7

ANTENNULES AND ANTENNAE IN THE CRUSTACEA

Geoff Boxshall and Damià Jaume

Abstract

The remarkable diversity in form and function of the antennules and antennae of crustaceans is reviewed. The basic form of the crustacean antennule is a single-axis segmented limb, but in malacostracans it is typically biflagellate, and in remipedes it comprises a dorsal segmented axis and ventral flagellum. The form of the antenna is also compared across the major crustacean taxa. It is plesiomorphically biramous, with a multisegmented exopod and up to four-segmented endopod; the segmentation of the protopodal part is variable.

The antennules are primarily sensory and form a major sensory interface with the environment. The distribution patterns of chemosensors, mechanosensors, and bimodal elements along the antennules are compared across major taxa. The structure of selected sensors is briefly described, and their roles in feeding, mating, and predator detection behavior are discussed. Crustaceans also use their antennules for such purposes as holding food, grasping a mate, and attaching to a host or other substrate. Morphological adaptations exhibited by these multifunctional limbs are described. Antennae are used for a wide range of tasks. They often perform a sensory role but are used in swimming, attachment, feeding, mating, brooding, and respiration. The manner in which this multifunctionality is reflected in morphology is outlined.

The balance among the different functional roles performed by antennules and antennae changes during development. In crustaceans with planktotrophic nauplii, for example, the antennal coxa bears one or two feeding endites that are subsequently lost during development as the mandibular gnathobase takes over their function. The ontogenetic development of both limbs is briefly reviewed. The enhancement of the chemosensory array on the antennules of males as they attain sexual maturity is found to be common to many different crustacean groups.

Functional Morphology and Diversity. Edited by Les Watling and Martin Thiel.

ANTENNULES AND ANTENNAE IN THE CRUSTACEA

The spectacular adaptive radiation of crustaceans is reflected in the diversity of morphology, behavior, and mode of life they exhibit. The traditional definition of a crustacean usually refers to the possession of a mandible in combination with two pairs of antennae. This serves to distinguish them from chelicerates and fossil taxa such as trilobites, megacheirans, and marrellomorphs, which lack mandibles, and from hexapods and myriapods, which have mandibles but only a single pair of antennae. While in many different crustaceans the antennae provide the primary sensory interface with the environment, they can also be involved in locomotion, attachment, feeding, and mating behavior. The morphology of the antennae differs from group to group, reflecting their different functional roles, and it can vary during development, as the balance of functional roles changes from larva to adult. The patterns of antennal morphology and their relationships are explored here.

ANTENNULES

The anteriormost paired limb on the head of arthropods goes by a variety of names: in crustaceans either *antennule* or *first antenna* is used, according to group or personal preference, whereas in the other mandibulatan groups (hexapods and myriapods) and in the trilobites it is most commonly referred to as the *antenna*. In modern chelicerates, the anteriormost limbs on the prosoma are the paired chelicerae, which, on the basis of Hox gene expression patterns (Telford and Thomas 1998, Damen et al. 1998), can be interpreted as positional homologues of the antennules in these other arthropods (Akam 2000), but they are not considered here. In some Paleozoic fossil arthropods of uncertain affinity, such as *Leanchoilia superlata*, the first limb is simply termed the "great appendage" (Bruton and Whittington 1983). We use *antennule* here for the anteriormost limb pair arising from the deuterocerebral somite of the head of crustaceans and their mandibulatan relatives (see Scholtz and Edgecombe 2005).

Structure

The typical arthropodan antennule comprises a single proximodistal axis composed of few to multiple subdivisions, which have been referred to variously as antennulomeres, podomeres, flagellomeres, segments, articles, annuli, or annulations. The terminology for the subdivisions is dependent upon their anatomy. An antennule is segmented if it consists of a linear series of true segments, as defined by the presence of intrinsic muscles that insert or attach at each intersegmental articulation. Each articulation is typically provided with a hoop of arthrodial membrane that allows slight telescoping of the proximal rim of the more distal segment within the distal rim of the more proximal segment. Segmented antennules, therefore, have segmentally arranged intrinsic musculature, typically along the entire length of the limb (see Boxshall 2004).

The other type of single-axis antennule is flagellate. At least two different types of flagellate antennules are found within recent arthropods: those with terminal flagella formed by annulation of the distal segment, as in some collembolans, ectognathan insects, and malacostracan crustaceans, and those with nonterminal or intercalary annulations, such as scutigeromorph centipedes and some crustacean larvae (see Boxshall 2004). Terminal flagella are by far the most common. Flagella are also composed of few to multiple external subdivisions of the axis, but they lack intrinsic musculature. These subdivisions are referred to here as *annuli*.

Interpreting the nature of the antennules of fossil arthropods can be problematic since information on intrinsic musculature is usually lacking. Without evidence derived from knowledge of the internal anatomy, the subdivisions of the limb cannot be identified as either segments or annuli, and descriptive terms such as *antennulomeres* should be used. Whether segmented or flagellate, antennules are essentially modular in construction, and this modularity confers important functional attributes, permitting, for example, the enhancement of a sensory array by the addition of extra modules or by the specialization of individual modules.

Single-Axis Antennules

Single-axis antennules are found in the great majority of fossil arthropod taxa from the early Paleozoic, as exemplified by the Cambrian arthropods of the Burgess and Maotianshan Shale faunas. Single-axis, segmented antennules are found in the Myriapoda (with the exception of the Pauropoda), in some basal Hexapoda (Diplura and Collembola only) (Imms 1939), and in the Crustacea, with the exception of the Remipedia and the Malacostraca only (see Boxshall et al. 2010).

In the Crustacea, the maximum number of segments expressed varies with taxon. In recent Branchiopoda, the antennules are either one- or two-segmented, although the spinicaudatan *Caenestheriella australis* has a distal flagellar section comprising a linear series of lobes that resemble segments (Boxshall 2004). Fossil branchiopods have more antennulary segments: the Devonian lipostracan *Lepidocaris* has short, three-segmented antennules (Scourfield 1926, 1940), but in the Kazacharthra (fossil relatives of the Notostraca) up to 15 antennulomeres have been reported in *Almatium gusevi* (McKenzie et al. 1991). In Cambrian branchiopods such as *Rehbachiella* and *Bredocaris*, the antennules comprise a proximal zone of incomplete annuli and a distal zone of cylindrical segments (Walossek 1993). The presence of proximal annuli is possibly indicative of intercalary annulation (*sensu* Boxshall 2004), but the absence of data on musculature makes it impossible to interpret these fossils unequivocally.

In the Cephalocarida the single-axis antennule comprises only six segments in *Hutchinsoniella macracantha* (Hessler 1964), and no segments are added during development (Sanders 1963). In the Mystacocarida the maximum number of segments is eight (Hessler and Sanders 1966), and this is constant throughout larval development in *Derocheilocaris remanei* (Olesen 2001). In any extant copepod species, a maximum of 27 antennulary segments is found, although Huys and Boxshall (1991) demonstrated that a total of 28 different segments are expressed within the Copepoda as a whole. These multisegmented antennules are not flagellate—all segments are primitively provided with intrinsic musculature (Fig. 7.1). Reductions in antennulary segmentation are common across the Copepoda and are primarily a result of failure of expression of intersegmental articulations during development rather than secondary fusion of segments that were expressed earlier in ontogeny (Boxshall and Huys 1998).

The antennule of Myodocopa is a single axis with up to eight segments, as found in extant forms and in fossil taxa from the Silurian (Siveter et al. 2003, 2007). Podocopan ostracods have single-axis antennules, and a maximum of eight segments is expressed, although most recent taxa have fewer (Maddox 2000). Developmental data indicate that reductions in segmentation in adults result primarily from failures of expression of intersegmental articulations rather than secondary fusions (Smith and Tsukagoshi 2005, Smith and Kamiya 2008). It has been suggested that a reduced exopod, represented by a setose marginal expansion, is present in some podocopans (e.g., Kesling 1951, Rossetti and Martens 1996, Karanovic 2005), but a recent review of developmental and other studies found no evidence to support this interpretation (Boxshall et al. 2010).

