Sexual dimorphism in calanoid copepods: morphology and function

Susumu Ohtsuka[1] & Rony Huys[2]
[1]*Fisheries Laboratory, Hiroshima University, 5-8-1 Minato-machi, Takehara, Hiroshima 725-0024, Japan.*
E-mail: ohtsuka@hiroshima-u.ac.jp
[2]*Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
E-mail: rjh@nhm.ac.uk

Key words: copepod, calanoid, sexual dimorphism, mating, post-mating, phylogeny

Abstract

Mate location and recognition are essentially asymmetrical processes in the reproductive biology of calanoid copepods with the active partner (the male) locating and catching the largely passive partner (the female). This behavioural asymmetry has led to the evolution of sexual dimorphism in copepods, playing many pivotal roles during the various successive phases of copulatory and post-copulatory behaviour. Sexually dimorphic appendages and structures are engaged in (1) mate recognition by the male; (2) capture of the female by the male; (3) transfer and attachment of a spermatophore to the female by the male; (4) removal of discharged spermatophore(s) by the female; and (5) fertilization and release of the eggs by the female. In many male calanoids, the antennulary chemosensory system is enhanced at the final moult and this enhancement appears to be strongly linked to their mate-locating role, i.e. detection of sex pheromones released by the female. It can be extreme in calanoids inhabiting oceanic waters, taking the form of a doubling in the number of aesthetascs on almost every segment, and is less expressed in forms residing in turbulent, neritic waters. Mate recognition is a process where chemoreception and mechanoreception presumably work in conjunction. The less elaborate male chemosensory system in the Centropagoidea is counterbalanced by females playing a more active role in generating hydromechanical cues. This is reflected in females in the shape of the posterior prosomal margin, the complexity of urosomal morphology and the size of the caudal setae. Visual mate recognition may be important in the Pontellidae, which typically show sexual dimorphism in eye design. The most distinctive sexual dimorphism is the atrophy of the mouthparts of non-feeding males, illustrating how copepod detection systems can be shifted to a new modality at the final moult. In the next phase, the male captures the female using the geniculate antennule and/or other appendages. Three types of antennulary geniculations are recognized, and their detailed morphology suggests that they have originated independently. Grasping efficiency can be enhanced by the development of supplemental hinges. The scanty data on capture mechanisms in males lacking geniculate antennules are reviewed. It is suggested that the loss of the antennulary geniculation in many non-centropagoidean calanoids has evolved in response to increasing predator pressure imposed on pairs in amplexus. Spermatophore transfer and placement are generally accomplished by the modified leg 5 of the male. In some males, leg 5 consists of both a chelate grasping leg and a spermatophore-transferring leg, whereas in others, only the latter is developed. Tufts of fine setules/spinules and/or sclerotized elements on the terminal portion of the leg are involved in the transfer and attachment of the spermatophore. The configuration of gonopores, copulatory pores and their connecting ducts in the female genital double-somite is diversified in the early calanoid offshoots such as Arietellidae and Metridinidae, whereas in more derived groups, it is constant and invariable, with paired gonopores and copulatory pores located beneath a single genital operculum. The absence of seminal receptacles in most Centropagoidea limits the female's ability to store sufficient sperm for multiple egg batches, suggesting that repeated mating is necessary for sustained egg production. Discharged spermatophores are usually removed by the female leg 5 and/or specialized elements on other legs. In *Tortanus* (*Atortus*) Ohtsuka, which has rudimentary fifth legs in the female and complex coupling devices in the male, a spermatophore supposedly remains on the female urosome, since eggs appear to be released from a ventral opening of the spermatophore. The type of sexual dimorphism is closely related to habitat and biology. Some hyperbenthic families never show multiplication of aesthetascs on the male antennule, whereas families of the open pelagic realm such as the Aetideidae always have non-feeding males exhibiting secondary multiplication of antennulary aesthetascs. The various aspects and diversity of calanoid sexual dimorphism are herein considered in an evolutionary context.

442

Introduction

During the hundreds of millions of years spanning the evolutionary history of the subclass Copepoda (Huys & Boxshall, 1991), the habitat shift from benthos to plankton performed by the Calanoida can be viewed as the major and probably earliest attempt by copepods to colonize the pelagic biome. It is largely through this evolutionary success, combining radiation, diversification and specialization, that copepods can be ranked among the most abundant animal groups on earth. Calanoids are highly adapted to the planktonic mode of life and dominate zooplankton communities, although members of the most primitive families such as the Pseudocyclopidae and Ridgewayiidae have retained their close association with the sediment–water interface, the ancestral hyperbenthic habitat where most copepod orders probably originated (Huys & Boxshall, 1991). They are morphologically distinguishable from other orders by the combination of the following characters: the gymnoplean tagmosis, the presence of a genital double-somite in the female and the unarmed sixth legs closing off the genital apertures in both sexes. Huys & Boxshall (1991) also recognized a number of plesiomorphies such as the presence of a coxal epipodite on the maxillule and an inner coxal seta on the antenna, but the evolutionary significance and diagnostic value of such characters are limited.

Although no single type of sexual dimorphism is universal in the order, in practice, adult male calanoids can be readily distinguished from other copepods by prominent modifications expressed in the antennules and fifth legs. The male antennule is primitively geniculate on the right side only, a morphological and functional asymmetry not noted in any other order. The fifth legs can be extremely modified in the males of many families and their profound transformation frequently hampers correct homologization with the female condition. In all other copepod orders, leg 5 sexual dimorphism is limited to modest transformation in segmentation and number of armature elements. Conversely, female calanoids – in contrast to males – show an amazing variety in genital structures. This diversity in configurations between genital apertures, copulatory pore(s) and their connecting ducts is unrivalled in the Copepoda (Huys & Boxshall, 1991; Ohtsuka et al., 1994; Cuoc et al., 1997; Barthélémy et al., 1998). The nature of each of these three categories of sexual dimorphism is unique to calanoids; however, homology-based unifying patterns that could provide

diagnostic apomorphies for the entire order have yet to be identified.

Mate location and recognition are essentially asymmetrical processes in the reproductive biology of copepods. The male is the active partner during these phases and its primary role is geared towards locating and catching the largely passive partner, the female. Consequently, the male is adapted for its locating role and its success can be enhanced through signals provided by the female. It is conceivable that this behavioural asymmetry led to the evolution of sexual dimorphism in copepods. This phenomenon is central to our understanding of the species-specific sequence of mating and post-mating behavioural processes observed in calanoids: (1) mate recognition by the male; (2) capture of the female by the male; (3) transfer and attachment of a spermatophore by the male; (4) fertilization and release of eggs by the female; and (5) removal of discharged spermatophores by the female (cf. Lee, 1972; Blades, 1977; Blades & Youngbluth, 1979; Jacoby & Youngbluth, 1983; Blades-Eckelbarger, 1991; Vaupel Klein, 1998; present study). Interspecific reproductive isolation mechanisms rely on chemical, mechanical and behavioral barriers, all of which can be collectively promoted by sexual dimorphism (Blades-Eckelbarger, 1991).

The aim of this review is to interpret calanoid sexual dimorphism and its putative functions from a behavioral and evolutionary perspective, primarily by addressing the following two questions: (1) Which sexually dimorphic structures are involved in each of the five sequential events identified during calanoid mating and post-mating? (2) What is the evolutionary significance of sexual dimorphism?

Materials and methods

Calanoid copepods examined in the present study were mainly collected from both shallow and deeper waters in the Seto Inland Sea and off the Nansei Islands, western Japan, during 1992–1999, using plankton nets, dredges and sledge-nets (mesh size 0.1–0.3 mm): (1) superfamily Pseudocyclopoidea: *Pseudocyclops* spp.; (2) superfamily Epacteriscoidea: *Ridgewayia boxshalli* Barthélémy, Ohtsuka & Cuoc, 1998; *Placocalanus inermis* Ohtsuka, Fosshagen & Soh, 1996; *P. longicauda* Ohtsuka, Fosshagen & Soh, 1996; and, *P. brevipes* Ohtsuka, Fosshagen & Soh, 1996; (3) superfamily Arietelloidea: *Lucicutia*

magna Wolfenden, 1903; *Metridia pacifica* Brodsky, 1950; *Neorhabdus latus* (Sars, 1905); *Pleuromamma xiphias* (Giesbrecht, 1889); *P. abdominalis* (Lubbock, 1856); and, *Nullosetigera helgae* (Farran, 1908); (4) superfamily Centropagoidea: *Candacia bipinnata* (Giesbrecht, 1889); *C. longimana* (Claus, 1863); *Labidocera acuta* (Dana, 1849); *L. japonica* Mori, 1935; *Pontellina plumata* (Dana, 1849); *Pontellopsis tenuicauda* (Giesbrecht, 1889); *P. strenua* (Dana, 1849); *P. yamadae* Mori, 1937; *Temora discaudata* Giesbrecht, 1889; *Tortanus Atortus longipes* Brodsky, 1948; *T. A. rubidus* Tanaka, 1965; and, *T. A. terminalis* Ohtsuka & Reid, 1998; (5) superfamily Megacalanoidea: *Acrocalanus gibber* Giesbrecht, 1888; *A. monachus* Giesbrecht, 1888; *Calanus sinicus* Brodsky, 1962; *Calocalanus styliremis* Giesbrecht, 1888; *Cosmocalanus darwini* (Lubbock, 1860); *Megacalanus princeps* Wolfenden, 1904; and, *Paracalanus parvus* (Claus, 1863) s.l.; (6) superfamily Bathypontioidea: *Temorites longicornis* (Tanaka, 1965); and, *T. spinifera* (A. Scott, 1909); (7) superfamily Eucalanoidea: *Eucalanus attenuatus* (Dana, 1849); *E. hyalinus* (Claus, 1866); and, *E. mucronatus* Giesbrecht, 1888; (8) superfamily Clausocalanoidea: *Euchaeta rimana* Bradford, 1974; *Gaetanus kruppi* Giesbrecht, 1903; *Lophothrix frontalis* Giesbrecht, 1895; *Paraeuchaeta barbata* (Brady, 1883); *P. media* (Giesbrecht, 1888); *P. sarsi* (Farran, 1908); *P. tuberculata* A. Scott, 1909; and, *Scottocalanus securifrons* (T. Scott, 1894). *Pseudocyclops minutus* Ohtsuka, Fosshagen & Putchakarn, 1999 was collected from Phuket, Thailand (Ohtsuka et al., 1999). In addition, material of *Ryocalanus bowmani* Markhaseva & Ferrari, 1995 (Ryocalanoidea) deposited in the Smithsonian Institution was also examined. Copepods were observed with light (Nikon Optiphoto) and scanning electron (JEOL T-20) microscopes. Terminology follows Huys and Boxshall (1991).

Results and discussion

(1) Mate recognition

Antennulary chemosensory system
It is now widely accepted that for successful mate recognition (and copulation) most copepods rely heavily on sensory modalities other than vision, such as mechano- and/or chemoreception. Although direct neurophysiological evidence is still lacking, it is generally assumed that the male actively searches for sex pheromones released by the female, mainly by means of its array of chemosensory aesthetascs on the antennules (Katona, 1973; Griffiths & Frost, 1976; Snell & Carmona, 1994 Boxshall et al., 1997). According to Katona (1973) and Snell & Morris (1993), these gynopheromones released by females attract males from a distance, are species-specific and appear highly soluble in order to minimize the energetic cost involved in loss of the diffusing signal.

Aesthetascs are generally more numerous and frequently larger in male copepods. Boxshall & Huys (1998) remarked that the most significant qualitative change in the ontogeny of the male calanoid antennules is the acquisition of additional aesthetascs at the final moult from the fifth copepodid stage to the adult. The timing of appearance of these sexually dimorphic aesthetascs strongly indicates their function in mate recognition. The ancestral condition for calanoids is the presence of one aesthetasc on every antennulary segment, except the segment representing the ancestral segment XXVI (Huys & Boxshall, 1991). In males of many marine calanoid families, secondary multiplication (mainly doubling) of aesthetascs is distinct, and it has been speculated that this enhancement of the chemosensory system is correlated with the colonization of the open pelagic environment where chemical cues are of paramount importance (Huys & Boxshall, 1991; Boxshall & Huys, 1998). In fact, in species residing in freshwater and neritic waters (superfamily Centropagoidea) or the hyperbenthic zone (families Arietellidae, Boholinidae, Pseudocyclopidae, Pseudocyclopiidae, Ridgewayiidae, Stephidae), where chemical cues may be less important than in oceanic regions, males rarely bear multiple aesthetascs on the antennules (Huys & Boxshall, 1991; Boxshall & Huys, 1998; Ferrari & Benforado, 1998; present study).

Doubling of aesthetascs in the male is usually restricted to the proximal segments of the antennule (segments I–XIV) except for *Eucalanus* Dana (Eucalanidae) in which each of the ancestral segments II–XXIV carries two aesthetascs. This addition at the final moult of male *E. attenuatus* is equivalent to a doubling of the aesthetascs present in the female (Fig. 1). Many of these additional aesthetascs are located within the high velocity zone of the scanning current generated by the antennae and the mandibular and maxillulary palps, and are well positioned to sample any gynopheromones which could reveal the presence of females (Katona, 1973; Griffiths & Frost, 1976; Boxshall et al., 1997). Aesthetasc multiplication

is typically expressed on odd ancestral segments III, V, VII, IX and XI, except for some genera such as *Clausocalanus* Giesbrecht, *Spinocalanus* Giesbrecht and *Euchaeta* Philippi which may have secondarily lost certain double aesthetascs (Boxshall et al., 1997; present study). The alternate distribution pattern of multiple aesthetascs on odd segments only may effectively avoid overlapping of aesthetascs across the scanning current.

Sexually dimorphic multiplication of aesthetascs seems to be almost exclusively restricted to males of certain genera in the relatively derived superfamilies Eucalanoidea (Eucalanidae), Clausocalanoidea (Aetideidae, Clausocalanidae, Euchaetidae, Phaennidae, Pseudocyclopiidae, Scolecitrichidae), Ryocalanoidea (Ryocalanidae), Bathypontioidea (Bathypontiidae), Megacalanoidea (Calanidae, Calocalanidae, Megacalanidae, Paracalanidae) and, extremely rarely, in the primitive Arietelloidea (Arietellidae). Exceptionally, secondary aesthetasc doubling is expressed on the antennules of both sexes. This evolutionary multiplication on the proximal segments took place in some genera of the families Augaptilidae within the superfamily Arietelloidea (*Augaptilus* Giesbrecht, *Centraugaptilus* Sars, *Euaugaptilus* Sars, *Haloptilus* Giesbrecht (in Giesbrecht & Schmeil), *Pseudhaloptilus* Wolfenden), Metridinidae (*Metridia* Boeck, *Pleuromamma* Giesbrecht (in Giesbrecht & Schmeil)) and Heterorhabdidae (*Neorhabdus* Heptner), and independently in the Candaciidae, the only family in the Centropagoidea that has successfully colonized the open-pelagic zone (Giesbrecht, 1892; Ohtsuka et al., 1997; Soh, 1998; present study). In these taxa aesthetascs may play a role not only in mate tracking but also in the detection of food and/or in the exchange of chemical information between both sexes. Indirect supporting evidence for the reciprocity of the latter mechanism is provided by recent behavioural studies of *Temora longicornis* (Müller, 1792) (Centropagoidea) which lacks multiple aesthetascs in both sexes. Females of this species seem to react to chemical exudates of male conspecifics by changes in their swimming motion (and hence, hydromechanical signal), in order to increase the encounter probability with potential mates (Van Duren & Videler, 1996; Van Duren et al., 1998).

