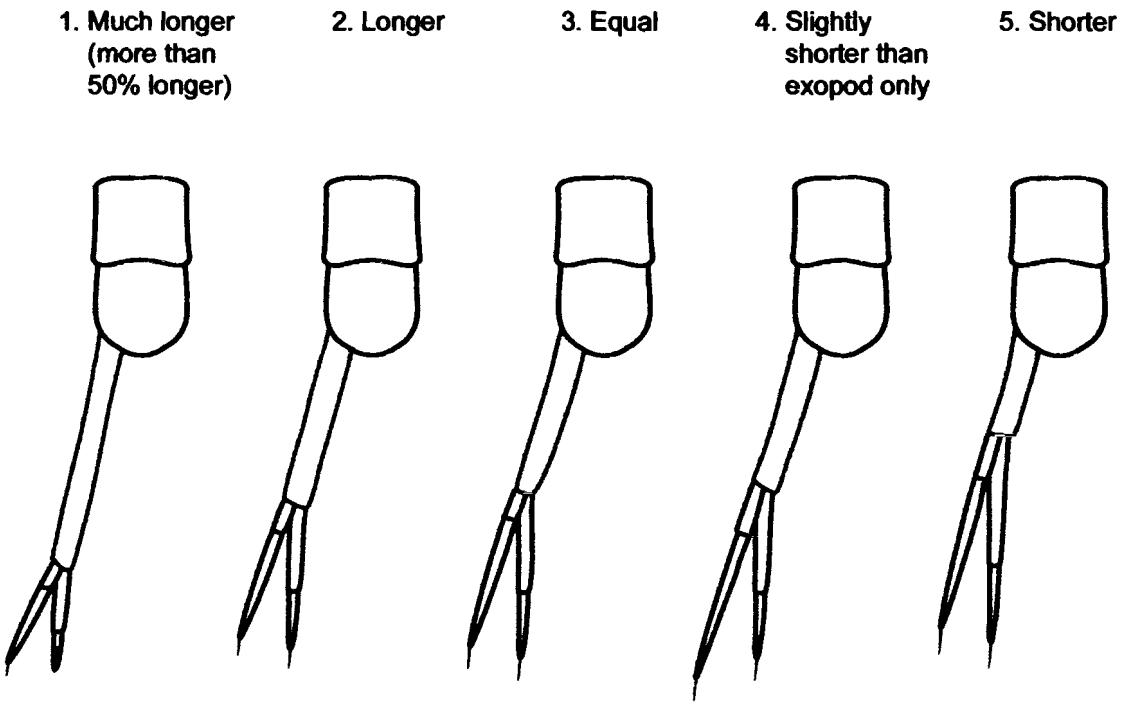


Figure C107. Pleon - uropod - rami length with respect to each other

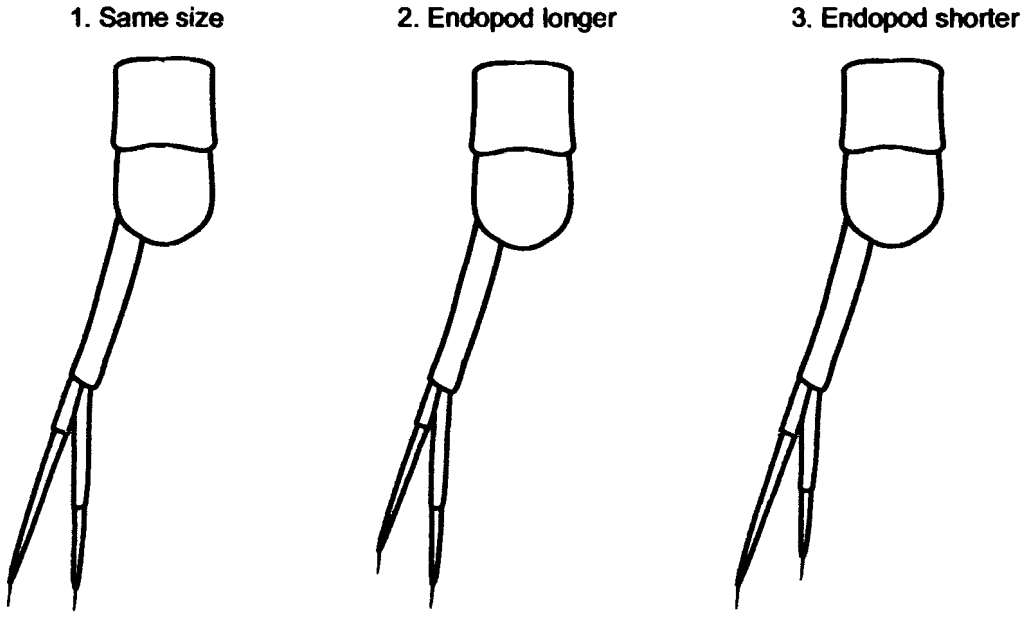
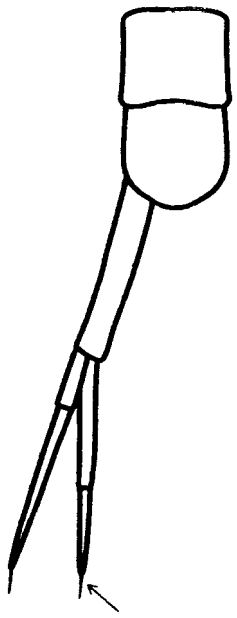