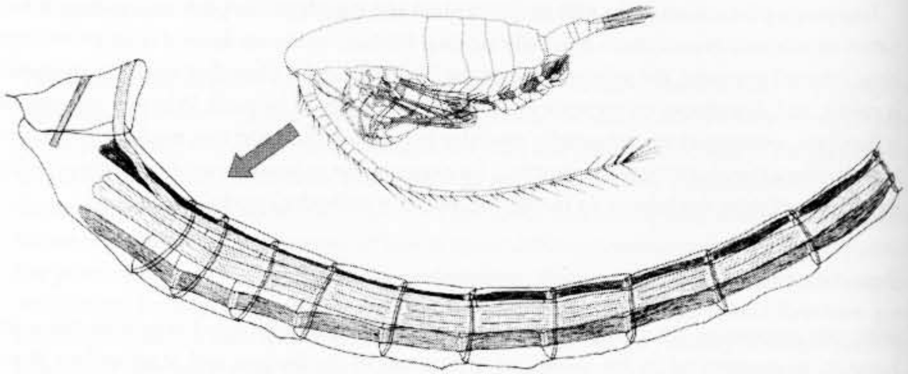

Fig. 7.1.
Proximal part of the antennule of a female *Euaugaptilus* (Copepoda: Calanoida) showing intrinsic muscles making intermediate attachments on the proximal rim of each segment. Modified from Boxshall (1985), with permission from the Royal Society of London.

In the bivalved Cambrian phosphatocopines, the antennules are small and comprise a single axis with a maximum of 13 irregular subdivisions (in *Waldoria*), referred to by Maas et al. (2003) as annuli. Setae are present on the two or three distal annuli only, and the setation pattern does not change during development.

Antennules of Thecostraca consist of a maximum of six expressed segments, as found in some Ascothoracida. In adults the prehensile antennule terminates in a clawlike subchela mechanism that secures attachment to the host. Developmental studies show that the ascothoracidan claw originates on the fourth segment of the six-segmented naupliar antennule, with the distal two segments becoming incorporated into the compound apical segment of the adult (Grygier 1984). A total of eight different segments are therefore expressed during development. In the Cirripedia, including the parasitic Rhizocephala, the antennules (Fig. 7.2) are short and four-segmented, but the apical segment is offset at an angle to the main axis that terminates in the attachment disc carried on the third segment. This disc is responsible for securing the larva to the substrate during settlement. A standardized terminology for the segments and their setae was proposed by Bielecki et al. (2009).

The antennule of the branchiuran fish lice comprises a two-segmented basal part armed with curved, hooklike outgrowths and a two-segmented distal part, bearing setae (Rushton-Mellor and Boxshall 1994). The Tantulocarida lack antennules in the tantulus larva stage (indeed, this larva lacks all cephalic limbs), and in adult males the antennules are represented only by paired clusters of aesthetascs arising anteriorly on the ventral surface of the cephalothorax (Boxshall and Lincoln 1987). In the adult sexual female, a pair of unsegmented antennules is present (Huys et al. 1993).

Double-Axis Antennules

Antennules with two proximodistal axes are found in adult malacostracans and remipedes. The malacostracan antennule typically comprises a robust basal part, the peduncle, bearing two multiannulate flagella. The antennulary peduncle in malacostracans is not homologous with the protopod of the postantennulary biramous limb—there is no evidence that the crustacean antennule is derived from a fundamentally biramous structure (Boxshall 2004). The peduncle

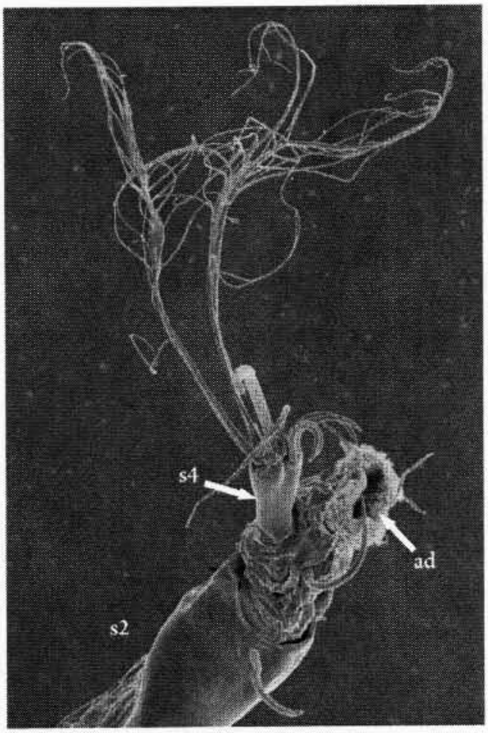

Fig. 7.2.
Scanning electron micrograph of distal segments (s2, s4) of antennule of cypris larva of *Megabalanus rosea* (Thecostraca: Cirripedia) showing offset apical segment (s4) with complex setal armature, and attachment disc (ad) on third segment. Photo courtesy of J. Høeg.

is the proximal segmented zone that contains intrinsic musculature and carries the flagella. It can be two-, three-, or four-segmented and houses the flagellar flexor and extensor muscles that insert inside the proximal rim of the basal annulus of each flagellum (Fig. 7.3). All malacostracan antennules thus far investigated lack intrinsic musculature in the annulated flagellar parts. In the terrestrial anomuran *Birgus latro*, the peduncle segments are long and slender, and the distal flagella are relatively short.

This biflagellate antennule is an autapomorphy of the Malacostraca (Richter and Scholtz 2001, Jenner et al. 2009) and is present in the earliest unequivocal fossil malacostracan, *Cinerocaris magnifica*, an archaeostracan phyllocarid from the Silurian (Briggs et al. 2003). The two flagella are sometimes referred to as inner and outer rami (Richter and Scholtz 2001) or, specifically, as exopod and endopod (e.g., Bruce 1986 for isopods, Clark et al. 1998 for decapods, and Perrier et al. 2006 for palaeocarid syncarids), but this terminology is inappropriate (see review in Boxshall et al. 2010). The flagella are also referred to as outer and inner (Jaume and Bréhier 2005), as medial and lateral (e.g., Goldman and Patek 2002, Reidenbach et al. 2008), or as primary and accessory (Jaume et al. 2006). The terms *primary* and *accessory flagella* are used here.

The biflagellate antennule comprises a laterally located primary flagellum, the annuli of which each typically carry one or two rows of aesthetascs, and an accessory flagellum. The more medially positioned accessory flagellum can be as long as or longer than the primary flagellum, but it never carries aesthetascs and typically appears later in development than the

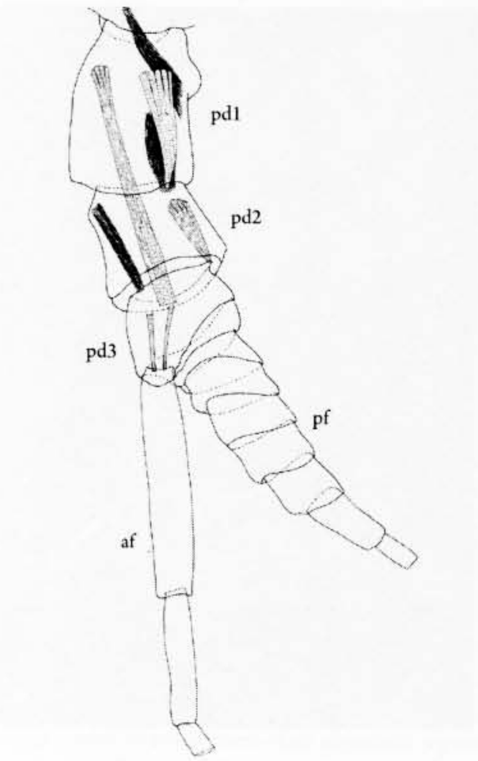

Fig. 7.3.
Antennule of the male of *Montucaris* (Peracarida: Bochusacea) showing intrinsic musculature within three-segmented peduncle (pd1–pd3) and inserting on the proximal rim of an accessory flagellum (af). No musculature is observed going to the base of the primary flagellum (pf) in the male. Modified from Jaume et al. (2006), with permission from Blackwell Publishing.

primary flagellum. Given the presence of aesthetascs only on the primary flagellum, we infer that it is homologous with the dorsal axis in remipēdes and with the sole axis in other nonmalacostracans. Most malacostracans, including the anaspidacean and palaeocaridacean Syncarida, Euphausiacea, Amphionidacea, Decapoda, and members of the peracaridan groups Mysidacea, Lophogastrida, Cumacea, and Spelaeogriphacea, primitively have two multiannulate flagella. Both flagella can be reduced; in the Mictacea and Bochusacea, for example, both consist of just a few annuli. The accessory flagellum is reduced and often absent in isopods, amphipods, and tanaidaceans. In oniscoidean isopods, perhaps as an adaptation to a terrestrial mode of life, the entire antennule can be reduced to one to three subdivisions, with subsequent loss of clear separation between the peduncle and flagellum (Vandel 1960). In the cirolanid isopod *Bathynomus giganteus*, the "scale" carried on the third antennulary segment has been interpreted as representing the reduced accessory flagellum, as indicated by the retained cluster of setal elements at its tip (Brusca and Wilson 1991).