Huys & Boxshall (1991) speculated that the addition of aesthetascs in males of derived superfamilies occurred secondarily when they colonized the open oceanic waters. Sexually dimorphic double aesthetascs evolved independently at least twice in the Calanoida, once (or possibly also twice) within the Arietelloidea, and a second time in the common ancestor of the lineage comprising the superfamilies Megacalanoidea, Bathypontioidea, Eucalanoidea, Clausocalanoidea and possibly Ryocalanoidea (Boxshall & Huys, 1998). The oceanic Candaciidae (Centropagoidea) represent an independent line of evolution, since double aesthetasc numbers, when present, always occur in both sexes. However, since some taxa of the most primitive families in the Arietelloidea, the Metridinidae and Augaptilidae, bear multiple aesthetascs on the proximal antennulary segments in both sexes (Soh, 1998), this pattern might well be the ancestral one in these families. Boxshall & Huys (1998) remarked that aesthetascs are evolutionary labile and character reversal cannot be excluded. We hypothesize that the secondary loss of double aesthetascs in females of the arietelloidean genera that have colonized the open pelagic is the result of suppression by heterochrony, either by progenesis (early cessation of development), neoteny (slower developmental rate) or post-displacement (later initiation of development). It is conceivable that various heterochronic processes may have played an important role in the enhancement or simplification of the chemosensory system when new habitat shifts occurred within families.

Trophic dimorphism

Planktonic calanoids belonging to a wide range of families have independently evolved non-feeding males. Mouthpart atrophy of males in some lineages can be correlated with enhancement of the chemosensory capacity of the male antennule (Boxshall et al., 1997). In the Euchaetidae, females are powerful predators, and the non-feeding strategy in the males may therefore have evolved as a means of preventing cannibalism. This is discussed in detail below.

Integumental organs

Other chemosensory organs, such as the cephalic dorsal humps in some males of the Megacalanoidea (Nishida, 1989), and, presumably, the complex cephalic dorsal structure in male *Pterochirella tuerkayi* Schulz, 1990 (Aetideidae) may also be involved in mate recognition, although Schulz (1990) speculated that the latter may be involved in attachment to the bottom or to an animal host.

Blades-Eckelbarger (1991) claimed that integumental organs such as hair-sensilla and glandular pores (e.g. Vaupel Klein, 1982; Hulsemann & Flem-

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXV	XXVI	XXVII	XXVIII
EUCALANIDAE		●	★	●	★	●	★	●	★	●	★	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
AETIDEIDAE (1)			★	●	★	●	★	●	★																			
AETIDEIDAE (2)			★		★		★	●	★		★																	
MEGACALANIDAE			★		★		★		★		★	●	●	●														
RYOCALANIDAE			★		★		★	●	★	●	★	●	●															
BATHYPONTIIDAE			★		★		★		★		★	●	●															
CALANIDAE			★		★		★		★		★																	
PARACALANIDAE			★		★		★		★		★																	
CALOCALANIDAE			★		★		★		★		★																	
SCOLECITRICHIDAE			★		★		★		★		★																	
SPINOCALANIDAE			★		★		★		★																			
ARIETELLIDAE		●	★	●																								
EUCHAETIDAE		●	★																									

Figure 1. Distribution of double aesthetascs on the male antennule of selected families. I–XXVIII: number of ancestral segment; closed asterisk: double aesthetascs on segments III, V, VII, IX and XI; closed circle: double aesthetascs on other segments. (1) *Aetideus armatus* (Boeck, 1873); (2) *Pterochirella tuerkayi* Schulz, 1990. Data from Giesbrecht (1892); Frost & Fleminger (1968); Damkaer (1975); Bradford et al. (1983); Fleminger (1985); Schulz (1990); Ohtsuka et al. (1994); Markhaseva & Ferrari (1996); Boxshall et al. (1997); Soh (1998); present study. Note: the family Calocalanidae is now relegated to a junior synonym of the family Paracalanidae (Andronov, 1970; Bradford–Grieve, 1994).

inger, 1990) may play an important role during mate recognition in calanoids which lack highly modified secondary sexual characters, such as the Eucalanoidea and Megacalanoidea (Fleminger, 1973; Fleminger & Hulsemann, 1977). It has been repeatedly suggested that such integumental organs may function as a communication system of receptors and effectors (Fleminger, 1973, 1975; Fleminger & Hulsemann, 1977; Hulsemann & Fleminger, 1990). At each step of ritualized mating behaviour, there may be signals recognized by each sex, particularly involving the integumental organs on the geniculate antennule (in some taxa), the urosome and leg 5 in male (see Fig. 9B), and the prosome and urosome in female. Integumental organs, in particular mechanoreceptive hair- and peg-sensilla, appear to play important roles in calanoids that produce spermatophores with complex coupling plates such as pontellids. For example, Hulsemann & Fleminger (1990) found that the pore signature pattern and other epicuticular structures on the female urosome differ greatly in sibling species of *Pontellina* Dana, and it is conceivable that similar interspecific differences are to be found on the urosome and leg 5 of their respective males. Such integumental features may provide the male with mechanical signals, confirming that he has captured a conspecific female, and may provide topographic information ne-

cessary to determine the orientation of the female genital double-somite during mating. The latter is a critical step in the mating encounter since the grip of the male's leg 5 on the female's urosome must be positioned precisely to enable the male to place the spermatophore coupler correctly (Blades, 1977; Blades & Youngbluth, 1979; Jacoby & Youngbluth, 1983; Blades-Eckelbarger, 1991).

Vision and bioluminescence

Visual mate recognition may be important in the Pontellidae, which are typically colorful and mostly live in well-lit, oceanic surface waters. The nauplius eye in these calanoids has separated into three separate eyes, and in genera such as *Anomalocera* Templeton, *Epilabidocera* Wilson, *Labidocera* Lubbock, *Pontella* Dana and *Pontellina* there is distinct sexual dimorphism in eye design, with the males having the larger eyes. The eye of *Pontella* males is a highly sophisticated 'centre and surround' spot detector (Land, 1984, 1988) and is almost certainly involved in mate recognition as it could provide a mechanism for detecting spots of one color against a background of another. Some pontellid genera are strongly colored with blue or green pigment (cf. Giesbrecht, 1892, Plate 1, Fig. 6; Plate 3, Fig. 9) and many display sexually dimorphic color patterns which may be related to mate recogni-
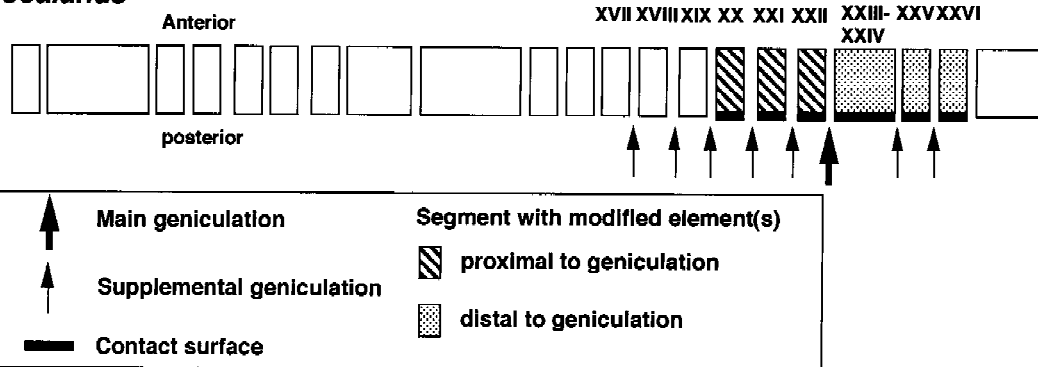
446
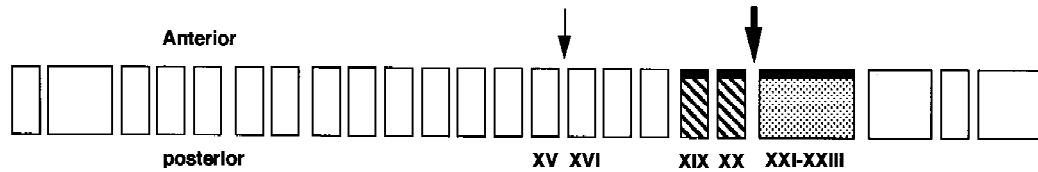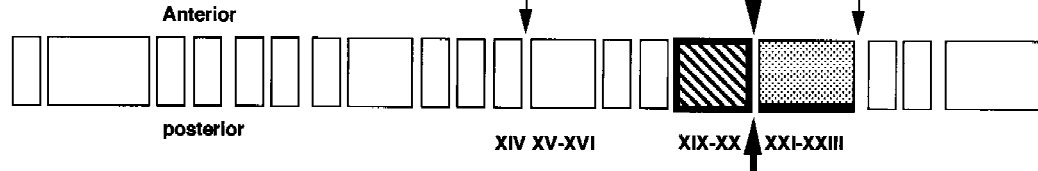
Figure 2. Schematic illustrations of 3 types of geniculate antennules in male calanoids. In *Bathypontia* the compound segment XIX-XX bears modified elements and functions as a contact surface in grasping females. Note: the genus *Barhypontia* Sars is relegated to a junior synonym of the genus *Temorites* sars (Bradford-Grieve, 1999).

tion. Recognition by means of color is presumably of limited importance in oceanic communities because of the rapid extinction of most wavelengths with depth. The presence of elaborate eyes in both pontellid sexes may also indicate partial involvement in prey-capture. Some representatives of the Centropagidae (*Centropages* Krøyer), Aetideidae (*Chiridius* Giesbrecht) and Phaennidae (*Cephalophanes* Sars) also have elaborate nauplius eyes, but no sexual dimorphism is expressed.

All species of Metridinidae and most Heterorhabdidae and Lucicutiidae are bioluminescent (Herring, 1988). At least some Augaptilidae and Megacalanidae also show luminous capability, but most other marine calanoids are non-luminous. Although males and females have a fundamentally similar distribution pattern of luminous glands, sexual differences in the intensity of light emission have been reported for some calanoid genera (e.g. *Pleuromamma*; see references in Herring (1988)) suggesting a signalling role in mate recognition or mating behavior in general.

Mechanical cues
It is likely that mate seeking in copepods, like searching for food, is a process where chemoreception and mechanoreception work in conjunction (Van Duren et al., 1998). In the low-to-intermediate Reynolds number regime, where planktonic copepods operate, a hydromechanical signal gives strongly directional information (Yen & Strickler, 1996; Yen et al., 1998). Recent experimental designs have produced accumulating evidence that males can detect and pursue females using mechanical cues from the females' swimming wake. Strickler & Bal (1973) first suggested that mechanical cues may be involved in mate recognition, and this hypothesis appears to be supported by the fact that sexual dimorphism in the shape of the posterior prosomal margin and the urosome is primarily found in the families of the Centropagoidea which
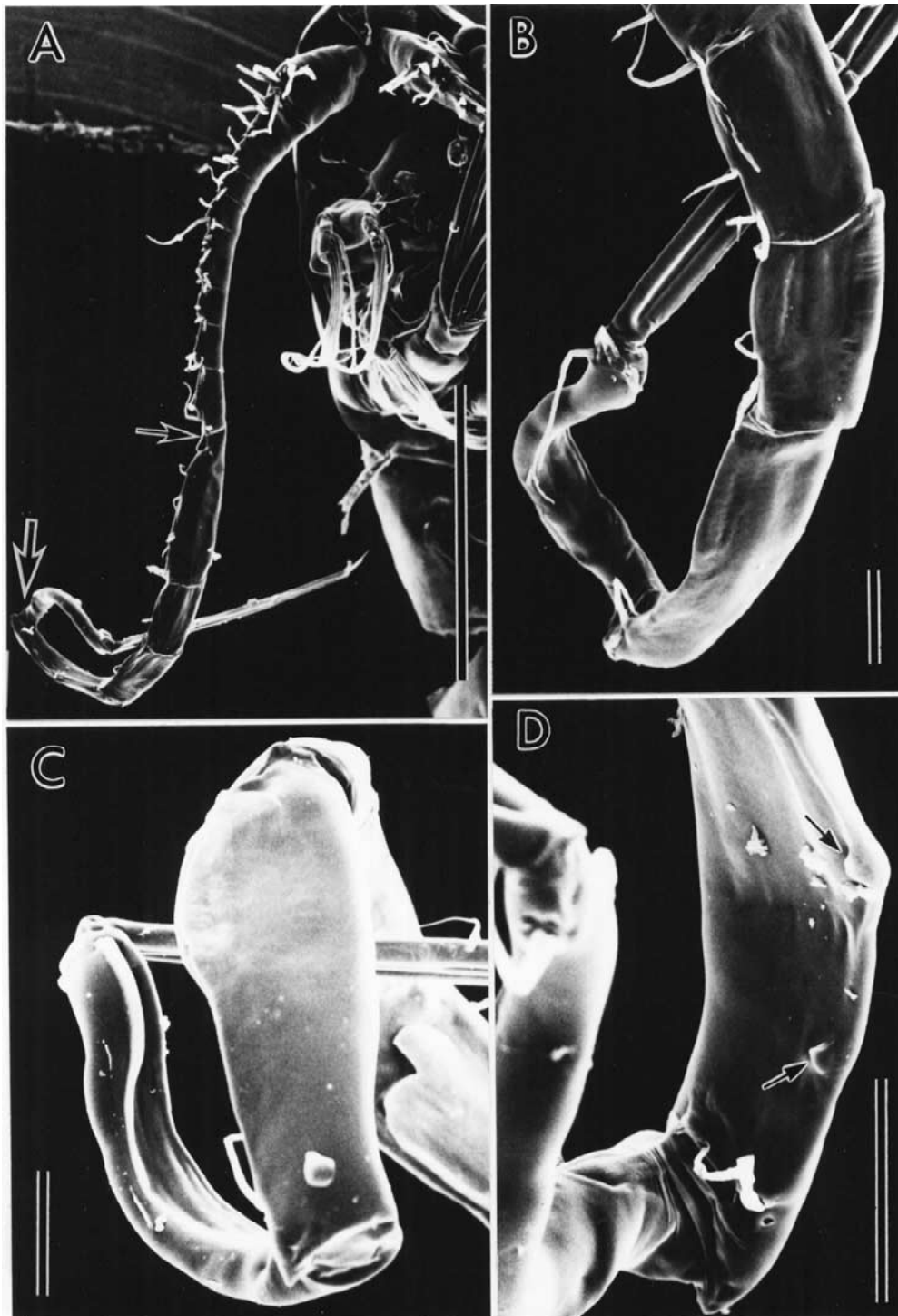
Figure 3. Antennules of male *Temorites longicornis* (Tanaka, 1965). (A) Right antennule (this specimen probably showing grasping position), main and supplemental geniculations indicated by large and small arrow, respectively; (B) Compound segment XVII–XXIV; (C) Compound segments XIX–XX and XXI–XXIII around hinge; (D) Compound segment XIX–XX, modified elements arrowed. Scale = 1 mm (A); 0.1 mm (B–D).
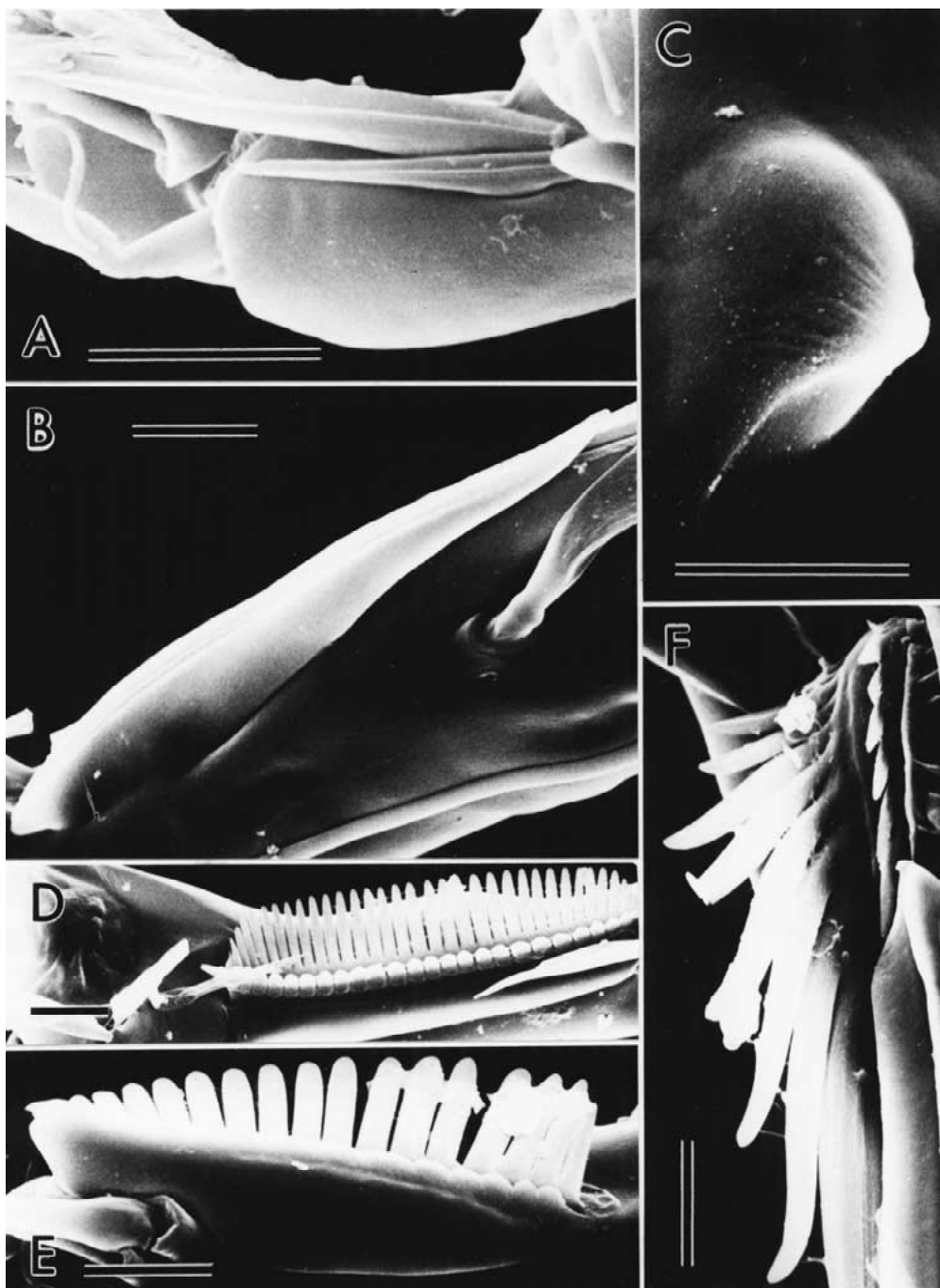
448