Figure C108. Pleon - uropod endopod - terminal setae

1. present



2. absent

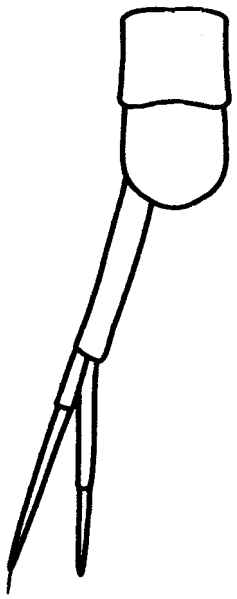
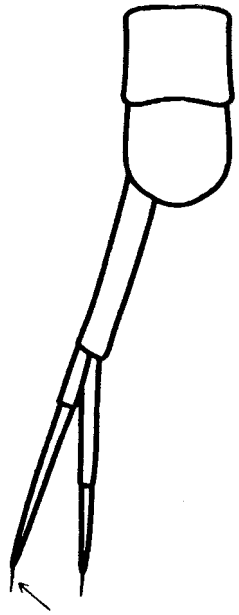


Figure C109. Pleon - uropod exopod - terminal setae

1. present



2. absent

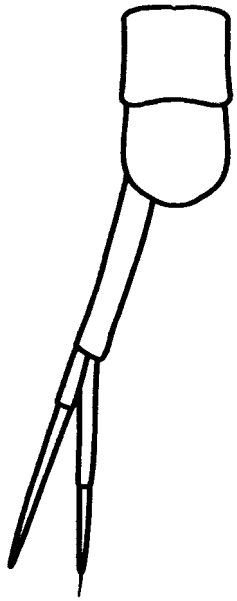


Figure C110. Pleon, male - number of pleopods present

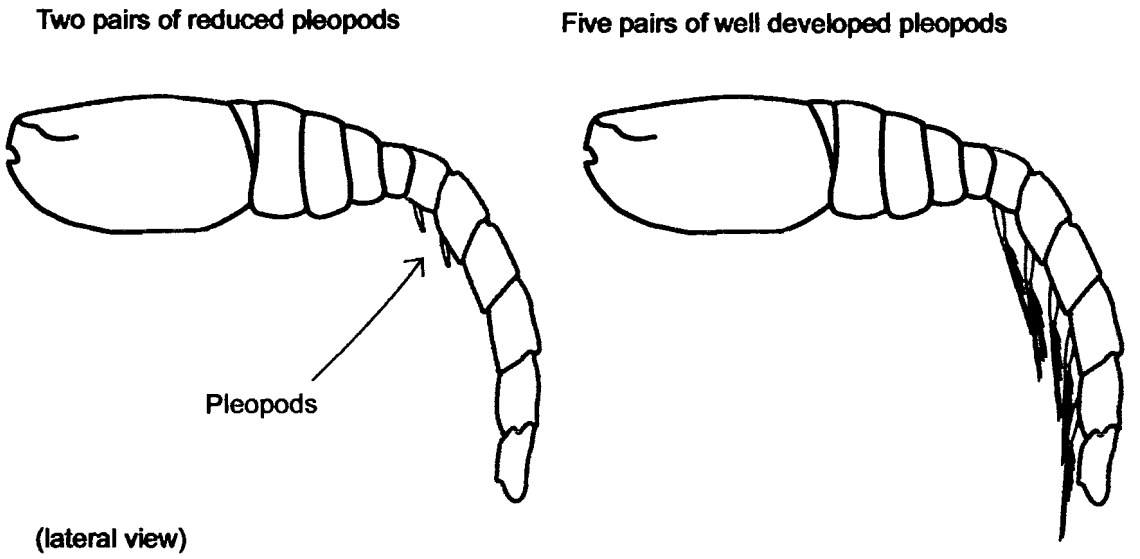
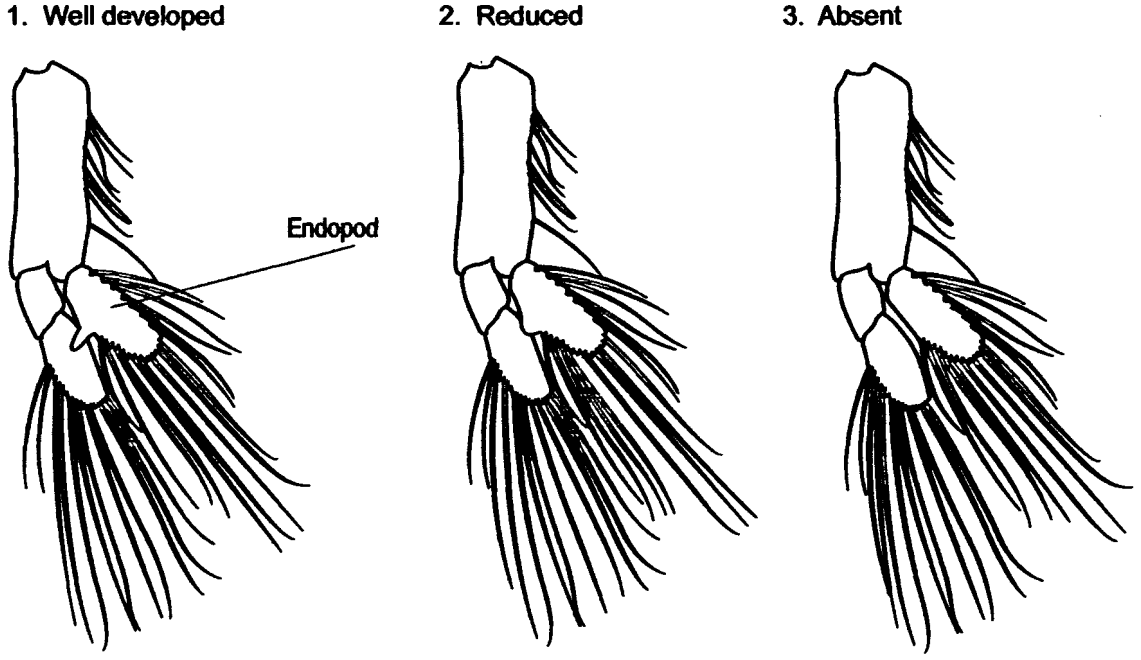


Figure C111. Pleon, male - pleopods - process on endopod



BIOGRAPHY OF THE AUTHOR

Pilar Haye was born in Santiago Chile, on May 15, 1974. Wonderful parents, Helia and Sergio, raised her and her numerous loving siblings. Pilar attended school and university in Santiago. She went to The Kent School middle and high school where she met the two biology teachers that would captivate her into the study and understanding of the nature of life ('El Moli' and 'El Señor Pozo'). She attended the Pontificia Universidad Católica de Chile from 1992 to 1996 from where she received the degree of Licentiate in Biological Sciences. While she was in college she interacted with inspiring teachers, particularly Dr. Ojeda that gave her support throughout her academic experience. Soon after graduation, she moved to Maine, U.S.A., and entered the graduate program at The University of Maine to follow an advanced degree in the Department of Biological Sciences. Her goals were to learn about crustaceans and about the theory and methods of systematic biology. She worked at Dr. kornfield's laboratory, where she did her thesis work on a charismatic group of marine organisms called cumaceans. Pilar is a candidate for the degree of Doctor of Philosophy in Biological Sciences from The University of Maine in December, 2002.