In the Leptostraca, the antennule consists of a three-segmented peduncle bearing a flagellum and an articulated scale. The externally located scale of the Leptostraca was interpreted by Richter and Scholtz (2001) as the "outer ramus" (presumably the homologue of the laterally located primary flagellum). It is probably independently derived within the Phyllocarida, since the archaeostracan phyllocarid *Cinerocaris magnifica* carries two long antennulary flagella

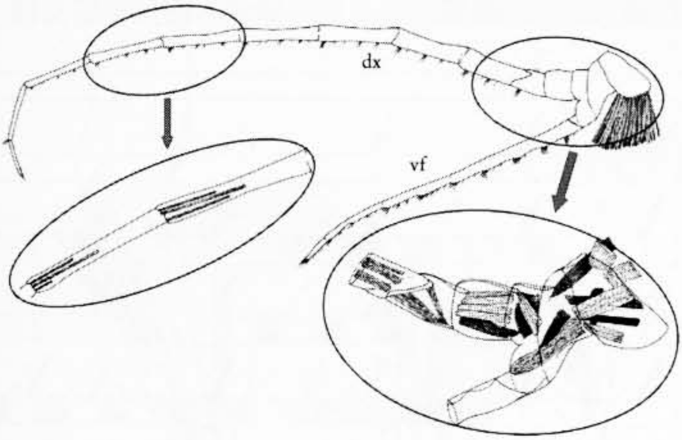

Fig. 7.4.
Antennule of *Speleonectes* (Remipedia) with details showing musculature within protopodal part extending into segmented dorsal axis (dx) and inserting on proximal rim of annulate ventral flagella (vf). Modified from Boxshall (2004), with permission from Wiley and Sons, Ltd.

(Briggs et al. 2003). We consider that the leptostracan outer scale is derived from the accessory flagellum despite its lateral origin. The evidence supporting this inference is the relatively late appearance of the scale after the main axis (the primary flagellum) during development (Olesen and Waloßek 2000) and the absence of aesthetascs, which are found only on the primary flagellum. In the Bathynellacea there is an antennulary scale carried internally, and it has been interpreted as a rudiment of the accessory flagellum (Siewing 1959, Richter and Scholtz 2001, as the "inner ramus").

When first discovered, the Remipedia were described as having biramous antennules (Yager 1981), but Boxshall (2004) revealed that the dorsal branch is the primary axis consisting of segments defined by intrinsic muscles, and the ventral branch lacks intrinsic musculature and is weakly annulated (Fig. 7.4). The ventral branch is not segmented and should not have been interpreted as a ramus: it is a flagellum. During development the primary axis only is present in the metanaupliar phase, and the ventral flagellum first appears in the postlarva, initially as a single "segment" lacking annulations (Koenemann et al. 2007). The remipede antennule therefore comprises the segmented primary axis typical of other Crustacea such as the Cephalocarida and Copepoda plus a ventral flagellum and differs from the biflagellate antennule of malacostracans. The common basal part of the remipede antennule is referred to as the *peduncle*. It is not homologous with the protopod of a biramous limb because, as for the Malacostraca, there is no evidence that the crustacean antennule is derived from a biramous limb (Boxshall 2004).

Multiple-Axis Antennules

A triflagellate antennule occurs in the Stomatopoda and in their Paleozoic relatives belonging to the hoplocaridan orders Aeschronectida and Palaeostomatopoda (Schram 1986). The triflagellate condition of the stomatopod antennule is an autapomorphy (Richter and Scholtz 2001). In stomatopods the ventrally located accessory flagellum is subdivided into two subflagella (Kunze 1983), but only the primary flagellum carries aesthetascs (Mead and Koehl 2000), as in other malacostracans.

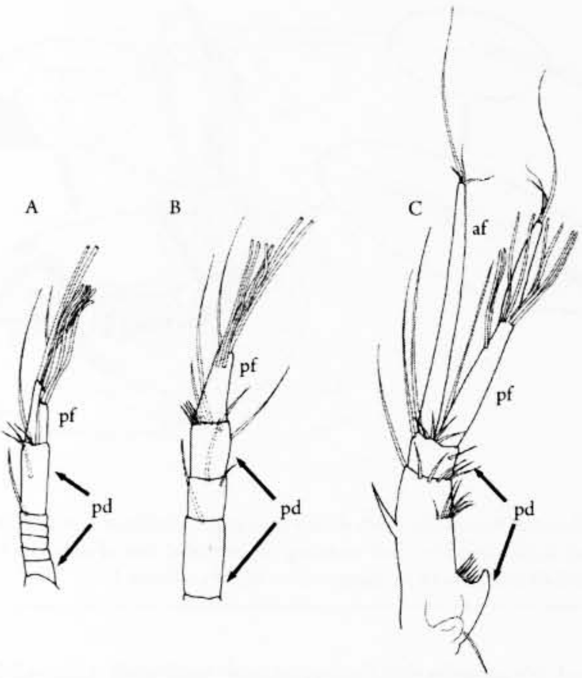

Fig. 7.5.
Development of antennule of *Pleoticus muelleri* (Decapoda) showing single-axis state in protozea I stage (A) and protozoea III stage (B), consisting of peduncle (pd) and primary flagellum (pf), and biflagellate condition of mysis II stage (C), after first appearance of accessory flagellum (af) at mysis I stage. Redrawn from de Calazans (1992).

Within the Caridea (Decapoda), some representatives of at least three families (Palaemonidae, Alpheidae, and Hippolytidae) also have the accessory flagellum divided to form two subflagella (see Bacescu 1967). Given current estimates of relationships, we infer that this condition has arisen independently in the Caridea, probably more than once.

Development

Studies on postembryonic development of crustaceans provide additional evidence supporting the secondary derivation of the biflagellate antennule (e.g., Scholtz 2000, Gruner and Scholtz 2004, Koenemann et al. 2007). The orthonauplius represents a primordial phylotypic stage for the Crustacea, and the naupliar antennule always comprises a single primary axis (Fig. 7.5A,B). Any additional flagellar structures present in malacostracans (e.g., the accessory flagellum) and remipedes (the ventral flagellum) develop at a subsequent, postnaupliar stage (Fig. 7.5C).

In segmented antennules, development follows a distal-to-proximal pattern. Articulations separating the more distal segments are typically expressed earlier than those separating the more proximal ones, and segmental setation is typically complete earlier on more distally located segments than on proximal ones (Boxshall and Huys 1998, Smith and Tsukagoshi 2005). The ground-plan development pattern from nauplius to adult was modeled by Boxshall and Huys (1998) for a hypothetical ancestral copepod (Fig. 7.6). The metamorphic molt from