Figure 4. Modified elements on geniculate antennule of male. (A) Compound segment XXI–XXIII of *Pseudocyclops ensiger* Ohtsuka, Fosshagen & Putchakarn, 1999; (B) Compound segment of *Nullosetigera helgae* (Farran, 1908); (C) Compound segment XIX–XX of *Temorites longicornis* (Tanaka, 1965); (D) Compound segment XXI–XXIII of *Temora discaudata* Giesbrecht, 1889; (E) Segment XIX of *T. discaudata*; (F) Compound segment XXI–XXIII of *Pontellina plumata* (Dana, 1849). Scale = 0.01 mm (A–F).

lack double aesthetascs on the male antennules. Females in these families typically possess wing-like expansions or acute protrusions on the posterior prosomal margins, complex urosomal morphology and enlarged modified caudal setae. Similarly, in the primitive anchialine cave-dwelling Epacteriscidae, females typically have asymmetrically modified caudal rami, with seta V elongated on one side only and with left seta VI ornamented with a setular tuft near the base (Fosshagen et al., 2001). Another example of caudal ramus sexual dimorphism is found in the Euchaetidae, where most members show distinct differences in the length and morphology of caudal ramus seta VI (e.g. *Paraeuchaeta norvegica* (Boeck, 1863): Sars (1902)). These sexually dimorphic modifications may produce species-specific hydrodynamic (mechanical) cues, which are short-lived, directional and traceable over time and distance. The less enhanced male chemosensory system in these families appears, therefore, to be counterbalanced by the females playing a more active role in attracting males.

(2) Mate capture

Males with a geniculate antennule capture the female's caudal rami or urosome before transfer and attachment of the spermatophore (Lee, 1972; Katona, 1973; Blades, 1977; Blades & Youngbluth, 1979; Jacoby & Youngbluth, 1983; Blades-Eckelbarger, 1991). In contrast, little is known about how males without a geniculate antennule capture their mates (Mauchline, 1998). In the former, the main hinge is usually located between ancestral segments XX and XXI (Huys & Boxshall, 1991), and it enables the antennule to fold in upon itself in such a way that the anterior edges of ancestral segments XX and XXI are opposed (Blades, 1977) (Fig. 2). The present study reveals another two types of male geniculate antennules, on the basis of the configuration of intrinsic and extrinsic muscles and the distribution of modified elements as grasping organs. In *Temorites* Sars (Bathypontiidae) (Figs 2 and 3), the main geniculation is located between ancestral segments XX and XXI, corresponding to the neocopepodan geniculation found in generalized forms. However, the posterior edge of the compound segment XXI–XXIII (Figs 2 and 3) is bent antero-laterally to form a grasping device opposing the dorsal side of the compound segment XIX–XX, which is expanded and carries two short hook-like grasping elements (Fig. 3D, arrowed; Fig. 4C). The posterior edge of XXI–XXIII is curved at the mid-point and

bears a groove with a longitudinal ridge, probably representing a highly modified element (Fig. 3C). The third type is found in *Ryocalanus* Tanaka (Ryocalanidae), which differs completely from the other two types, as Tanaka (1956) has already pointed out. The main hinge is located at segmental boundary XXII–XXIII, and the antennule folds back upon itself in such a way that the posterior edges of segments XX–XXVI are opposed. Judging from the configuration of antennulary elements proposed by Huys & Boxshall (1991), the proximal processes on segments XX, XXI, XXII, and probably XXIII are modified elements, whereas the serrated structures along the posterior edges of segments XXV and XXVI seem not to be true elements.

Grasping efficiency of the male antennules can be enhanced by the development of supplemental hinges. These are common in the Cyclopoida and Misophrioida, but generally rare in the Calanoida (Huys & Boxshall, 1991; Boxshall & Huys, 1998) although found in all three types of geniculated antennules (Fig. 2). In *Heterorhabdus* Giesbrecht (in Giesbrecht & Schmeil), which belongs to the first type, a supplemental hinge is found between segments XV and XVI (Boxshall & Huys, 1998) while in *Labidocera aestiva* Wheeler, 1901, a major accessory articulation point is located between segments XIX and XX (Blades & Youngbluth, 1979). In *Temorites* it is located at segmental boundary XIV–XV while in *Ryocalanus*, five and two supplemental geniculations are present proximal and distal to the neocopepodan geniculation, respectively. Supplemental geniculations in *Heterorhabdus*, *Labidocera* and *Temorites* are supposed to function in drawing the female close and/or in the male orientating himself with respect to the female just before transfer of the spermatophore with leg 5, rather than in the direct capture of the female. On the other hand, *Ryocalanus* seems to utilize these supplemental geniculations to capture the female directly.

The degree of modification of armature elements on either side of the geniculation is variable in the Calanoida (Fig. 4). The simplest modification is a sclerotized spiniform process with the proximal part fused to the segment and distally free (Fig. 4A, B). The Epacteriscoidea, Pseudocyclopoidea (Fig. 4A), Megacalanoidea and the majority of the Arietelloidea (Fig. 4B) exhibit such simple transformations of setae and spines. Elaborate modifications, involving the formation of comb-like or serrated structures along the anterior ridge of the modified element, are found in members of the superfamily Centropagoidea, such
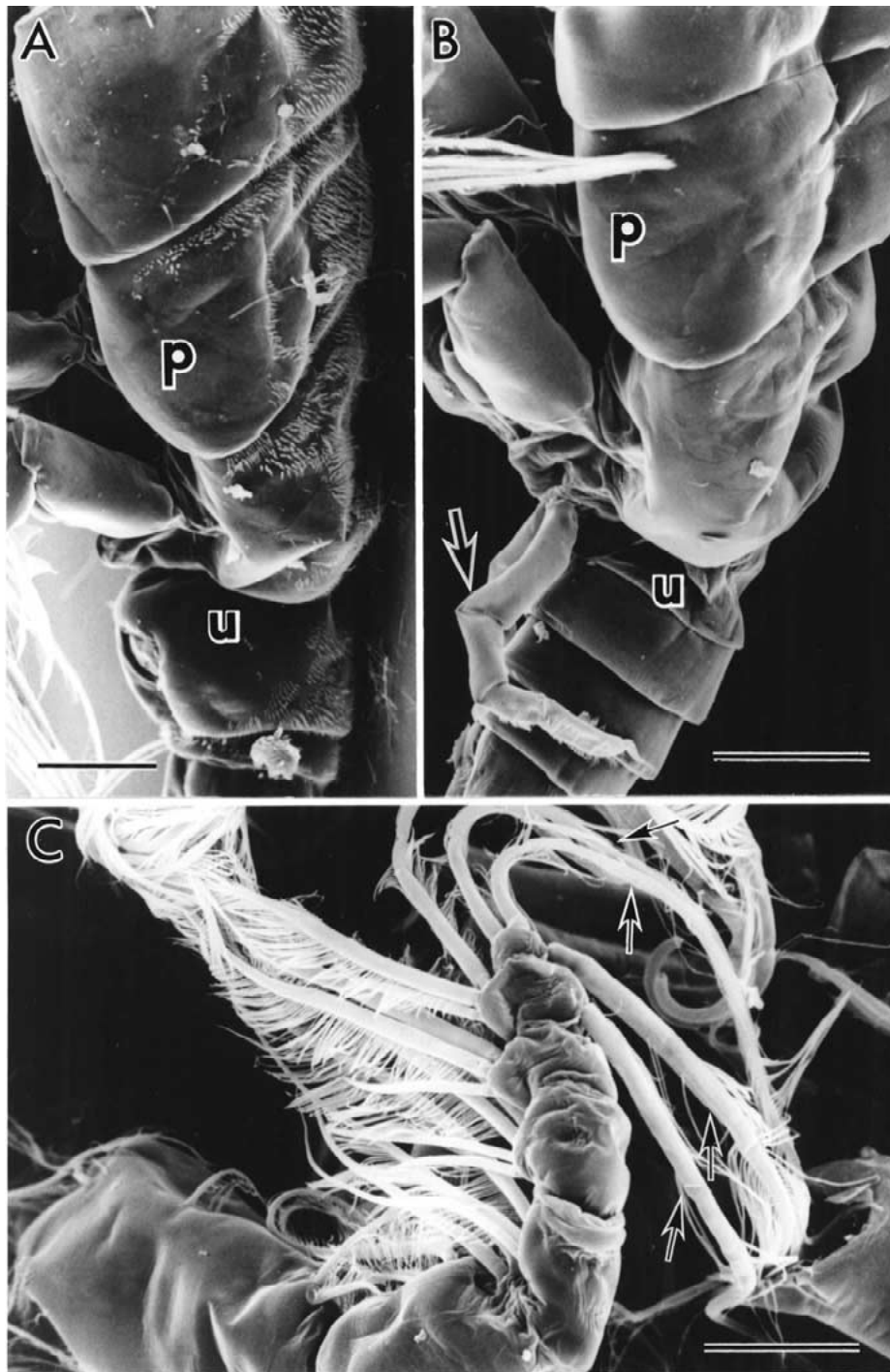
Figure 5. Eucalanus attenuatus (Dana, 1849), female (A), male (B, C). (A) Pedigers 2–5 (p) and urosome (u), lateral; (B) Pedigers 3–5 (p) and urosome (u), lateral, leg 5 arrowed; (C) Maxilliped, laterally directed setae arrowed. Scale = 0.2 mm (A, B); 0.1 mm (C).

as *Temora discaudata* (Fig. 4D, E) and *Pontellina plumata* (Fig. 4F), and parts of the Arietelloidea. In *Temorites*, two elements are modified into simple, short hook-like prominences (Fig. 4C). These modifications certainly guarantee secure clasping of the female during spermatophore transfer (Blades, 1977, Blades & Youngbluth, 1979).

Recently, some information on mechanisms of capture of females by males without a geniculate antennule has become available. In the Euchaetidae, the male grasps the female urosome with his right leg 5, facing in the opposite direction from the female (Mauchline, 1998). In the Calanidae, the male holds the lateral sides of the female prosome with both his maxillipeds (Tsuda & Miller, 1998). In several calanid genera, the outer setae of the last two endopod segments of the maxilliped are typically reflexed in the male (except for those with reduced mouthparts). This modification in combination with the size difference of the male maxilliped may be an adaptation for clasping the female's prosome by the male situated dorsally. Spermatophore transfer can be carried out by the left leg 5 in both Calanidae and Euchaetidae. Although the copulatory behaviour of the Eucalanoidea has not been observed yet, it may be similar to that of the Calanidae, based on the structure of the non-geniculate antennules and non-grasping fifth legs in males. In female *Eucalanus attenuatus* (Fig. 5A), the dorsal and lateral sides of the last three prosomites (pedigers 2–5) are covered with minute spinules, which may function in helping the male to grasp the female, as in the Calanidae (Tsuda & Miller, 1998). These spinules are completely lacking in the male (Fig. 5B). The maxilliped is relatively shorter in the male than in the female, and the plumose setae on the basis and endopod are much better developed in the male (Fig. 5C). The inwardly directed plumose setae on the basis and endopod of the male maxilliped may function in grasping, whereas outwardly directed setae (Fig. 5C, arrowed) on the fifth and sixth endopodal segments may play a restricted role in generating a scanning current, together with the antennae, mandibles and maxillules. Such sexual dimorphism has not been observed in the prosome of *Calanus sinicus* although both sexes of this species bear paired patches of minute integumental ridges dorsolaterally on the second to the fifth pedigerous somites (Fig. 6).
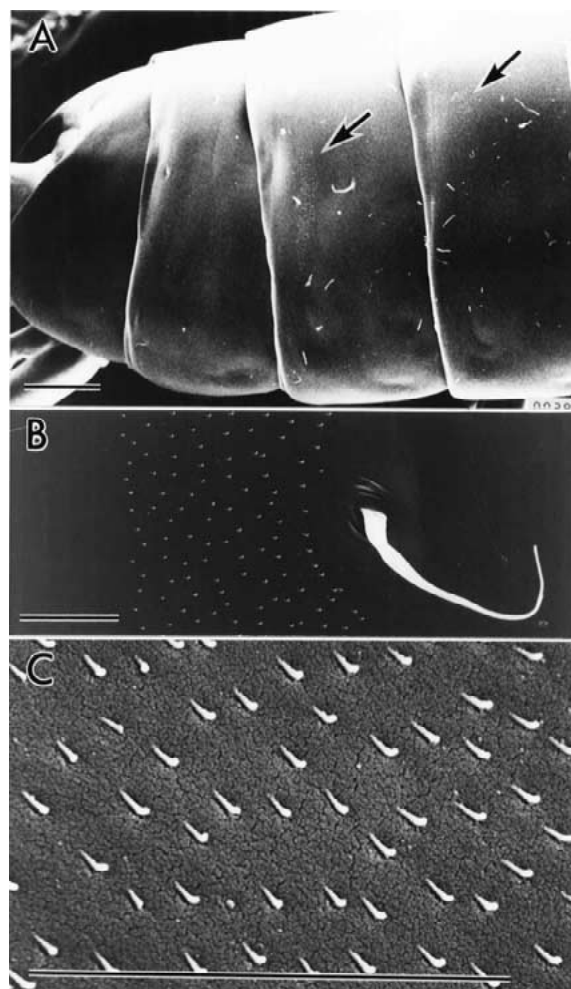

Figure 6. Lateral view of pedigers 2–5 of female *Calanus sinicus* Brodsky, 1962. (A) Pedigers 2–5, lateral, dorsolateral patch of minute ridges arrowed (not clearly seen in pedigers 4 and 5, but similar patches present); (B) Dorsolateral patch of minute ridges on pediger 3; (C) Magnification of dorsolateral ridges. Scale = 0.1 mm (A, B); 0.01 mm (C).

(3) Spermatophore transfer and attachment

Copulation comprises a series of sequential events during the transfer and attachment of a spermatophore from the male to the female (Blades, 1977). After a spermatophore is extruded from the posterior slit-like opening of the left (or right, in parts of the Arietelloidea, Clausocalanoidea and Spinocalanoidea) margin of the male genital somite (Heberer, 1932; Blades & Youngbluth, 1979), it is attached to the genital double-somite of the female by the male leg 5 (Blades, 1977; Blades & Youngbluth, 1979; Jacoby & Youngbluth, 1983; Blades-Eckelbarger, 1991). The

452

spermatophore provides an efficient vehicle by which the aflagellate and presumably amoeboid spermatozoa can be transferred to the female. Glycoproteins on the surface of the female genital double-somite can be informative as a potential signal for the male when attaching a spermatophore (Snell & Carmona, 1994).

In the centropagoideans with a geniculate antennule in the male, the chelate right leg 5 instead of the antennulary hold is used to grasp the female urosome, and the left leg 5 transfers and attaches an extruded spermatophore to the female genital double-somite (Katona, 1973, 1975; Blades, 1977; Blades & Youngbluth, 1979; Jacoby & Youngbluth, 1983). Although the function of leg 5 has never been elucidated in the taxa without a geniculate antennule in the male, it is possible to some degree to make inferences from a functional morphology point of view.

Basically, male fifth legs can be classified into three functional types: (1) both legs present, usually biramous, with functional swimming setae; (2) both legs present, uniramous or biramous, without functional swimming setae, sometimes highly modified into a grasping organ (see Fig. 9A, B); (3) only one functional leg present, uniramous, without functional swimming setae (see Fig. 5B). The first type retains not only mating but also swimming functions in association with legs 1–4, while the other two types are engaged only in mating. Since in most males, except for the Arietelloidea (Soh, 1998) and parts of the Spinocalanoidea and Clausocalanoidea (Frost & Fleminger, 1968; Damkaer, 1975), a single male genital aperture opens on the left side, the spermatophore is transferred to the female by the male left leg. In some taxa displaying the first and second types, the right leg retains its hold on the female until placement of the spermatophore is completed (Lee, 1972; Katona, 1975; Blades, 1977; Blades & Youngbluth, 1979; Blades-Eckelbarger, 1991). The spermatophore extruded from the genital aperture is either temporarily attached to a tuft of fine setules on the terminal or subterminal part of the left exopod as in the Pontellidae (Centropagoidea) (Blades & Youngbluth, 1979), gripped by terminal spines/spiniform processes on the left exopod as in the Centropagidae (Centropagoidea) (Blades, 1977), and/or grasped by some modified elements or segments as in the Euchaetidae (Clausocalanoidea) (Ferrari, 1978; Blades-Eckelbarger, 1991). These three spermatophore transfer mechanisms can probably be applied to other taxa.

Figure 7. Terminal exopodal segments of male left leg 5. (A) *Calanus sinicus* Brodsky, 1962; (B) *Candacia bipinnata* Giesbrecht, 1889; (C) *Eucalanus mucronatus* Giesbrecht, 1888; (D) *Paraeuchaeta tuberculata* A. Scott, 1909; (E) *Labidocera acuta* (Dana, 1849); (F) *Scottocalanus securifrons* (T. Scott, 1894). Scale = 0.1 mm (A, C); 0.2 mm (B, F); 0.5 mm (D, E).

Tufts of fine setules on the terminal/subterminal portion of the left exopod (right if the genital aperture is on the right side) are found in such taxa as: Arietellidae, Hyperbionychidae, Lucicutiidae, Metridinidae and Nullosetigeridae (Soh et al., 1999) (Arietelloidea); Acartiidae, Candaciidae (Fig. 7B), Diaptomidae, Pseudodiaptomidae, Pontellidae (Figs 7E and 9C), Temoridae and Tortanidae (Centropagoidea); Calanidae (Fig. 7A) (Megacalanoidea); *Temorites* (Bathypontioidea); Eucalanidae (Fig. 7C) (Eucalanoidea); *Ryocalanus* (Ryocalanoidea); Aetideidae, Clausocalanidae, Euchaetidae (Fig. 7D), Phaennidae, Scolecitrichidae, and Tharybidae (Clausocalanoidea); *Spinocalanus* (Spinocalanoidea) (cf. Giesbrecht, 1892; Frost & Fleminger, 1968; Deevey, 1973; Damkaer, 1975; Bradford et al., 1983; Ferrari & Dojiri, 1987; Blades-Eckelbarger, 1991; Andronov, 1992; Ohtsuka et al., 1993; Markhaseva, 1996; Markhaseva & Ferrari, 1996; Soh 1998; present study). Alternatively, in some members of the Clausocalanoidea and Mega-
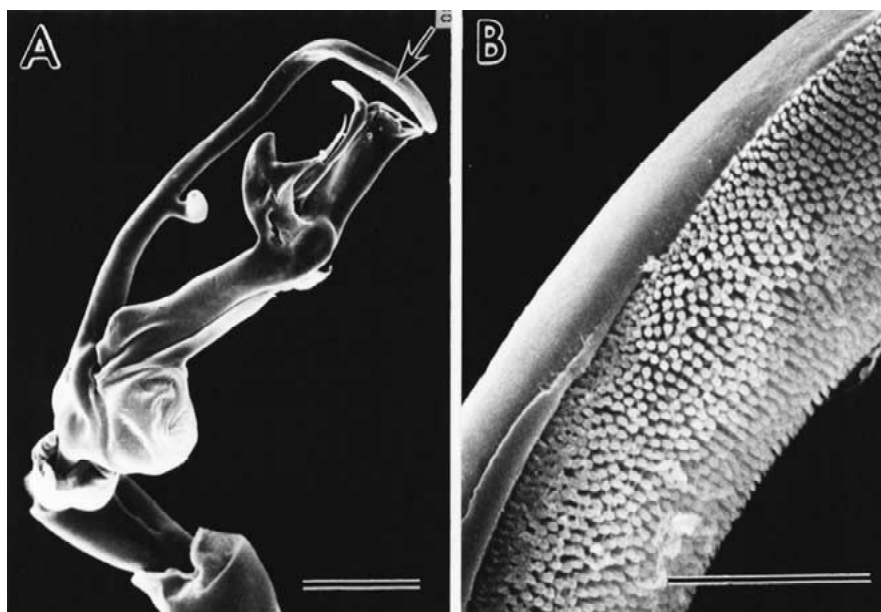
Figure 8. Left exopodal segments of male *Cosmocalanus darwini* (Lubbock, 1860). (A) Left exopod, arrowed part magnified in B; (B) Magnification of terminal inner surface of outer process on second segment. Scale = 0.1 mm (A); 0.01 mm (B).

calanoidea, the second exopodal segment of the left leg 5 bears patches of fine spinules (*Scottocalanus securifrons*; Fig. 7F) or granules (*Cosmocalanus darwini*; Fig. 8), which may also function in grasping the spermatophore.

Two or all of these three male leg 5 types may sometimes be found within a single superfamily. Members of the primitive superfamily Epacteriscoidea display the first type while members of the equally primitive Pseudocyclopoidea exhibit either the first or the second type. In contrast, species belonging to the derived superfamilies Bathypontioidea, Eucalanoidea, Ryocalanoidea, Spinocalanoidea and Clausocalanoidea usually display the second or the third type. Taxa belonging to the Arietelloidea and Centropagoidea are assignable to the first or the second type. Finally, the Megacalanoidea exhibit all three types. The distribution of each of the three leg types in the currently recognized superfamilies suggests that evolutionary plasticity in the mode of spermatophore transfer is considerable. It is conceivable that identical mechanisms have been adopted by different superfamilies but changed subsequently and independently many times in the course of evolution.

Calanoid spermatophores are basically classified into two morphological types (Blades-Eckelbarger, 1991). In the majority of the calanoids, spermatophores are simple, tube-shaped flasks, narrowing into a neck of variable length. They adhere to the female by a cement-like secretion present on the outside of the neck or by secretions extruded from the spermatophore itself. In some members of the Centropagidae, Pontellidae, Pseudodiaptomidae and Tortanidae (Centropagoidea) the spermatophore flask is connected to a coupling apparatus ('coupler'; Fig. 11), consisting of one or more chitinous plates and carrying an adhesive secretion (Ohtsuka & Kimoto, 1989; Walter, 1989; Blades-Eckelbarger, 1991; Ohtsuka & Reid, 1998). In calanoids producing the latter type, the female genital double-somite is usually ornamented with spines, processes and swellings which fit the shape of the coupler, constituting a key-and-lock mechanism (Lee, 1972). Closely related species employing this key-and-lock mechanism (with coupler) are reproductively isolated primarily at the copulation stage, rather than at the premating search and capture stages (Vaupel Klein, 1982; Blades-Eckelbarger, 1991).

Some males appear to bear a specialized structure on the terminal portion of the transferring leg 5, that is used for tactile inspection and cleaning of the genital area prior to transfer and attachment of a spermatophore. This cleaning device can be located on either the exopod or the endopod. In the Euchaetidae, the second exopodal segment of the left leg 5 bears a serrate process and a digitiform process with fingerprint-like ornamentation (Fig. 7D),

which may clean the female genital area before copulation (Mauchline, 1998; present study). Members of the superfamily Centropagoidea require multiple copulations in order to fertilize all the egg clutches because of the lack of seminal receptacles in the female (Barthélémy et al., 1998). This change in reproductive strategy is reflected in structural modifications in the leg 5 endopod and/or the urosome of the males. Observations of male *Labidocera aestiva* showed that the left ridged endopod is used to stroke the female genital area before copulation, suggesting that it may function to clean the female body surface, where waste products of previous matings and broods remain (Blades & Youngbluth, 1979). In some males of the Tortanidae, the terminal portion of the left leg 5 bears a file-like structure which could serve a similar purpose (Ohtsuka & Reid, 1998). It is noteworthy that in some males of the families Pontellidae, Candaciidae and Tortanidae, peculiar structures are present also on the right side of the urosome. In *Pontellopsis yamadae* (Figs 9A and 10A, B) highly specialized, file-like structures are found on the right side of the second and third urosomites, whereas in *Labidocera japonica* a single, acute process is present on the right ventrolateral side of the genital somite. In *Candacia bipinnata,* the right lateral process on the genital somite bears a fingerprint-like structure (Fig. 10C, D). In some male tortanids, a process or swelling is present on the right lateral side of the second urosomite (Ohtsuka & Reid, 1998). The idea that all these sexually dimorphic structures could serve as auxiliary cleaning devices is particularly attractive, however, the copulatory behaviour of each species must be directly observed in order to reveal their precise function. Many of these putative cleaning devices are usually associated with mechanoreceptors such as peg- and hair-sensilla (see Fig. 10B, C), which suggests that grooming may also be important during mating (see 'Mate recognition').

(4) Removal of discharged spermatophore(s)

The empty spermatophore is usually removed after the spermatozoa and seminal secretions are fully discharged. In numerous calanoid families, this process appears to be accomplished by the specialized female leg 5. Blades & Youngbluth (1979) demonstrated how female pontellids position the long exopods of their fifth legs under the lateral edges of the anterior shield to remove the whole spermatophore apparatus. Specialized pit-pores on the female genital double-somite, underlying the spermatophore attachment area, may

facilitate the removal by secreting a substance which structurally modifies and thus loosens the cement of the posterior coupling plate.

Calanoid female fifth legs can be classified into three types according to their modification (cf. Vaupel Klein, 1998). (1) The modification is not particularly prominent; leg 5 is biramous and essentially similar to the preceding legs. This type may remove discharged spermatophores using the stout outer spines on the exopod (Boholinidae, Epacteriscidae, Pseudocyclopidae, Ridgewayiidae) or the large inner spine/process on the second exopodal segment (Augaptilidae, Heterorhabdidae, Lucicutiidae, Centropagidae). In *Calanus* Leach, *Cosmocalanus* Bradford & Jillett and *Nannocalanus* Sars (Calanidae), the female leg 5 bears serrations along the inner coxal margin which may be engaged in removing discharged spermatophores. Since this structure is found in both sexes (Bradford, 1988), it may play an alternative role in grooming the tips of the antennules (cf. Price et al., 1983). (2) Leg 5 is reduced, usually uniramous, with well developed spines and/or processes terminally (most other taxa). (3) Leg 5 is completely absent or reduced to a rudimentary appendage which is apparently without function (some Arietellidae, Augaptilidae, Tortanidae (Fig. 11, indicated by small arrow), Paracalanidae, Eucalanidae, Ryocalanidae, Spinocalanidae, Aetideidae, Clausocalanidae, Diaixidae, Euchaetidae, Parkiidae and Scolecithricidae).