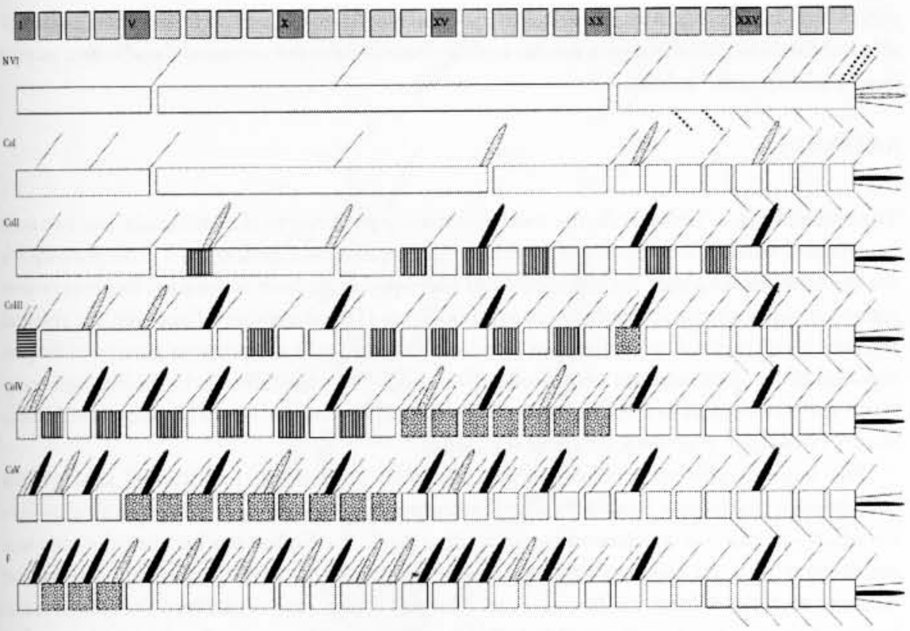

Fig. 7.6.
Schematic showing hypothetical development of segmentation and setation through the copepodid stages of Copepoda. The scale at the top indicates the presumed 28 segments of the ancestral copepod. Setae are shown as lines, and aesthetascs, as solid elements. A segment carrying a seta not present at the preceding stage is shaded with vertical stripes if the newly added seta is anterodistal or with stippling if the new seta is anteroproximal. The basal segment is shown with horizontal stripes when its second and third setae appear. Aesthetascs are shown stippled when they first appear, and then in black. Abbreviations: CoI–CoV, copepodid stages I–V; F, female; NVI, nauplius VI stage. Adapted from Boxshall and Huys (1998) with permission from the Royal Society of London.

the sixth and final nauplius stage to the first copepodid stage was marked by the subdivision of the apical segment of the nauplius to form the distal eight segments of the adult antennule. No further divisions occur in this distal section of the antennule throughout the five copepodid-phase molts to adult. During the copepodid phase, the two proximal antennulary segments of the nauplius undergo a sequence of subdivisions to form segments 1–20 of the adult. Antennules with fewer expressed segments are envisaged as being generated by early cessation of the process of subdivision (Boxshall and Huys 1998, Schutze et al. 2000), a pedomorphic process.

Proximal annulation is expressed transiently during the naupliar phase of development of some podoplean copepods but is lost by the first copepodid stage (e.g., Dahms 1992). The protozoeal larvae of penaeid decapods similarly exhibit transient annuli in the proximal part of the antennule (Fig. 7.5A), which are lost by the end of the zoeal phase. The proximal annulated part of the antennule of *Rehbachiella* and *Bredocaris* may be interpreted as additional evidence of their larval status but may also indicate that a proximal annulated zone is plesiomorphic for the Crustacea.

In decapod malacostracans such as *Panulirus argus* and *Cherax destructor*, the primary antennulary flagellum develops by the production of new annuli at the base of the flagellum, in a meristematic zone (Sandeman and Sandeman 1996, Steullet et al. 2000). In both species

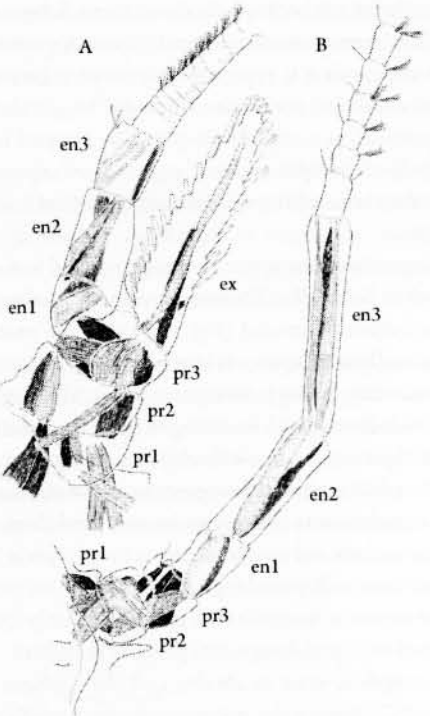

Fig. 7.7.
(A) Biramous antenna of *Hemimysis* (Peracarida: Mysidacea) showing intrinsic musculature within three-segmented protopod (pr1–pr3), within the proximal three endopodal segments (en1–en3) inserting on the proximal rim of the endopodal flagellum and within the exopod (ex). (B) Uniramous antenna of *Typhlocirolana* (Peracarida: Isopoda) showing intrinsic musculature within three-segmented protopod (pr1–pr3) and proximal three endopodal segments (en1–en3), inserting on the proximal rim of the endopodal flagellum. The exopod is absent.

and elaborate ornamentation, whereas in females they are typically smaller and simpler in construction (Linder 1941). In conchostracan branchiopods the antenna is biramous, and both of the large rami appear to be flagellate, but both exopod and endopod comprise numerous segments as defined by the presence of intrinsic muscles (Shakori 1968, Boxshall 2004). The multisegmented nature of the endopod was interpreted as secondarily derived within the Conchostraca by Boxshall (2004). In cladocerans the number of exopodal and endopodal segments does not exceed three in Anomopoda, Onychopoda, and Ctenopoda or four in Haplopoda and the fossil order Cryptopoda. In *Holopedium*, the antenna is uniramous due to loss of the endopod.

The cephalocaridan antenna is biramous, comprising a protopod divided into coxa and basis, a short two-segmented endopod, and a well-developed, multisegmented exopod (Sanders 1963). The number of exopodal segments and associated setal elements increases during ontogeny; *Hutchinsoniella*, for example, has 13 segments bearing 15 setae at the metanauplius stage, rising to 19 and about 70 setae in the adult (Elofsson and Hessler 1991). The setae are structurally similar, with the lumen of each containing 6–12 unbranched outer dendritic segments surrounded by two layers of sheath cells. All the setae were interpreted as chemosensors by Elofsson and Hessler (1991), who remarked on the lack of mechanoreceptors, not having found scolopale bodies associated with any of the setal sensory cells (see chapter 6).

subdivision takes place in annuli distal to the basal meristematic annulus. Few details are available but the basic process seems similar to that described for the antennal flagellum in isopods (see "Development," below).

ANTENNAE

The second limb in arthropods, the one immediately posterior to the antennule, has two main names: in Crustacea, it is the *second antenna* or just *antenna*; in Chelicerata, it is the *pedipalp*. We use the term *antenna* here. In Hexapoda and Myriapoda this limb is missing; its absence serving as a diagnostic character of the taxon Atelocerata (Heymons 1901). However, the antennal segment is represented by the limbless intercalary segment. The expression pattern of the gene *engrailed* in the epidermal and neural cells of hexapods unequivocally marks the intercalary segment, and its existence is further supported by the expression pattern of the Hox gene *labial* in insects (Diederich et al. 1989, Peterson et al. 1999).

The Silurian arthropod *Tanazios* was described by Siveter et al. (2007) as a possible stem-lineage crustacean. Boxshall (2007) reinterpreted the antenna of *Tanazios* as missing in the adult—its absence is indicated by the marked gap in the limb series between the antennule and the mandible. He concluded that the lack of differentiation in the postmandibular limbs of *Tanazios* excludes it from the Eucrustacea. Boxshall (2007, 322) considered the lack of antennae in a Silurian marine arthropod to be "of immense significance both to our understanding of deep mandibulate phylogeny, and to the emerging, but as yet unstable, picture of hexapod origins within the Pancrustacea."

Structure

The basic postantennulary limb of arthropods is widely regarded to be biramous (see Walossek 1993, Hou and Bergström 1997, Boxshall 2004), comprising a proximal stem, the protopod, bearing an inner endopod and outer exopod. These rami are major limb axes and are carried distally on the protopod. They are plesiomorphically supplied with intrinsic muscles originating within the protopod and are commonly segmented. The antenna of crustaceans is plesiomorphically biramous: the protopod is two-segmented, comprising coxa and basis; the exopod is usually multisegmented, and the endopod typically comprises only four expressed segments. In malacostracans the protopod may be three-segmented (Fig. 7.7), but there is no evidence for the existence of a precoxa in the antenna of cephalocaridans, remipedes, branchiopods, copepods, mystacocaridans, podocopan ostracods, myodocopans, or branchiurans. The Tantulocarida lack antennae at all stages of the described life cycle (Huys et al. 1993). The nonfeeding planktonic adults of monstrilloid copepods lack all cephalothoracic limbs from antennae to maxillipeds, inclusive. The infective nauplius phase, however, has biramous antennae with a setose, natatory exopod and an endopod that carries a terminal clawlike seta (Grygier and Ohtsuka 1995). The antennal endopod together with the clawed mandible are used to grasp the host surface during infection.