In some calanoids exhibiting the third type, the preceding legs 1–4 seem to compensate for the loss of leg 5 (Vaupel Klein, 1998). For example, some aetideids such as *Euchirella* Giesbrecht, *Gaetanus* Giesbrecht, and *Pseudochirella* Sars bear one or more inner acute processes on the coxa of leg 4 only in females. These processes are supposed to function in the removal of empty spermatophores (cf. Bradford & Jillett, 1980; Markhaseva, 1996; Vaupel Klein, 1998). In the Diaixidae and Ryocalanidae, females also have strong inner coxal processes on leg 4, as in these aetideids (cf. Andronov, 1992; Markhaseva & Ferrari, 1996). In female *Paraeuchaeta tuberculata* (Euchaetidae), with the genital area located ventroposteriorly on the genital double-somite, the inner coxal setae of leg 4 are longer and thicker than those of the preceding legs 1–3, and sufficiently elongate to reach the genital area, whereas those of the male are similar to those of legs 1–3. However, these setae seem not to be sclerotized sufficiently for scraping off spent spermatophores, and might be used only to clean the female genital area. In the Euchaetidae, the male may
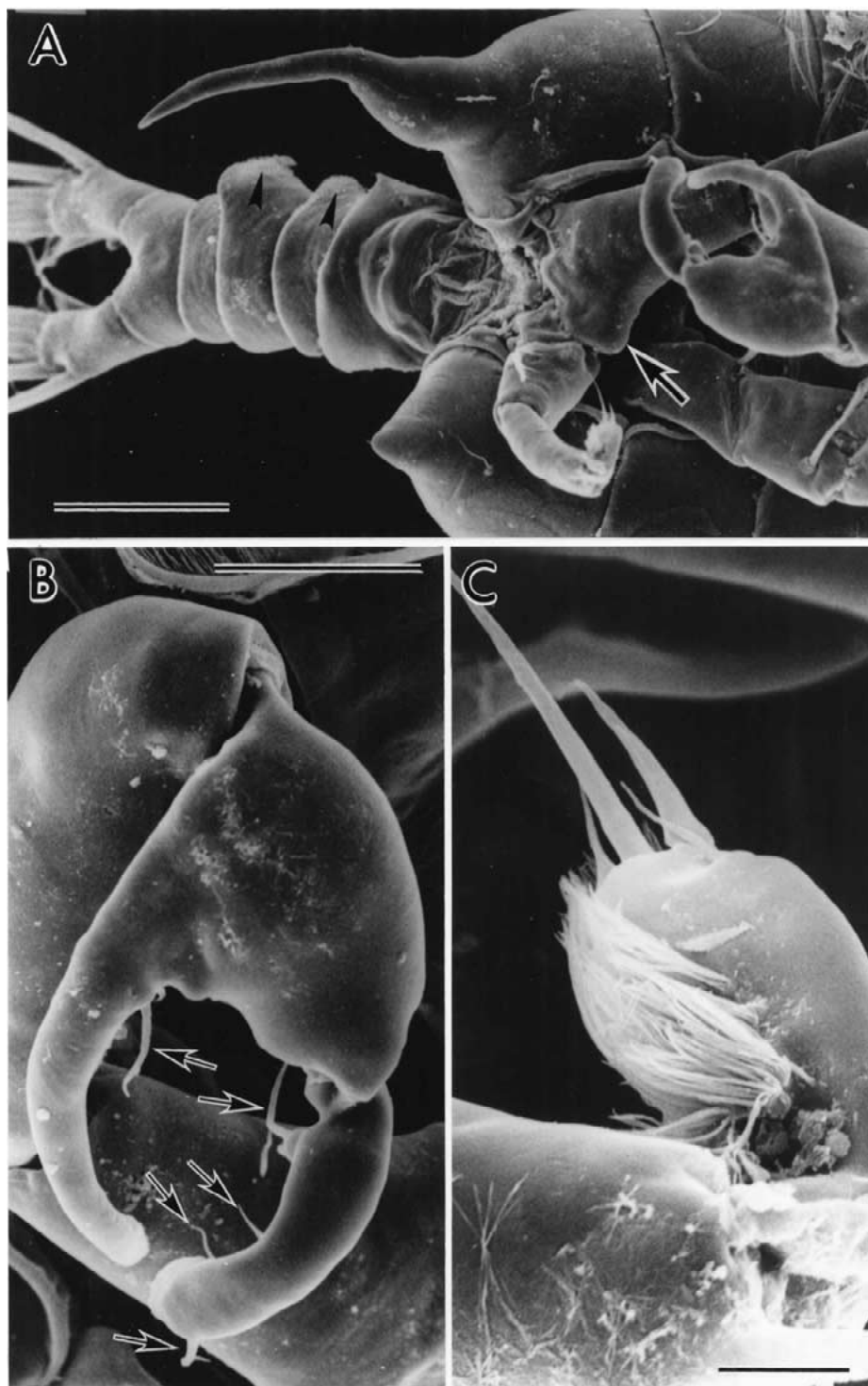
Figure 9. Male *Pontellopsis yamadae* Mori, 1937. (A) Ventral view of pediger 5 and urosome, leg 5 indicated by large arrow, putative cleaning organ indicated by small arrows; (B) Chelate structure of exopod of right leg 5, hair-sensilla arrowed; (C) Terminal exopod segment of left leg 5, posterior. Scale = 0.1 mm (A); 0.05 mm (B); 0.01 mm (C).

456
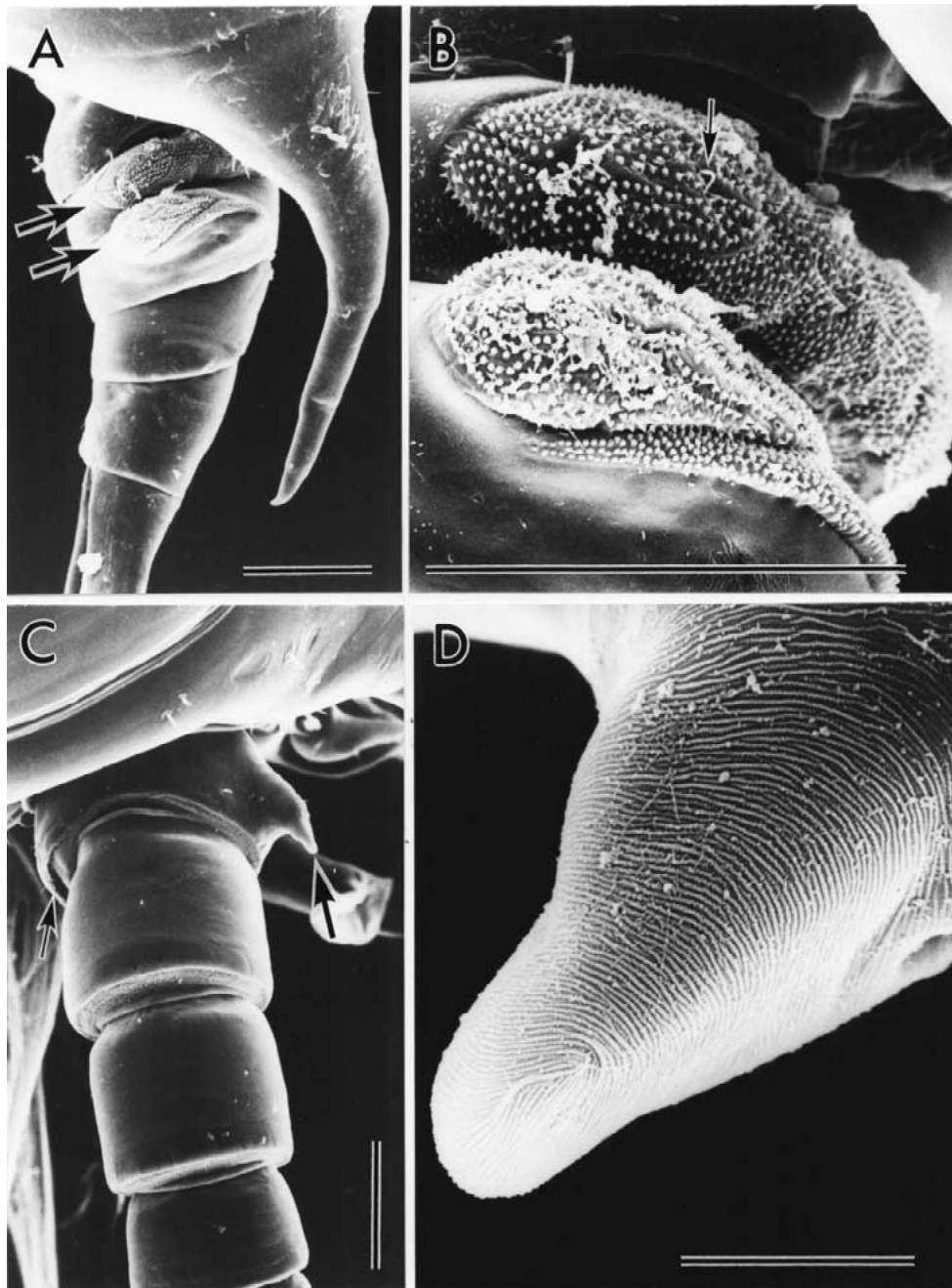
Figure 10. Putative cleaning organs in males of *Pontellopsis yamadae* Mori, 1937 (A, B) and *Candacia bipinnata* Giesbrecht, 1889 (C, D). (A) Urosome, right lateral, cleaning device on second and third urosomites arrowed; (B) Cleaning organs on second and third urosomites, hair-sensillum arrowed; (C) Urosome, cleaning device and gonopore indicated by large and small arrow, respectively; (D) Cleaning device. Scale = 0.1 mm (A–C); 0.01 mm (D).
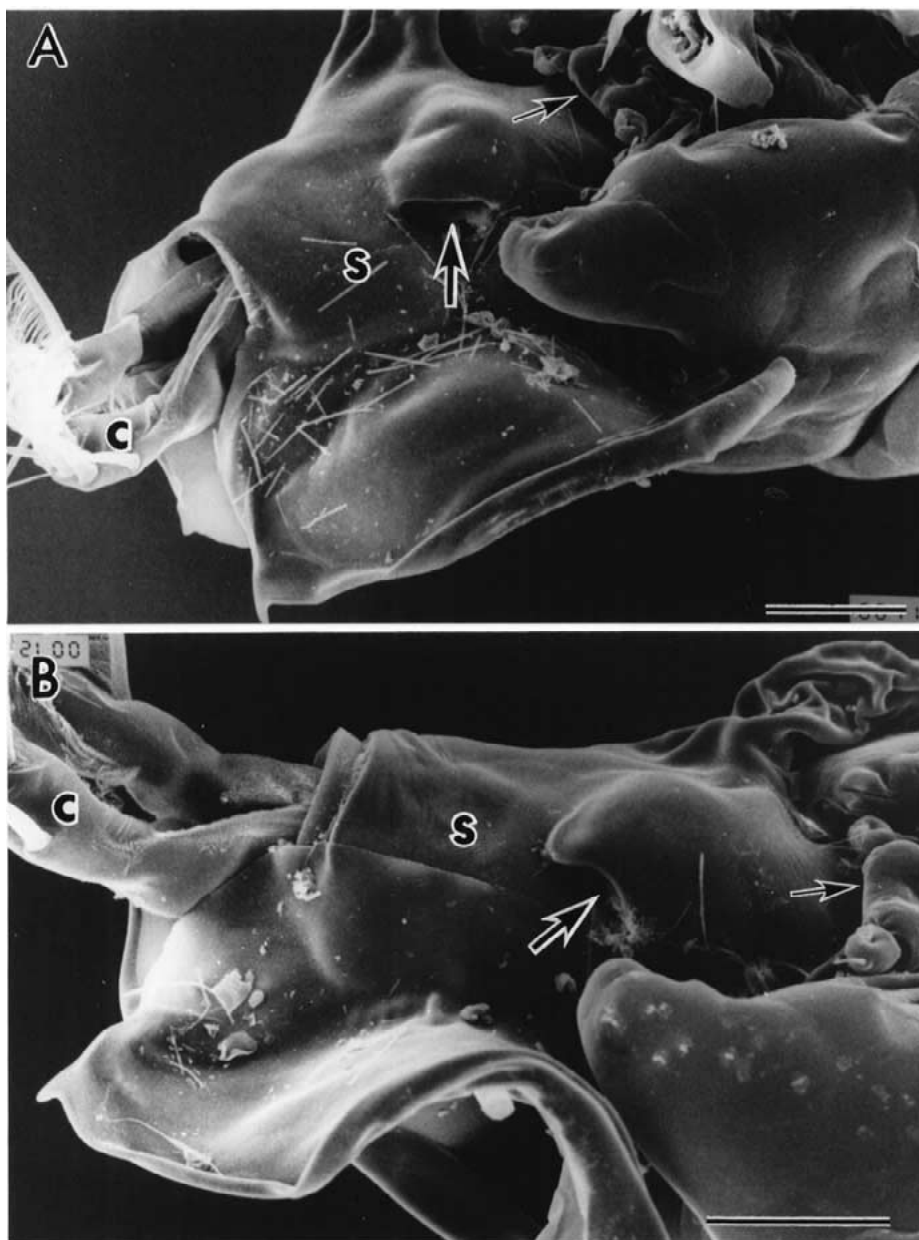
Figure 11. Ventral view of female urosome of *Tortanus* (*Atortus*) *rubidus* Tanaka, 1965, covered by complex spermatophore. (A, B) Two different specimens. s: spermatophore; c: caudal rami; large arrow: opening of spermatophore from which fertilized eggs may be released; small arrow: rudimentary leg 5. Scale = 0.1 mm (A, B).

scrape off an empty spermatophore, and the terminal serrated and ridged processes on the second exopodal segment of the male left leg 5 in effect, compensate for the loss of the female leg 5 (see Fig. 7D).

Some species of *Tortanus* (*Atortus*) Ohtsuka (Tortanidae) with a rudimentary plate-like leg 5 (Fig. 11A, B, indicated by small arrow) have a complex coupling device on the spermatophore which almost entirely covers the urosome of the female (Fig. 11, s) (cf. Othman, 1987; Ohtsuka & Kimoto, 1989; present study), and is not readily detached from it using dissecting needles (Ohtsuka, pers. obs.). A spermatophore so firmly glued onto the female urosome may remain on it after all egg clutches have been fertilized within the

458

Figure 12. Reduced mouthparts of males. (A) Ventral view of mouthparts of *Acrocalanus gibber* Giesbrecht, 1888; (B) Proximal parts of mandible, maxillule and maxilla of *Acrocalanus gibber*; (C) Ventral view of reduced mouthparts of *Eucalanus attenuatus* (Dana, 1849); (D) Proximal parts of mandible, maxillule and maxilla of *Lophothrix frontalis* Giesbrecht, 1895. 1: labrum; small arrow: reduced mandibular cutting edge; large arrow: reduced maxilla; asterisk: reduced precoxal arthrite of maxillule. Scale = 0.1 mm (A, D); 0.01 mm (B); 0.5 mm (C).
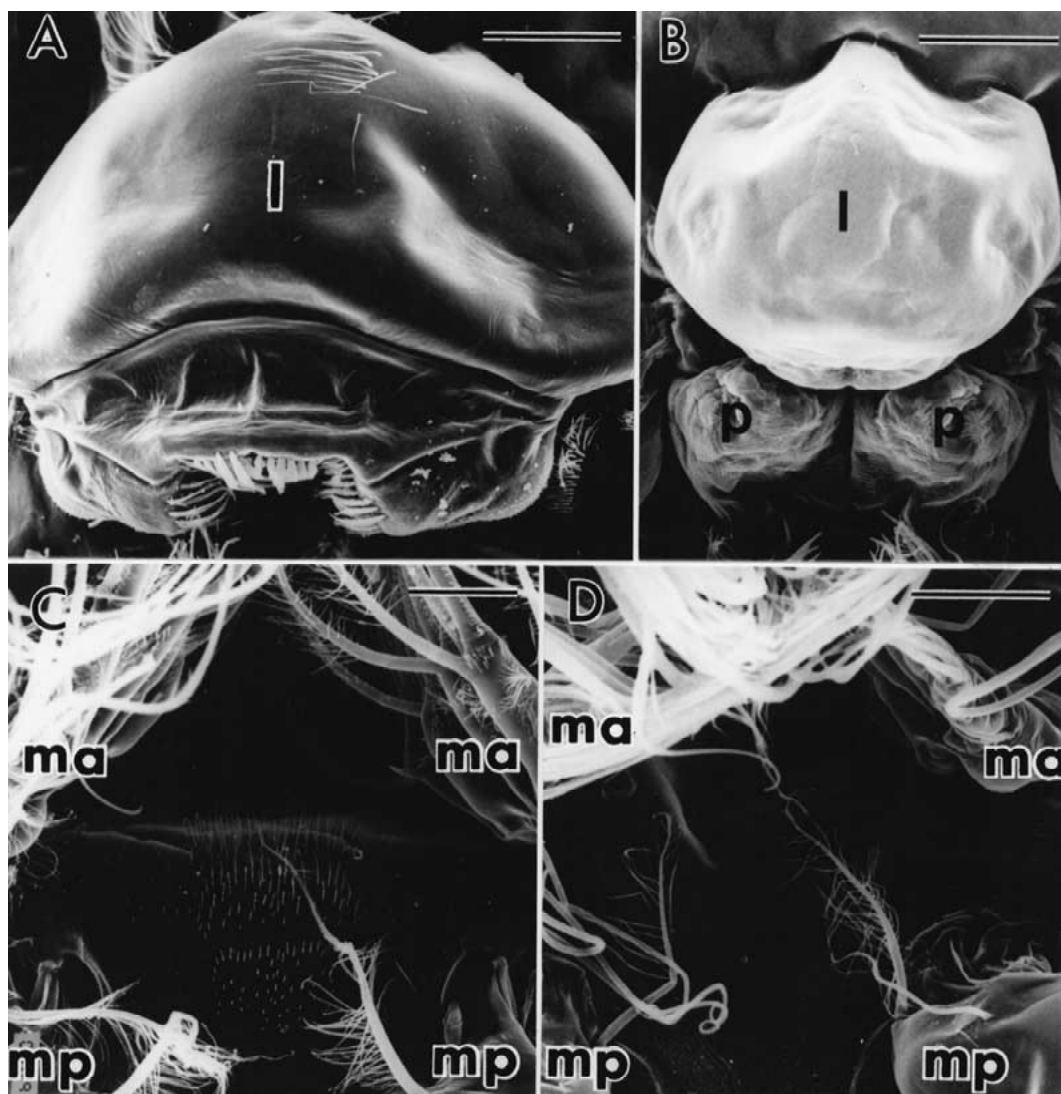
Figure 13. Eucalanus attenuatus (Dana, 1849), female (A, C), male (B, D). (A) Labrum (l); (B) Labrum (l) and paragnath (p); (C, D) Dorsal wall of filter basket between maxillae (ma) and maxillipeds (mp). Scale = 0.1 mm (A–D).

genital atrium (Barthélémy et al., 1998) and released. In *T.* (*A.*) rubidus, a large pore, ca. 60 μm in diameter, is present on the ventral side of the spermatophore (Fig. 11, indicated by large arrow), beneath which the gonopore is located. This pore seems to be the only opening for releasing the fertilized eggs.

Females of some species of the Pseudocyclopiidae (Clausocalanoidea) bear an inner elongate coxal spine on legs 2–4, which may be involved in removal of discharged spermatophores, presumably in conjunction with leg 5 (Ohtsuka, 1992).

In addition to spermatophore removal, the female leg 5 is supposed to play a role in handling, posi-

tioning, and/or protecting either spermatophore and/or egg sac (Vaupel Klein, 1998), but this has never been confirmed directly.

(5) Genital system in female

This section briefly deals with the female genital system in relation to fertilization and release of eggs by the female. The spermatophore extruded by the male is cemented onto the female genital double-somite (Blades & Youngbluth, 1979; Jacoby & Youngbluth, 1983). Recent detailed observations have revealed that the structure of female genital systems is surprisingly

diversified in the Calanoida, compared with those of other orders (Huys & Boxshall, 1991; Ohtsuka et al, 1993, 1994; Cuoc et al., 1997; Barthélémy et al., 1998). Particularly in the primitive superfamilies Pseudocyclopoidea and Arietelloidea, the female genital structures are extremely diverse (see Cuoc et al., 1997). However, this complexity of the female genital systems seems not to be directly correlated to particular reproductive structures in the males. The reason probably is that in copepods, insemination occurs via a spermatophore rather than a copulatory intromittent organ, such as a penis (cf. Ostracoda: Tsukagoshi, 1988, 1989).

In the majority of Centropagoidea, the female genital system is radically divergent from the ancestral calanoid condition by the presence of a single genital operculum and the complete absence of seminal receptacles (Barthélémy et al., 1998; Barthélémy, 1999). Spermatophores discharge their contents over the ventral surface of the genital double-somite of the female, forming an attached spermatophoral mass. This major evolutionary change in storage of seminal products, from internal (seminal receptacles) to semi-external (genital atrium) or fully external (Sulcanidae, Diaptominae), limits the ability of females to store sufficient spermatozoa for multiple egg batches. Further inseminations are effectively prevented until the old supply of spermatozoa is being displaced by extrusion of eggs (or in some taxa, egg-sacs). Barthélémy et al. (1998) suggested that in most species repeated mating is necessary for the sustained production of egg clutches and that this unusual reproductive strategy is reflected in the near-parity sex ratio commonly observed in centropagoidean populations.

In contrast, more derived superfamilies always bear a single genital operculum, beneath which paired gonopores and copulatory pores open (Cuoc et al., 1997). Eggs are then typically released into the water, or exceptionally carried in multiseriate sacs (Arietellidae) or linear strings (some Aetideidae). Ohman & Townsend (1998) hypothesized that the presence of ventrally carried egg-sacs in some species of *Euchirella* may be associated with the evolutionary loss of leg 5 in the female.

(6) Trophic dimorphism

The most distinct sexual dimorphism is the reduction or atrophy of mouthparts in non-feeding males. This is restricted to superfamilies such as the Arietelloidea, Megacalanoidea, Eucalanoidea, Clausocalanoidea and
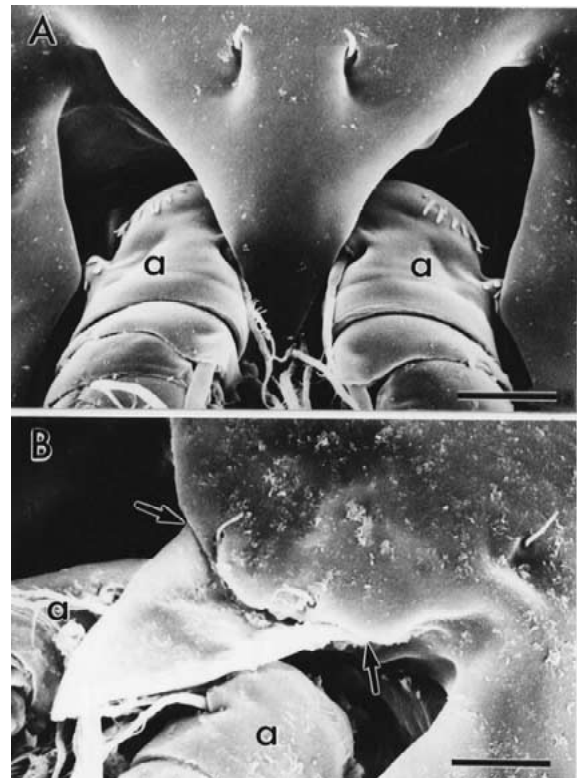

Figure 14. Rostrum of *Pseudocyclops minutus* Ohtsuka, Fosshagen & Putchakarn, 1999, female (A), male (B); a: antennule; suture separating pseudorostrum from dorsal cephalic shield arrowed. Scale = 0.1 mm.

Spinocalanoidea, and is a strategy adopted irrespective of the feeding habits exhibited by the corresponding females. The non-feeding strategy in the male has probably evolved independently many times during calanoid evolution.

Non-feeding males generally exhibit reductions in the mandibular gnathobases (Fig. 12A–D: indicated by small arrow), inner lobes of the maxillule (Fig. 12B, D: indicated by asterisk), the entire maxilla (Fig. 12A–D: indicated by large arrow), and, in some cases, particular inner setae on the maxilliped, irrespective of feeding habit. These parts are involved in catching, handling, and ingesting food in females with multifunctional mouthparts. In the carnivorous Euchaetidae, females have maxillulary endopods modified as grasping devices which may assist the maxillae and the maxillipeds to capture and consume active prey, while those of the males are reduced in addition to the usually reduced parts mentioned above. The remaining parts of these mouthpart appendages of the non-feeding male play roles in gen-
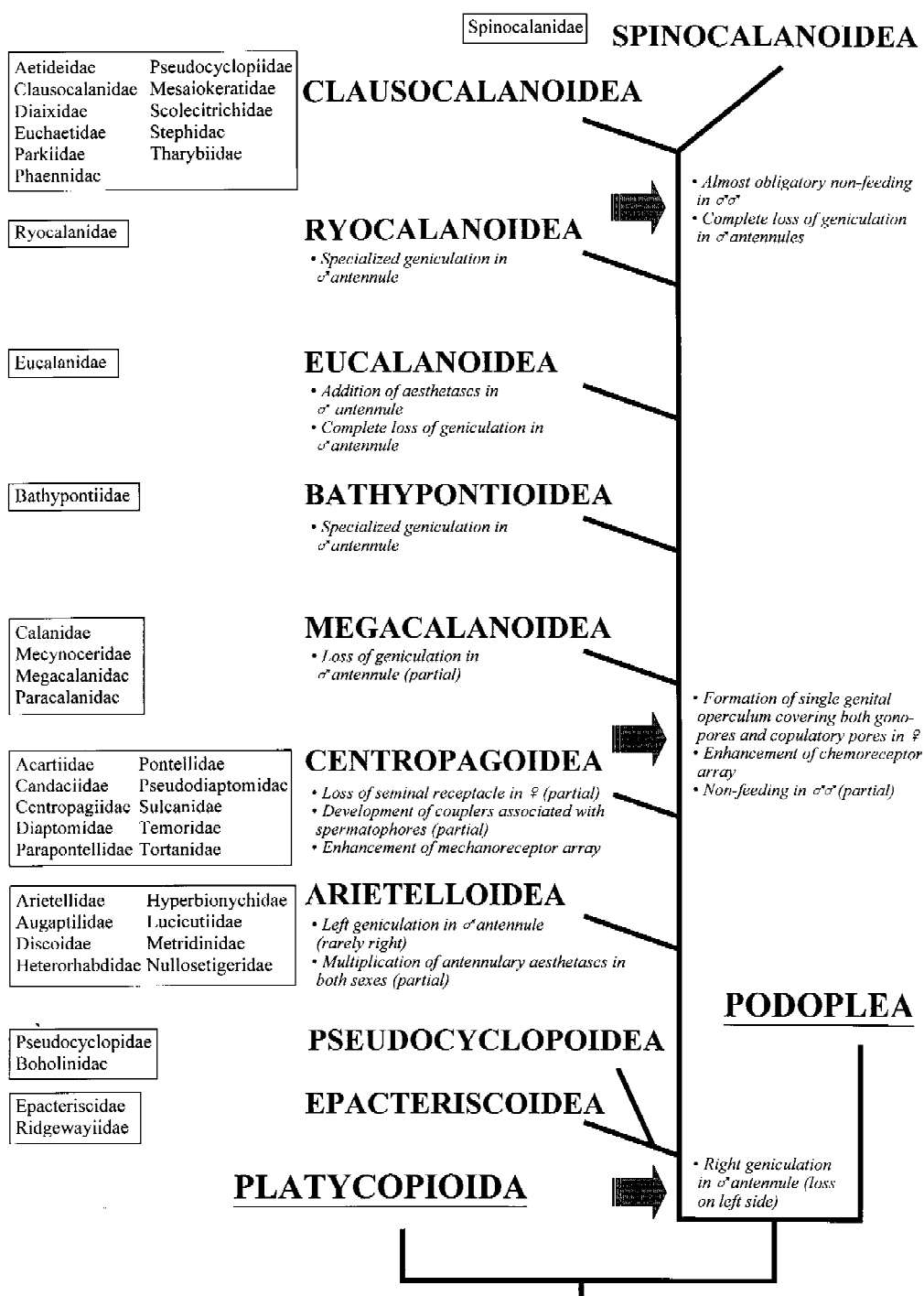
Spinocalanidae **SPINOCALANOIDEA**

Aetideidae Pseudocyclopiidae
Clausocalanidae Mesaiokeratidae
Diaixidae Scolecitrichidae
Euchaetidae Stephidae
Parkiidae Tharybiidae
Phaennidae

CLAUSOCALANOIDEA

• *Almost obligatory non-feeding in ♂♂*
• *Complete loss of geniculation in ♂ antennules*

Ryocalanidae

RYOCALANOIDEA

• *Specialized geniculation in ♂ antennule*

Eucalanidae

EUCALANOIDEA

• *Addition of aesthetascs in ♂ antennule*
• *Complete loss of geniculation in ♂ antennule*

Bathypontiidae

BATHYPONTIOIDEA

• *Specialized geniculation in ♂ antennule*

Calanidae
Mecynoceridae
Megacalanidae
Paracalanidae

MEGACALANOIDEA

• *Loss of geniculation in ♂ antennule (partial)*

Acartiidae Pontellidae
Candaciidae Pseudodiaptomidae
Centropagiidae Sulcanidae
Diaptomidae Temoridae
Parapontellidae Tortanidae

CENTROPAGOIDEA

• *Loss of seminal receptacle in ♀ (partial)*
• *Development of couplers associated with spermatophores (partial)*
• *Enhancement of mechanoreceptor array*

• *Formation of single genital operculum covering both gono-pores and copulatory pores in ♀*
• *Enhancement of chemoreceptor array*
• *Non-feeding in ♂♂ (partial)*

Arietellidae Hyperbionychidae
Augaptilidae Lucicutiidae
Discoidae Metridinidae
Heterorhabdidae Nullosetigeridae

ARIETELLOIDEA

• *Left geniculation in ♂ antennule (rarely right)*
• *Multiplication of antennulary aesthetascs in both sexes (partial)*

PODOPLEA

Pseudocyclopidae
Boholinidae

PSEUDOCYCLOPOIDEA

Epacteriscidae
Ridgewayiidae

EPACTERISCOIDEA

PLATYCOPIOIDA

• *Right geniculation in ♂ antennule (loss on left side)*

Figure 15. Phylogenetic tree of calanoid superfamilies, after Andronov (1974) and Park (1986). Each superfamily is defined by sexually dimorphic characters (apomorphies). Arrows indicate synapomorphies.

erating scanning currents for detection of pheromones and hydromechanical cues, in mating, in swimming and possibly in grooming (Boxshall et al., 1997).