The antenna of Cambrian phosphatocopines is biramous: the protopod is unsegmented or subdivided into coxa and basis, the endopod is two- or three-segmented, and the exopod is described as multiannulate (Maas et al. 2003). When undivided, the protopod forms an entire gnathobase; when divided, both coxa and basis are drawn out medially into a spine-bearing endite (Siveter at al. 2001). The number of "annuli" in the exopod ranges from about 8 up to 24, and these typically carry a single seta each, with two at the apex (Maas et al. 2003).

In the Anostraca, the antennae exhibit extreme sexual dimorphism. In adult males they may be modified as enormous grasping structures, often with species-specific basal outgrowths

In mystacocarids, cirripedes, and copepods, the antenna is typically biramous, comprising coxa and basis, which bears the exopod and endopod. The endopod is apparently six-segmented in mystacocarids, but in copepods it is typically only three-segmented, although traces of an ancestral four-segmented condition are retained in some basal calanoids (Huys and Boxshall 1991). It is only two-segmented in cirripede nauplii. The exopod has at most nine segments in mystacocarids and cirripede nauplii and ten segments in copepods. However, within the Thecostraca, ascothoracid metanauplii have antennal exopods of 12 or more segments (Boxshall and Böttger-Schnack 1988).

In malacostracans the protopod has typically been regarded as two-segmented, comprising coxa and basis, but we find in *Tulumella* (Thermosbaenacea), *Hemimysis* (Fig. 7.7A), *Stygiomysis* (Mysidacea), and *Typhlocirolana* (Isopoda) (Fig. 7.7B) that the protopod is three-segmented. The coxa articulates proximally with a precoxa that may have been interpreted as a pedestal, but the presence of muscles inserting at this joint indicates that it is a segment. The antennal endopod in malacostracans is well developed, consisting of up to three defined segments proximally, plus a terminal flagellum representing a subdivided fourth segment. The proximal endopodal segments are usually referred to as peduncle segments, so the six-segmented peduncle of some peracaridans comprises a combination of three protopodal and three endopodal segments (Fig. 7.7), whereas in other peracaridans and euphausiaceans the peduncle is five-segmented, consisting of two protopodal and three endopodal segments. Muscles are present only in the peduncle segments (Fig. 7.7). In the syncarid *Anaspides* the peduncle is only four-segmented, comprising coxa, basis, and two defined endopodal segments plus the flagellum.

In leptostracans the exopodal scale is absent, and the antenna is uniramous, but in the archaeostracan phyllocarid *Cinerocaris* the antenna is biramous with two slender flagellate rami (Briggs et al. 2003). In eumalacostracans the exopod is reduced to a scale, although in stomatopods the scale has a well-defined proximal segment (Schram and Hof 1998). The exopodal scale, also referred to as the *scaphocerite*, is greatly enlarged in the Amphionidacea and in decapod shrimps but can be reduced or lost in anomurans and brachyurans. In asellote isopods and in the thermosbaenacean *Tulumella*, there is also a scalelike exopod, but other members of these orders, as well as members of the Cumacea and Amphipoda, have uniramous antennae lacking any trace of the exopod (Fig. 7.7B). The flattened, platelike antenna of scyllarid lobsters is derived from the flagellum, not from the exopodal scale.

Extreme development of the antennal flagellum is exhibited in penaeidean decapods, in which it can attain a total length more than three times that of the body. In these penaeideans, the flagellum comprises a relatively rigid proximal section and a long whiplike distal section, separated by a flexure zone. During normal swimming, the proximal section is held out from the body, and the flexible distal part trails out parallel to and at a distance from the animal (Foxton 1969). Distal to the flexure zone, each annulus typically carries a pair of arched, plumose setae that together effectively form a tube running the entire length of the distal section. Within this "tube" a linear array of finely plumose setae can be present, although there is not necessarily one per annulus. This system allows the detection of near-field vibrating sources and can indicate the direction of the source because the near-field effect attenuates rapidly (i.e., along the length of the flagellum) (Denton and Gray 1986).

The stiffness of the flagellum is nonuniform. In *Cherax destructor*, the flagellum is tapered and consists of 220–250 annuli that increase in length and decrease in diameter toward the tip (Sandeman 1989). The flagellum is oval in cross section and exerts the greatest mechanical resistance against medial deflection and the lowest against dorsal deflection. Medial mechanical resistance decreases markedly toward the tip. When bent passively, curvature is confined to a small part of the flagellum, but with increasing force, the apex of the bend moves toward the base. Sensing curvature at several locations along the flagellum is likely to provide sufficient information to enable the crayfish to distinguish whether the bending is caused by the flow fields in the surrounding medium or by physical contact with an obstacle (Barnes et al. 2001).

Development

During the early naupliar phase, the antenna bears one or two feeding endites, referred to as the *naupliar* or *antennal processes*, on the proximal segment (the coxa) of the two-segmented protopod. These naupliar processes are found in copepods, mystacocarids (Fig. 7.8A), cephalocarids (Fig. 7.8B), and branchiopods—taxa that retain nonlecithotrophic nauplii. They decrease in size during later development and are lost at or before the molt to the postnaupliar phase.

In dendrobranchiate decapods, the antenna of the naupliar and protozoeal phases has a multisegmented exopod that gradually ceases to express segmentation during development until, by the megalope phase (= mysis I stage), the exopod has transformed into the unsegmented antennal scale (Fig. 7.9) so characteristic of the adult caridoid facies (Hessler 1983). This transition from segmented naupliar ramus to unsegmented scale is unique to these malacostracans. It is accompanied by a change in form of the endopod, from a two-segmented ramus (Fig. 7.9A) to an annulate flagellum (Fig. 7.9C).

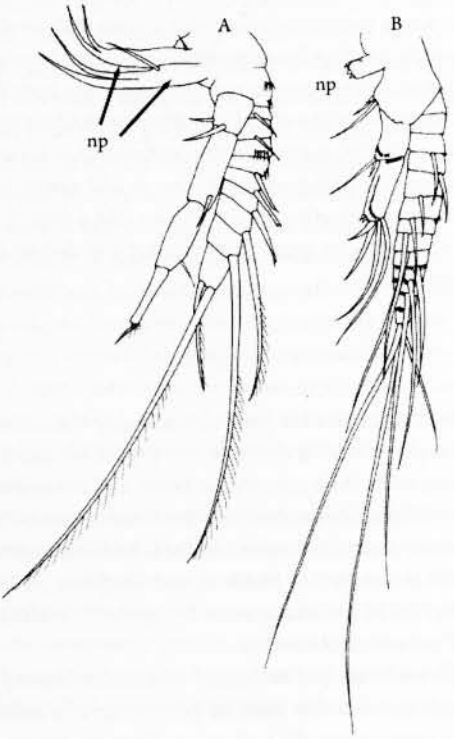

Fig. 7.8.
(A) Antenna of first stage metanauplius of *Derocheilocaris* (Mystacocarida) showing large feeding naupliar processes (np) on coxa (redrawn from Hessler and Sanders 1966). (B) Antenna of first stage nauplius of *Hutchinsoniella* (Cephalocarida) showing developing naupliar process on coxa (redrawn from Sanders 1963).

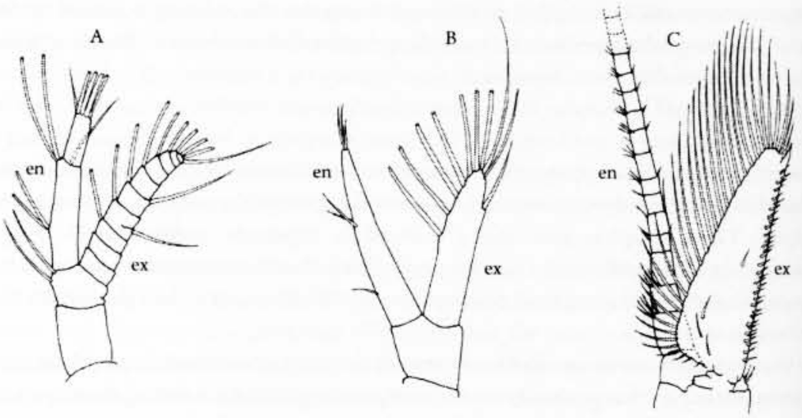

Fig. 7.9.
Developmental of the antenna of *Pleoticus muelleri* (Decapoda) showing transition in form of exopod (ex) and endopod (en) from protozoea III stage (A) to mysis I stage (B), and megalopa stage (C). Redrawn from de Calazans (1992).