On the ventral integumental wall between the maxillae and maxillipeds of female *Eucalanus attenuatus*, fine spinules and setules are present, all of which are directed anteriorly (Fig. 13C). These are lacking in the non-feeding male (Fig. 13D). Probably these structures reduce leakage of particles captured within the 'filter basket' (cf. Boxshall, 1985). The posterior margin of the labrum in the female bears short, stout spinules directed toward the esophagus (Fig. 13A), whereas that of the non-feeding male is naked (Fig. 13B). This presumably also plays a role in reducing leakage of food particles during chewing with the mandibular gnathobases.

In addition to the reduction in mouthparts, the array of elements on the antennules differs between both sexes of the Euchaetidae. At the last moult, non-feeding males in this carnivorous family, simultaneously shed the 3-dimensional, 4-point setal array on the proximal antennulary segments, which is the primary prey detection system in the feeding female (Boxshall et al., 1997).

(7) Other sexually dimorphic characters

Other sexually dimorphic characters except for the basic Bauplan (the number of urosomites) are found in the shape of the posterior prosomal margin, the ornamentation of the urosome, the mobility of the rostrum, and the structure of the setal elements on the legs. Since knowledge of the mating behaviour of calanoids is restricted mainly to particular genera in the Centropagoidea, most of their functions remain unknown.

Within the Centropagoidea, some taxa of the Diaptomidae, Centropagidae, Pontellidae, Pseudodiaptomidae, Temoridae and Tortanidae, exhibit distinct sexual dimorphism in the shape of the prosomal rear margins. As discussed above, the wing-like expansions or large projections of the posterior prosomal end margins of the female may provide a hydromechanical cue utilized by the seeking male.

In some males of *Pleuromamma* (Arietelloidea), the urosome is considerably asymmetrical, covered with numerous long setules on the dorsal, lateral and, in particular, ventral sides, which are not found in the females (see Giesbrecht, 1892: Plate 33, Figs 49 and 50). In females of *Calocalanus plumulosus* (Claus, 1863) and *C. pavo* (Dana, 1849) (Megacalanoidea),

the caudal seta(e) are extremely decorated (cf. Giesbrecht, 1892: Plate 3, Fig. 5; Plate 4, Fig. 15). These structures may be involved in mate recognition (wakes as mechanical cues) or in the diffusion of sex pheromones (as chemical cues).

In some species of the hyperbenthic family Pseudocyclopidae, the rostrum ('pseudorostrum' sensu Huys & Boxshall, 1991) is mobile at the base only in the male (Fig. 14B) but not in the female (Fig. 14A). This juncture may facilitate grasping of the female by the right geniculate antennule of the male during the initial phase of copulation, since the female is an active swimmer (Bowman & González, 1961).

In the Euchaetidae, in particular the genus *Paraeuchaeta* A. Scott, the female antennule bears dense rows of fine setules along the posterior margin of the proximal segments (in female *Euchaeta rimana* only the 3rd, 7th and 8th segments with an elongate seta bear such row of setules), whereas the non-feeding male lacks them. The female shows a horizontal swimming pattern, swimming smoothly and continuously for detection of prey and mate, whereas the male swims vertically displaying a hop-and-sink pattern (Greene & Landry, 1985; Landry & Fagerness, 1988; Yen, 1988). These antennulary setules, present only in the female, are suggested to function as "a hydrodynamic faring to reduce the separation of the boundary layer and shedding of vortices as the antennules (continuously) pass through the water", which can be "important in reducing background noise to enhance the sensitivity of the receptor" (Landry & Fagerness, 1988). The "hop-and-sink" swimming pattern of the adult male seems to conserve energy because of its non-feeding stage. In this family additional sexual dimorphism is found in legs 1 and 2 (cf. Bradford et al., 1983), but the function is unknown.

(8) Phylogenetic implications

A modern scheme of the phylogenetic relationships between calanoid superfamilies was first proposed by Andronov (1974) and later modified by Park (1986) (Fig. 15). These systems are not based on cladistics, but generally correspond well to a phylogenetic tree generated by a cladistic analysis (Boxshall, pers. comm.). Their topology is also approximately supported by a 28 S rRNA-based phylogenetic study (Braga et al., 1999). According to Braga et al. (1999), the Centropagoidea is an earlier offshoot than the Arietelloidea, whereas the reverse position is supported in Park's (1986) tree. The new superfamily Fosshagenioidea, recently established by Suárez-Morales &

Iliffe (1996), is not considered in the present study because of its potential synonymy with another named superfamily (Boxshall, pers. comm.). We noted some confusion in the correct application of the superfamily name for the Megacalanoidea, Centropagoidea and Epacteriscoidea since all contain families which are older than their respective coordinate families (Calanidae Dana, 1849 vs Megacalanidae Sewell, 1947; Diaptomidae Baird, 1850 vs Centropagidae Giesbrecht, 1892; Ridgewayiidae M.S. Wilson, 1958 vs Epacteriscidae Fosshagen, 1973) which is in contradiction with the Principle of Coordination traditionally applied to family-group names. On priority alone, all three superfamily names would require substitution by their older synonym, however, according to Art. 35.5 of the new Code (4th edition), which came into effect on 1 January 2000, preference should be given to prevailing usage rather than priority, and consequently the older name is not to displace the younger one.

Each superfamily is well defined by its own characteristic sexual dimorphism. Recent studies have added new information about their distinct evolutionary trends. The early diverging branches comprising the originally hyperbenthic superfamilies Pseudocyclopoidea, Epacteriscoidea and Arietelloidea are generally characterized by: (1) the absence of multiplication of antennulary aesthetascs in the male (or exceptionally, in both sexes of some Arietelloidea); (2) the presence of a geniculate antennule on either the right or left side in the male; (3) the absence of non-feeding males (except for a few arietelloideans); (4) female genital system without a single genital operculum covering paired gonopores and copulatory pores. Most of the Centropagoidea share the first three symplesiomorphies. In addition, the Centropagoidea have the following autapomorphies: (1) loss of seminal receptacles (except for a few taxa); (2) development of complex coupling devices (in part) (Vaupel Klein, 1982; Blades-Eckelbarger, 1991; Barthélémy et al., 1998; Ohtsuka & Reid, 1998; Barthélémy, 1999).

The main lineage of calanoids seems to have acquired the following derived sexually dimorphic characteristics after the divergence of the Centropagoidea: (1) formation in the female of a single genital operculum, beneath which gonopores and copulatory pores open; (2) duplication of antennulary aesthetascs being strictly confined to the males. Moreover, there is a distinct tendency in males towards loss of antennulary geniculations and adoption of a non-feeding strategy, yet the pattern of both morphological changes within each superfamily appears to be erratic. Non-feeding is completely adopted by the terminal clade, comprising the open-water Spinocalanoidea and Clausocalanoidea. The Bathypontioidea and Ryocalanoidea have independently developed specialized and supplemental geniculations in the male antennules. However, as Boxshall et al. (1997) suggested, the putative secondary loss of doubled aesthetascs on the male antennule is found in the Euchaetidae (Clausocalanoidea). This may be related to a mate-seeking behavior in which the female actively searches for the male (Yen, 1988).

Centropagoideans without seminal receptacles in the female are supposed to need a copulation before the production of each egg clutch, while in other taxa (with seminal receptacles), one or two matings at the beginning of the reproductive season provide the female with a sufficient stock of sperm throughout her life (Barthélémy et al., 1998). Centropagoideans are usually the predominant calanoids in the epipelagic zone and freshwater habitats (Grice & Hulsemann, 1965; Mauchline, 1998), and sometimes form dense swarms or schools (Ueda et al., 1983; Kimoto et al., 1988), which seems to guarantee multiple copulations.

Non-feeding and doubling of antennulary aesthetascs in males, both of which can enhance the capacity for chemosensory mate recognition (Boxshall et al., 1997), are adopted by the mainly open-water families Aetideidae, Calocalanidae, Clausocalanidae, Euchaetidae, Paracalanidae and Spinocalanidae, and facultatively by the neritic/oceanic families Calanidae, Eucalanidae, Phaennidae and Scolecitrichidae. These families belong exclusively to the derived Clausocalanoidea, Eucalanoidea, Megacalanoidea and Spinocalanoidea, all of which possess a single genital operculum and paired seminal receptacles in the female. The configuration of the genital system in females in conjunction with the enhanced chemosensitivity in males seem to be linked to their secondary invasion of open pelagic waters (the first was supposedly by the Arietelloidea; see Soh, 1998). In particular, chemosensitivity is likely to be more important for communication between the sexes in open waters than in shallow waters (Huys & Boxshall, 1991). On the other hand, non-feeding males have a short life span (Matthews, 1964). Therefore, synchronized maturation in both sexes is advantageous for taxa with non-feeding males. In fact, many cold-water species of the Megacalanoidea and Eucalanoidea reproduce in a restricted season in deep, calm waters where turbulence is low and chemical cues are very effective

464

(Miller et al., 1984; Atkinson, 1991; Schnack-Schiel & Mizdalski, 1994).

Observations of mating behaviour in centropagoideans and non-centropagoideans showed that the duration of mating is relatively long in the former (45–77 min. in *Pseudodiaptomus* spp.; Jacoby & Youngbluth, 1983), whereas in the latter it is much faster (0.1 to a few seconds; Tsuda & Miller, 1998). Prolonged mating involving complex coupling apparatuses clearly places couples at a greater risk of encountering predators since it reduces their escape ability and renders them more conspicuous to visual predators (cf. Svensson, 1992). Pairs in amplexus are more readily detected and consumed by visual predatory fish than is a single individual, because meso- and bathypelagic fish tend to prefer larger prey (Tsuda, 1995). The loss of the antennulary geniculation in many non-centropagoidean males may be related to this predation pressure. Calanoids which do not employ a key-and-lock mechanism have probably become more efficient in mate recognition (keeping tactile inspection to a minimum) and spermatophore transfer (direct attachment to female genital aperture), making antennulary geniculations largely redundant. Highly evolved pheromonal or hydromechanical cues (Van Duren et al., 1998) in these calanoids would clearly reduce the need for physical contact during mate recognition, facilitating rapid separation of the couple after successful spermatophore transfer. In families where mating is short to very short such as the Euchaetidae, males typically hold a spermatophore in the left leg 5, ready for attachment to the female before mating takes place (Ferrari, 1978; Hopkins et al., 1978). The majority of the Centropagoidea, however, retain the spermatophore internally in the ductus ejaculatorius until both sexes have assumed the correct mating position (e.g. Blades & Youngbluth, 1979, 1980; Blades-Eckelbarger, 1991; Mauchline, 1998).

References

Andronov, V. N., 1970. Some problems of taxonomy of the family Paracalanidae (Copepoda). Zool. Zh. 49: 980–985 (in Russian with English abstract).

Andronov, V. N., 1974. Phylogenetic relations of large taxa within the suborder Calanoida (Crustacea, Copepoda). Zool. Zh. 53: 1002–1012 (in Russian with English abstract).

Andronov, V. N., 1992. *Ryocalanus admirabilis* sp. n. (Copepoda, Calanoida, Ryocalanidae) from the central-eastern Atlantic. Zool. Zh. 71: 140–144 (in Russian with English abstract).

Atkinson, A., 1991. Life cycles of *Calanoides acutus*, *Calanus simillimus* and *Rhincalanus gigas* (Copepoda: Calanoida) within the Scotia Seas. Mar. Biol.109: 79–91.

Barthélémy, R.-M., 1999. Functional morphology and taxonomic relevance of the female genital structures in the Acartiidae (Copepoda: Calanoida). J. mar. biol. Ass. U.K. 79: 857–870.

Barthélémy, R.-M., C. Cuoc, D. Defaye, M. Brunet & J. Mazza, 1998. Female genital structures in several families of Centropagoidea (Copepoda: Calanoida). Phil. Trans. r. Soc. Lond. B 353: 721–736.

Blades, P. I., 1977. Mating behaviour of *Centropages typicus* (Copepoda: Calanoida). Mar. Biol. 40: 57–64.

Blades, P. I. & M. J. Youngbluth, 1979. Mating behavior of *Labidocera aestiva* (Copepoda: Calanoida). Mar. Biol. 51: 339–355.

Blades, P. I. & M. J. Youngbluth, 1980. Morphological, physiological and behavioural aspects of mating in calanoid copepods. In Kerfoot W. C. (ed.), Evolution and Ecology of Zooplankton Communities. The University Press of New England, Hanover (N.H.): 39–51.

Blades-Eckelbarger, P. I., 1991. Functional morphology of spermatophores and sperm transfer in calanoid copepods. In Bauer R. T. & J. W. Martin (eds), Crustacean Sexual Biology. Columbia University Press, New York: 246–270.

Bowman, T. E. & J. G. González, 1961. Four new species of *Pseudocyclops* (Copepoda: Calanoida) from Puerto Rico. Proc. U.S. natn. Mus. 113: 37–59.

Boxshall, G. A., 1985. The comparative anatomy of two copepods, a predatory calanoid and a particle-feeding mormonilloid. Phil. Trans. r. Soc. Lond. B311: 303–377.

Boxshall, G. A. & R. Huys, 1998. The ontogeny and phylogeny of copepod antennules. Phil. Trans. r. Soc. Lond. B 353: 765–786.

Boxshall, G. A., J. Yen & J. R. Strickler, 1997. Functional significance of sexual dimorphism in the cephalic appendages of *Euchaeta rimana* Bradford. Bull. mar. Sci. 61: 387–398.

Bradford, J. M., 1988. Review of the taxonomy of the Calanidae (Copepoda) and the limits to the genus *Calanus*. Hydrobiologia 167/168: 73–81.

Bradford, J. M., L. Haakonssen & J. B. Jillett, 1983. The marine fauna of New Zealand: pelagic calanoid copepods: families Euchaetidae, Phaennidae, Scolecithricidae, Diaixidae and Tharybidae. Mem. N.Z. oceanogr. Inst. 90: 1–150.