The isopod *Asellus aquaticus* is a useful model for the development of the endopodal flagellum, which consists of a single segment divided into annuli that are devoid of intrinsic musculature (Wege 1911). The antennal flagellum comprises a proximal meristematic region, a central region composed of quartets (sets of four annuli, each having a specific arrangement of setae), and an apical complex consisting of the apical annulus plus the four preceding annuli with specific setal patterns. The number of quartets in the central region is variable in *Asellus aquaticus* since this species never ceases molting and continues to add annuli throughout life (Maruzzo et al. 2007). The proximal meristematic annulus divides into a copy of itself (the meristem) and a distal annulus that is effectively an incomplete quartet and divides following a set pattern to produce the complete quartet.

SENSORS

In most crustaceans, the antennules are primarily sensory in function and carry rich arrays of sensory receptors that play a role in almost every aspect of their behavior. The main setal receptor types can be defined by their sensory modality, and although the sensitivity and functional responses of most setal elements have not been experimentally investigated, comparative studies allow for putative functions to be inferred. Setal elements with a sensory function are commonly referred to as *sensilla* (see Hallberg and Skog 2011), but the terminology has not yet stabilized (see chapter 6). In some taxa, such as copepods, aesthetascs are regarded as distinct from setae rather than as a setal subtype.

Various terminologies are employed to discuss crustacean sensory modalities, and this can generate confusion. Chemosensors that mediate perception of a remote chemical are referred to as *olfactory*. Olfaction (sense of smell) is distance chemoreception and usually involves the detection of a gradient of chemical entrained within a plume originating at its source, such as a pheromone produced by congeneric females or amino acids originating from food items. Chemosensors that mediate perception of a chemical stimulus at extremely close range, or when in direct physical contact, are often referred to as *gustatory* or *taste receptors*. This is contact chemoreception (Atema 1977). Distance and contact chemoreceptors represent extremes in sensitivity along a continuous spectrum, so the separation is somewhat artificial although widely adopted (see Hallberg and Skog 2011).

There is a similar functional division in mechanoreceptors. Mechanosensors that mediate remote perception of hydrodynamic signals, such as disturbances in flow fields caused by particles suspended in the water column or by the swimming motions of a live prey, are distance mechanosensors. Sensors that detect the presence of objects only when they come into direct physical contact with a surface are tactile sensors. Again, distance and tactile sensors represent extremes in sensitivity along a continuous spectrum of mechanosensors. Displacement of a mechanosensory setal shaft in its socket or the bending of a seta in direct contact with an object can both constitute a stimulus.

The Aesthetasc

Aesthetascs are the most studied crustacean chemosensor. They are typically elongate, thin-walled, cylindrical elements (Fig. 7.10), which lack internal enveloping cells in their outer part (Hallberg and Skog 2011). They are innervated by sensory cells that vary in number from a few to hundreds, for example, 400 in *Pagurus hirsutiusculus* (Ghiradella et al. 1968a). The sensory cells are surrounded by enveloping cells basally. They have dendrites from which cilia emerge, usually two cilia in malacostracans, sometimes only one, sometimes more. The cilia typically, but not always, branch dichotomously and repeatedly to form a dense mass of outer branches called *outer dendritic segments* (Laverack 1964, Hallberg et al. 1992). Grünert and Ache (1988) reported 8,000–10,000 such outer dendritic segments per aesthetasc in *Panulirus argus*.

Aesthetascs' function as a chemoreceptor has been confirmed experimentally by direct neurophysiological studies in various decapod malacostracans (Anderson and Ache 1985, Michel et al. 1993, Steullet et al. 2000). The permeability of the thin cuticle allows water-borne compounds to enter over the entire surface area, but the cuticle remains sufficiently impermeable to prevent loss of physiologically important molecules (Derby et al. 1997).

The aesthetasc can vary in external form: curved aesthetascs can be found, for example, in some isopods (Kaïm-Malka et al. 1999) and some cavernicolous copepods (Boxshall and Jaume 2000). They vary in size with taxa: body size is a factor influencing aesthetasc length. Aesthetascs in *Cancer productus* can attain a length of >1700 μm, one of the longest in the Crustacea, whereas those of small cladocerans or interstitial copepods may reach only 10–12 μm in length (Hallberg et al. 1992, Boxshall et al. 1993). Aesthetascs increase in size during development in the stomatopod *Gonodactylus mutatus* (Mead 2002). As well as varying in size with species, aesthetascs can be sexually dimorphic, with males carrying larger aesthetascs than conspecific females (Boxshall and Huys 1998).

Terrestrial crustaceans retain functional aesthetascs (Ghiradella et al. 1968b). In the robber crab *Birgus latro*, the antennules consist of an elongate, three-segmented peduncle bearing two short distal flagella, and the aesthetascs are arrayed in rows across the central groove of the primary flagellum. They differ from those of aquatic relatives in being relatively short and blunt. In addition, they have an asymmetric profile, with the side nearest the surface of the annulus being thickened and the exposed surface being thin and wrinkled (Stensmyr et al. 2005). The thickened surface and flattened profile presumably enhance the rigidity of the aesthetasc out of water.

The arrangement of aesthetascs on the antennule varies but is normally taxon specific and relatively highly conserved within a higher taxon. Cephalocarids, for example, carry just a single terminal aesthetasc. In adult *Hutchinsoniella* the aesthetasc is located in a terminal tuft, together with 11 other setae, and a further 11 setae are distributed over the more proximal segments (Elofsson and Hessler 1991). In anostracan and cladoceran branchiopods the aesthetascs

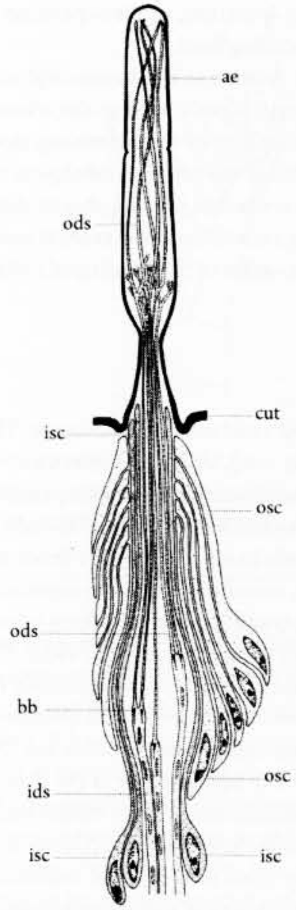

Fig. 7.10.
Fine structure of typical malacostracan aesthetasc. The aesthetasc (ae) has a short stalk attached to the cuticle (cut), and its lumen is filled with a mass of branching outer dendritic segments (ods), which arise from inner dendritic segments (ids) within the antennule. Just proximal to the origin of the outer dendritic segments are the 9 × 2 + 0 ciliary basal bodies (bb). The array of dendritic segments is sheathed with multiple layers formed by inner (isc) and outer (osc) sheath cells. Schematic shown with reduced numbers of components, there are multiple dendrites and a variable number of sheath cells. Adapted from Heimann (1984), with permission from Springer.

are typically found in a tuft on the apex of the antennule, whereas in the Notostraca and most Spinicaudata they are arrayed along the margin (Martin 1992). In mystacocarids, there is a single aesthetasc located subterminally on the apical segment (Olesen 2001). The sensory tubes described from the antennules of the myodocopan *Conchoecia spinirostris* are probably aesthetascs, although they differ from the typical decapod aesthetasc (Heimann 1979). In the remipede *Speleonectes tanumekes* the antennule carries several dozen aesthetascs arranged in parallel rows on the peduncle (van der Ham and Felgenhauer 2006).

In planktonic copepods, Giesbrecht (1893) observed that, with the exception of the basal and a few distal segments, all antennule segments carry a trithek of setal elements (one aesthetasc and two setae). Traces of this pattern can be identified in all copepods, whether planktonic, benthic, or parasitic (Huys and Boxshall 1991). Giesbrecht also noted that males in some calanoid families possess two aesthetascs per segment, giving a quadrithek arrangement (two setae plus two aesthetascs) compared with the trithek of the female. Quadritheks occur on one or more segments of the male antennules in many calanoids (Huys and Boxshall 1991). In its extreme form, double aesthetascs are present along almost the entire length of the male antennules (from segments II to XXIV in *Eucalanus attenuatus*), whereas in other calanoid families they are restricted to the proximal part of the antennule.

In malacostracans aesthetascs are found only on the primary (= lateral) flagellum. They are typically aligned in regular rows, either one or two rows per annulus, and the number of aesthetascs per row varies with taxon (Table 7.1). The rows may be distributed along the length of the flagellum or restricted to the more proximal part. In some amphipods, the proximal annuli are completely or partially fused and bear multiple transverse rows of aesthetascs, forming an organ referred to as the *callynophore* by Lowry (1986). Similarly, in the isopod *Idotea baltica*, aesthetascs are carried in six or seven rows on the distal antennulary "segment" (Guse 1983), but this is undoubtedly a compound unit representing several annuli that failed to separate during

Table 7.1. Arrangement of aesthetascs on the primary flagellum of malacostracans.

Higher taxon	Species	No. rows per annulus	No. aesthetascs per row	Reference
Stomatopoda	*Gonodactylus mutatus*	1	3	Mead 2002
Decapoda	*Panulirus argus*	2	8–12	Daniel et al. 2008
Decapoda	*Orconectes virilis*	2	3–4	Mead 2008
Decapoda	*Homarus americanus*	2	~12	Derby 1982
Decapoda	*Typhlatya arfeae*	1	1–3	Jaume and Bréhier 2005
Decapoda	*Lysmata boggessi*	2	4–5	Zhang et al. 2008
Decapoda	*Birgus latro*	2	~12–14	Stensmyr et al. 2005
Lophogastrida	*Lophogaster typicus*	2	1–2 (30–40 in males)	Johansson et al. 1996
Isopoda	*Bathynomus pelor*	1	4–5	Thomson et al. 2009
Isopoda	*Natatolana borealis*	1	10	Kaïm-Malka et al. 1999
Isopoda	*Asellus aquaticus*	1	1	Heimann 1984
Isopoda	*Idotea baltica*	—	2	Guse 1983
Amphipoda	*Metacrangonyx dominicanus*	1	1–2	Jaume and Christenson 2001
Amphipoda	*Bathymedon longirostris*	2	4–5	Jaume et al. 1998

development. Fusion of proximal annuli and subsequent concentration of aesthetasc rows occur elsewhere in eucaridan and peracaridan malacostracans. In the Brachyura, the aesthetascs are arrayed in a dense tuft on the ventral surface at the tip of the flagellum.

The fine scale arrangement of aesthetascs, such as the precise angle at which they are carried relative to the segment, can have functional significance (Mead and Weatherby 2002, Thomson et al. 2009). The guard setae located on either side of the aesthetasc rows in *Panulirus argus* have a dual function: protecting the array from damage and conditioning the flow to allow for the correct leakiness during a flick and return sequence (Reidenbach et al. 2008).

Unimodal Nonaesthetasc Chemosensors

Several different morphologies of nonaesthetasc chemosensory setae are found in the Crustacea (Hallberg and Skog 2011). The presence of a terminal pore on a setal element is often taken as an indication of a chemoreceptive function. Such setae often have their outer dendritic segments shielded by a dendritic sheath of enveloping cells, so their sensory surfaces are exposed only near the tip. This setal type probably functions as a contact chemoreceptor. Several are present on the antennule of the cirripede cyprid larva (see Bielecki et al. 2009) that carry a single terminal setal element (TS-D in terminology of Bielecki et al. 2009) identified as an aesthetasc on the basis of external morphology. However, at least in *Megabalanus rosa*, seta TS-D has a terminal pore, which is typically absent from true aesthetascs, and Bielecki et al. (2009) preferred to call it "aesthetasc-like." Its inferred function was detection of waterborne chemicals along its entire length.

The setae on the cephalocaridan antennule all share a similar structure: each contains an outer dendritic segment that arises from a single ciliary body (9 × 2 + 0 microtubule pattern), which in turn arises from a basal body connected to the sensory cell via the inner dendritic segment. All the setae lack scolopale bodies and display features suggesting chemoreception (Elofsson and Hessler 1991).

In two superfamilies of Podocopa (Cypridoidea and Pontocypridoidea), a modified seta known as "aesthetasc Y" is carried on the first endopodal segment of the antenna. Its internal structure was studied in detail by Andersson (1975), who inferred that it is a chemoreceptor. Kaji and Tsukagoshi (2008) compared the development and structure of "aesthetasc Y" and the linear array of so-called grouped setae located in a similar position on the first endopodal segment on five other ostracod superfamilies. They suggested that "aesthetasc Y" is derived from grouped setae.

In cypridoidean ostracods, the Wouters organ is found on the dorsal surface of the first antennulary segment, and the Rome organ is found on the ventral side of the second moveable segment of the antennule in cypridoideans (Smith and Matzke-Karasz 2008). Both the Rome and Wouters organs vary in form from buttonlike to tubular and may be derived from setae. They were presumed to be chemosensors by Smith and Matzke-Karasz (2008).

Unimodal Mechanosensors

Mechanosensory setae are rigid structures with relatively thick cuticles, and in copepods each is usually innervated by two dendrites, sometimes only one (Gresty et al. 1993a). The structure and innervation of the mechanosensory seta of *Pleuromamma xiphias* (Fig. 7.11), a calanoid copepod, was described in detail by Weatherby and Lenz (2000). A pair of long dendritic processes extends from the paired sensory cell bodies (the somata), located in the antennule itself, to the seta. Distal to each soma, the basal body is located within the dendrite about at the level where the scolopale begins. The scolopale tube extends almost to the socket at the base of the

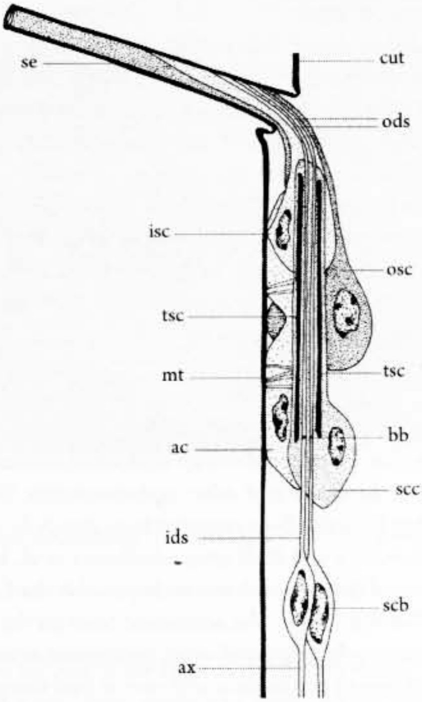

Fig. 7.11.
Schematic of typical copepod mechanosensory seta. The seta (se) articulates basally with the cuticle (cut). It is innervated by a pair of mechanosensory dendrites which pass from the cell bodies, through the tubular scolopale (tsc) contained within the scolopale cell (scc) sensory cell body (scb) before entering the base of the seta and inserting on its inner wall. The whole structure is enclosed by inner (isc) and outer (osc) sheath cells and is anchored to the cuticle by microtubules (mt) within the anchor cell (ac). At the level where the dendrite enters the scolopale are the 9 × 2 + 0 ciliary basal bodies (bb), marking the division of the dendrite into inner (ids) and outer segments (ods). The nerve cell connects to the central nervous system via an axon (ax). Adapted from Weatherby and Lenz (2000), with permission from Elsevier.

setal shaft. More distal dendrites become densely packed with a regular array of proliferating microtubules. Distally the microtubule array and surrounding dendrites bend and enter the lumen of the seta, inside which the dendrites are enveloped by inner and outer sheath cells. The dendrites and their microtubules terminate at attachments to the setal cuticle.

The scolopale cell is typical of arthropodan mechanosensors, and many of the cuticular setae in decapods are scolopidial in structure (Ball and Cowan 1977). The copepod mechanoreceptor described above (from Weatherby and Lenz 2000) differs from a typical scolopidial organ, which is characterized by the possession of a ciliary body with very large rootlets. These are in close contact with the dendritic membrane that itself makes desmosomal connections to the scolopale, firmly anchoring it to the scolopale (Schmidt and Gnatzy 1984). In *Pleuromamma*, dendrite anchoring appears to occur by the tight fit of the microtubule-packed dendrites within the tubular scolopale. In many crustaceans there is an extracellular dendritic sheath or cap that ensheathes the distal dendrites (Guse 1978), but none is present in *Pleuromamma*.