Bradford, J. M. & J. B. Jillett, 1980. The marine fauna of New Zealand: pelagic calanoid copepods: family Aetideidae. N.Z. oceanogr. Inst. Mem. 86: 1–102.

Bradford-Grieve, J. M., 1994. The marine fauna of New Zealand: pelagic calanoid Copepoda: Megacalanidae, Calanidae, Paracalanidae, Mecynoceridae, Eucalanidae, Spinocalanidae, Clausocalanidae. Mem. Z. Z. oceanogr. Inst. 102: 1–160.

Bradford-Grieve, J. M., 1999. The marine fauna of New Zealand: pelagic calanoid Copepoda: Bathypontiidae, Arietellidae, Augaptilidae, Heterorhabdidae, Lucicutiidae, Metridinidae, Phyllopodidae, Centropagidae, Pseudodiaptomidae, Temoridae,

Candaciidae, Pontellidae, Sulcanidae, Acartiidae, Tortanidae. Mem. N.Z. oceanogr. Inst. 111: 1–268.

Braga, E., R. Zardoya, A. Meyer & J. Yen, 1999. Mitochondrial and nuclear rRNA based copepod phylogeny with emphasis on the Euchaetidae (Calanoida). Mar. Biol. 133: 79–90.

Cuoc, C., D. Defaye, M. Brunet, R. Notonier & J. Mazza, 1997. Female genital structures of Metridinidae (Copepoda, Calanoida). Mar. Biol. 129: 651–665.

Damkaer, D. M., 1975. Calanoid copepods of the genera *Spinocalanus* and *Mimocalanus* from the central Arctic Ocean, with a review of the Spinocalanidae. NOAA tech. Rep. NMFR Circ. 391: 1–88.

Deevey, G. B., 1973. *Bathypontia* (Copepoda: Calanoida): six species, one new, from the Sargasso Sea. Proc. biol. Soc. Wash. 86: 357–372.

Ferrari, F. D., 1978. Spermatophore placement in the copepod *Euchaeta norvegica* Boeck 1872 from deepwater dumpsite 106. Proc. biol. Soc. Wash. 91: 509–521.

Ferrari, F. D. & A. Benforado, 1998. Setation and setal groups on antenna 1 of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias* and *Pseudocalanus elongatus* (Crustacea: Copepoda: Calanoida) during the copepodid phase of their development. Proc. Biol. Soc. Wash. 11: 209–221.

Ferrari, F. D. & M. Dojiri, 1987. The calanoid copepod *Euchaeta antarctica* from Southern Ocean Atlantic sector midwater trawls, with observations on spermatophore dimorphism. J. crust. Biol. 7: 458–480.

Fleminger, A., 1973. Pattern, number, variability and taxonomic significance of integumental organs (sensilla and glandular pores) in the genus *Eucalanus* (Copepoda, Calanoida). Fishery Bull. natn. ocean. atmos. Adm. 71: 956–1010.

Fleminger, A., 1975. Geographical distribution and morphological divergence in American coastal-zone planktonic copepods of the genus *Labidocera*. In Cronin L. E. (ed.), Chemistry, Biology and the Estuarine System. Estuar. Res. 1: 392–419.

Fleminger, A., 1985. Dimorphism and possible sex change in copepods of the family Calanidae. Mar. Biol. 88: 273–294.

Fleminger, A. & K. Hulsemann, 1977. Geographical range and taxonomic divergence in North Atlantic *Calanus* (*C. helgolandicus*, *C. finmarchicus* and *C. glacialis*). Mar. Biol. 40: 233–248.

Fosshagen, A., G. A. Boxshall & T. M. Iliffe, 2001. The Epacteriscidae, a cave-living family of calanoid copepods. Sarsia 86, in press.

Frost, B. W. & A. Fleminger, 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. Bull. Scripps Inst. Oceanogr., tech. Ser. 12: 1–235.

Giesbrecht, W., 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna Flora Golf. Neapel 19: 1–831.

Greene, C. H. & M. R. Landry, 1985. Patterns of prey selection in the cruising calanoid predator *Euchaeta elongata*. Ecology 66: 1408–1416.

Grice, G. D. & K. Hulsemann, 1965. Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the north-east Atlantic. J. Zool., Lond. 146: 213–262.

Griffith, A. M. & B. W. Frost, 1976. Chemical communication in the marine planktonic copepods *Calanus pacificus* and *Pseudocalanus* sp. Crustaceana 30: 1–8.

Heberer, G., 1932. Untersuchungen über Bau und Funktion der Genitalorgane der Copepoden. I. Der männliche Genitalapparat der calanoiden Copepoden. Z. mikrosk. anat. Forsch. 31: 250–424.

Herring, P. J., 1988. Copepod luminescence. Hydrobiologia 167/168: 183–195.

Hopkins, C. C. E., J. Mauchline & D. S. McLusky, 1978. Structure and function of the fifth pair of pleopods of male *Euchaeta norvegica* (Copepoda: Calanoida). J. mar. biol. Ass. U.K. 58: 631–637.

Hulsemann, K. & A. Fleminger, 1990. Taxonomic value of minute structures on the genital segment of *Pontellina* females (Copepoda: Calanoida). Mar. Biol. 105: 99–108.

Huys, R. & G. A. Boxshall, 1991. Copepod evolution, The Ray Society, London: 468 pp.

Jacoby, C. A. & M. J. Youngbluth, 1983. Mating behavior in three species of *Pseudodiaptomus* (Copepoda: Calanoida). Mar. Biol. 76: 77–86.

Katona, S. K., 1973. Evidence for sex pheromones in planktonic copepods. Limnol. Oceanogr. 18: 574–583.

Katona, S. K., 1975. Copulation in the copepod *Eurytemora affinis* (Poppe,1880). Crustaceana 28: 89–94.

Kimoto, K., J. Nakashima & Y. Morioka, 1988. Direct observations of copepod swarm in small inlet of Kyushu, Japan. Bull. Seikai reg. Fish. Res. Lab. 66: 41–58.

Land, M. F., 1984. Crustacea. In Ali M. A. (ed.), Photoreception and Vision in Invertebrates. NATO ASI Series A, Life Sciences 74: 401–438.

Land, M. F., 1988. The functions of eye and body movements in *Labidocera* and other copepods. J. exp. Biol. 140: 381–391.

Landry, M. R. & V. L. Fagerness, 1988. Behavioral and morphological influences on predatory interactions among marine copepods. Bull. mar. Sci. 43: 509–529.

Lee, C. M., 1972. Structure and function of the spermatophore and its coupling device in the Centropagidae (Copepoda: Calanoida). Bull. mar. Ecol. 8: 1–20.

Markhaseva, E. L., 1996. Calanoid copepods of the family Aetideidae of the world ocean. Proc. Zool. Inst. russ. Acad. Sci. 268: 1–331.

Markhaseva, E. L. & F. D. Ferrari, 1996. Three new species of *Ryocalanus* from the eastern tropical Pacific (Crustacea, Copepoda: Ryocalanidae). Zoosystematica Rossica 4: 63–70.

Matthews, J. B. L., 1964. On the biology of some bottom-living copepods (Aetideidae and Phaennidae) from western Norway. Sarsia 16: 1–46.

Mauchline, J., 1998. The biology of calanoid copepods. Adv. mar. Biol. 33: 1–710.

Miller, C. B., B. W. Frost, H. P. Batchelder, M. J. Clemons & R. E. Conway, 1984. Life histories of large, grazing copepods in a sub-arctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus* and *Eucalanus bungii* in the northeast Pacific. Prog. Oceanogr. 13: 201–243.

Nishida, S., 1989. Distribution, structure and importance of the cephalic dorsal hump, a new sensory organ in calanoid copepods. Mar. Biol. 101: 173–185.

Ohman, M. D. & A. W. Townsend, 1998. Egg strings in *Euchirella pseudopulchra* (Aetideidae) and comments on constraints on egg brooding in planktonic marine copepods. J. mar. Syst. 15: 61–69.

Ohtsuka, S., 1992. Calanoid copepods collected from the near-bottom in Tanabe Bay on the Pacific coast of the Middle Honshu, Japan. IV. Pseudocyclopiidae. Publ. Seto mar. biol. Lab. 35: 295–301.

Ohtsuka, S., G. A. Boxshall & H. S. J. Roe, 1994. Phylogenetic relationships between arietellid genera (Copepoda: Calanoida), with the establishment of three new genera. Bull. nat. Hist. Mus. Lond. (Zool.) 60: 105–172.

Ohtsuka, S., A. Fosshagen & S. Putchakarn, 1999. Three new species of the demersal calanoid copepod *Pseudocyclops* from Phuket, Thailand. Plankton Biol. Ecol. 46: 132–147.

466

Ohtsuka, S. & K. Kimoto, 1989. *Tortanus* (*Atortus*) (Copepoda: Calanoida) of southern Japanese waters, with description of two new species, *T.* (*A.*) *digitalis* and *T.* (*A.*) *ryukyuensis*, and discussion on distribution and swarming behaviour of *Atortus*. J. crust. Biol. 9: 392–408.

Ohtsuka, S. & J. W. Reid, 1998. Phylogeny and zoogeography of the planktonic copepod genus *Tortanus* (Calanoida: Tortanidae), with establishment of a new subgenus and descriptions of two new species. J. crust. Biol. 18: 774–807.

Ohtsuka, S., H. S. J. Roe & G. A. Boxshall, 1993. A new family of calanoid copepods, the Hyperbionycidae, collected from the deep-sea hyperbenthic community in the northeastern Atlantic. Sarsia 78: 69–82.

Ohtsuka, S., H. Y. Soh & S. Nishida, 1997. Evolutionary switching from suspension feeding to carnivory in the calanoid family Heterorhabdidae (Copepoda). J. crust. Biol. 17: 577–595.

Othman, B. H. R., 1987. Two new species of *Tortanus* (Crustacea, Copepoda) from Sabah, Malaysia. Malayan nat. J. 41: 61–73.

Park, T., 1986. Phylogeny of calanoid copepods. Syllogeus 58: 191–196.

Price, H. J., G.-A. Paffenhöfer & J. R. Strickler, 1983. Modes of cell capture in calanoid copepods. Limnol. Oceanogr. 28: 116–123.

Sars, G. O., 1902. Copepoda Calanoida. An Account of the Crustacea of Norway, with short descriptions and figures of all the species 4: 29–144, pls. 17–96.

Schnack-Schiel, S. B. & E. Mizdalski, 1994. Seasonal variations in distribution and population structure of *Microcalanus pygmaeus* and *Ctenocalanus citer* (Copepoda: Calanoida) in the eastern Weddell Sea, Antarctica. Mar. Biol. 119: 357–366.

Schulz, K., 1990. *Pterochirella tuerkayi*, a new genus, new species, an unusual calanoid copepod from the deep Gulf of Aden (Indian Ocean). Mitt. hamb. zool. Mus. Inst. 87: 181–189.

Snell, T. W. & M. J. Carmona, 1994. Surface glycoproteins in copepods: potential signals for mate recognition. Hydrobiologia 292/293: 255–264.

Snell, T. W. & P. D. Morris, 1993. Sexual communication in copepods and rotifers. Hydrobiologia 255/256: 109–116.

Soh, H. Y., 1998. Phylogenetic studies of the calanoid copepod superfamily Arietelloidea, with notes on distribution and feeding habits. Doctoral thesis, Hiroshima University, Hiroshima.

Soh, H. Y., S. Ohtsuka, H. Imabayashi & H.-L. Suh, 1999. A new deep-water calanoid copepod and the phylogeny of the genus *Nullosetigera* nom. nov. in the Nullosetigeridae nom. nov. (pro *Phyllopus*: Phyllopodidae) from Japanese waters. J. nat. Hist.: 1581–1602.

Strickler, R. & A. K. Bal, 1973. Setae of the first antennae of the copepod *Cyclops scutifer* (Sars): their structure and importance. Proc. natn. Acad. Sci., U.S.A. 70: 2656–2659.

Suárez-Morales, E. & T. M. Iliffe, 1996. New superfamily of Calanoida (Copepoda) from an anchialine cave in the Bahamas. J. crust. Biol. 16: 754–762.

Svensson, J. E., 1992. The influence of visibility and escape ability on sex-specific susceptibility to fish predation in *Eudiaptomus gracilis* (Copepoda, Crustacea). Hydrobiologia 234: 143–150.

Tanaka, O., 1956. Rare species of Copepoda Calanoida taken from the Izu region. Breviora 64: 1–8.

Tsuda, A., 1995. "The paradox of the plankton" and species diversity in plankton communities: a review. Bull. Plankton Soc. Japan 42: 105–121 (in Japanese with English abstract).

Tsuda, A. & C. B. Miller, 1998. Mate finding behavior in *Calanus marshallae* Frost. Phil. Trans. r. Soc. Lond. B353: 713–720.

Tsukagoshi, A., 1988. Reproductive character displacement in the ostracod genus *Cythere*. J. crust. Biol. 8: 563–575.

Tsukagoshi, A., 1989. The character of male copulatory organ and the distributional pattern of normal pore canals in the ostracod genus *Cythere*. Bull. Jap. Assoc. Benthol. 35/36: 89–96 (in Japanese with English abstract).

Ueda, H., A. Kawahara, M. Tanaka & M. Azeta, 1983. Underwater observations on copepod swarms in temperate and subtropical waters. Mar. Ecol. Prog. Ser. 11: 165–171.

Van Duren, L. A. & J. J. Videler, 1996. The trade-off between feeding, mate seeking and predator avoidance in copepods: behavioral responses to chemical cues. J. Plankton Res. 18: 805–818.

Van Duren, L. A., E. J. Stamhuis & J. J. Videler, 1998. Reading the copepod personal ads: increasing encounter probability with hydromechanical signals. Phil. Trans. r. Soc. Lond. B353: 691–700.

Vaupel Klein, J. C. von, 1982. A taxonomic review of the genus *Euchirella* Giesbrecht, 1888 (Copepoda, Calanoida). II. The type-species, *Euchirella messinensis* (Claus, 1863). A. The female of f. *typica*. Zool. Verh. Leiden 198: 1–131.

Vaupel Klein, J. C. von, 1998. Interpretation of character phylogenies in calanoid copepods by implementing Dollo's law. J. crust. Biol. 18: 153–160.

Walter, T. C., 1989. Review of the New World species of *Pseudodiaptomus* (Copepoda: Calanoida), with a key to the species. Bull. mar. Sci. 45: 590–628.

Yen, J., 1988. Directionality and swimming speeds in predator-prey and male-female interactions of *Euchaeta rimana*, a subtropical marine copepod. Bull. mar. Sci. 43: 395–403.

Yen, J. & J. R. Strickler, 1996. Advertisement and concealment in the plankton: what makes a copepod hydrodynamically conspicuous? Invert. Biol. 115: 191–205.

Yen, J., M. C. Weissburg & M. H. Doall, 1998. The fluid physics of signal perception by mate-tracking copepods. Phil. Trans. r. Soc. Lond. B 353: 787–804.