Transduction in a mechanosensor is the process by which a mechanical stimulus—a force acting to displace the seta—is transformed into a cellular physiological response. Weatherby and

Lenz (2000) suggest a likely mechanism for mechanotransduction involving linkages between individual microtubules and mechanogated channels in the dendritic membrane. The scolopale increases the rigidity of the system, and this rigidity probably contributes to high-frequency sensitivity. The attachment of the distal dendrites within the setal lumen instead of at the base probably enhances the physical displacement at the transduction site, promoting high sensitivity. The highly specialized receptor allows this planktonic copepod to detect the hydrodynamic disturbances generated by an incoming predator.

It is almost always the movement of the shaft in its socket that serves as the stimulus, but during molting in *Panulirus argus* the scolopale body is briefly located in the basal region of the setal shaft, and Schmidt and Derby (2005) suggested that, in this configuration, bending of the setal shaft itself could serve as an adequate stimulus.

Bimodal Chemo- and Mechanosensors

Antennulary setal elements that are bimodal—with both mechanosensory and chemosensory function—are well known in decapods and other malacostracans (Schmidt and Ache 1996, Kaïm-Malka et al. 1999). They have also been reported from cirripede cyprid larvae (Lagersson et al. 2003), in copepods (Laverack and Hull 1993, Weatherby et al. 1994), and in anostracan Branchiopoda (Tyson 1980), and they are probably widespread in the Crustacea.

In the model decapod *Panulirus argus*, the aesthetasc rows on the antennulary annuli are accompanied by setal elements, including guard setae, companion setae, and asymmetric setae. Guard setae flank the distal row of aesthetascs, and one or two companion setae are located lateral to each guard seta. The asymmetric seta is located between the end of the aesthetasc row and the guard seta. Only the asymmetric seta has been studied both ultrastructurally and electrophysiologically (Schmidt and Derby 2005). The asymmetric seta of *Panulirus argus* is bimodal. It has a terminal pore at the tip of the setal shaft, indicative of a chemosensory function, plus an associated scolopale body located in the annulus below its base, indicative of a mechanosensory function. Its position on the annulus provides for a loose mechanical coupling with the aesthetasc row.

The hooded sensillum of decapods is another bimodal element. In *Panulirus argus* the hooded sensillum is the second most abundant setal type on the antennulary flagella after the aesthetascs. Each has a porous cuticle and is innervated by nine or ten chemosensory and three mechanosensory neurons whose dendrites project to the tip (Cate and Derby 2002). The chemosensory neurons respond to waterborne chemical stimuli, while the mechanosensory neurons respond to direct tactile stimulation, not to distant hydrodynamic signals. Similarly, the pocilliform seta on the antenna of the scavenging isopod *Natatolana borealis* has a subapical pore and is probably a chemosensor (Kaïm-Malka et al. 1999).

Statocysts

Statocysts are paired equilibrium organs that contain mechanosensory setae responsive to changes in spatial orientation. In dendrobranchiate, caridean, and reptantian Decapoda, they are carried in the basal segment of the antennulary peduncle. They are also present in *Anaspides* and in the mysid *Hansenomysis*, according to Siewing (1956). In decapods, each statocyst consists of an invaginated cavity containing a statolith formed from sand grains cemented together by a secretion from integumental glands in the floor of the cyst (Prentiss 1901). Cysts are closed to the external environment and house two circular canals, one vertical and one horizontal, formed by compression of the cyst walls. Three groups of

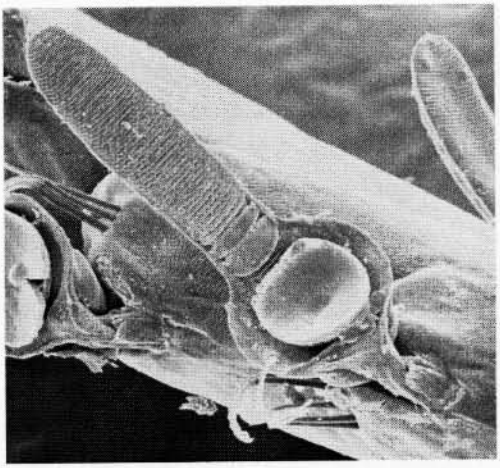

Fig. 7.12.
Scanning electron micrograph of calceolus from antenna of *Eusirus perdentatus* (Amphipoda). Photo courtesy of R. Lincoln.

mechanosensory setae are located in the floor of the statocyst and support the statolith. The setae, known as "statolith hairs," form concentric rows and are stimulated by shearing force created by movement of the statolith or by fluid movement within the circular canals. As the animal changes its orientation relative to gravity, the statolith is displaced creating a shearing force on the "statolith hairs." Responses of receptors within the decapod statocyst control reflexive compensatory and righting movements of the animal (see references in Cate and Roye 1997).

The Calceolus

Calceoli are enigmatic setal elements found in gammaridean amphipods (Lincoln and Hurley 1981). Each calceolus (Fig. 7.12) typically consists of a cup-shaped proximal element and a transversely banded distal element, both supported by a main receptacle and attached to the antenna by a short stalk. They can occur singly or in small groups on the flagellar annuli, and occasionally also on the peduncle. They frequently occur in males only, sometimes in both sexes, but never in females only. They can occur on the peduncle and flagellum of the antennule and antenna but are often confined to the antenna only. Dahl et al. (1970) inferred that calceoli are chemoreceptors, functioning as pheromone detectors, but Lincoln and Hurley (1981) concluded that they were mechanosensors despite being unable to confirm the presence of a nerve supply.

FUNCTIONAL MORPHOLOGY AND BEHAVIOR

The antennules of recent crustaceans are primarily sensory in function and form an important sensory interface with the environment. However, the hallmark of the arthropodan limb is its multifunctional potential, and antennules may play a role in many other behaviors, including locomotion, attachment, feeding, and mating. Performance of multiple functions is usually reflected in morphological adaptations, but in addition, comparative studies have revealed numerous examples of adaptive fine-tuning of the sensory array, by changes in the number of modular sets of sensory elements, by increasing or decreasing annulation, or by changes in the size or density of receptors. The antennae often perform a sensory role but can be similarly involved in a variety of other behaviors, including swimming, attachment, respiration, feeding, and brooding.

Swimming

Nauplii have only three pairs of limbs that perform a range of functions. The antennules already fulfill the sensory role that continues through to the adult, but in addition they may be involved in swimming and feeding in certain taxa. In cirripede nauplii, for example, the antennules are typically held directed forward while the paired antennae and mandibles generate the swimming motions (Rainbow and Walker 1976). In such cases, the role of antennules is presumably mainly sensory, whereas in calanoid copepods the antennules are often paddle shaped and setose and can contribute significantly to swimming (Bjørnberg 1986). The antennae are important locomotory limbs in all swimming nauplii.

Pelagic myodocopans such as *Conchoecia* swim almost continuously in the laboratory, using their antennal exopods, and begin sinking as soon as swimming motions cease during feeding episodes (Lochhead 1968). In podocopan Ostracoda, the antennules often have a locomotory function. This includes swimming in the Cypridoidea and crawling or digging in many Cytheroidea and in Darwinuloidea. Podocopans, such as *Cypridopsis vidua*, use both antennules and antennae in swimming. The motions of thrust-producing limbs are uniquely coordinated with the power strokes synchronized diagonally so that the left antennule and right antenna start together and end just as the right antennule and left antenna commence their power stroke (Hunt et al. 2007). During the power stroke, the long setae located on the four distal segments of the antennule and the array of setae on segment 3 of the antenna splay out into a fanlike configuration that accounts for >75% and about 50%, respectively, of the surface area in contact with the medium. During the recovery stroke, these natatory setae collapse back against the limb shaft. Swimming in this species is smoothly continuous because power strokes occur throughout the stroke cycle, in contrast to other small crustaceans, such as *Daphnia*, which exhibit rapid accelerations and decelerations due to the alternate power and recovery strokes of the antennae (the swimming limbs).

Cladocerans propel themselves through the water by the swimming motions of the paired antennae that have robust protopods housing powerful muscles. The zone of conspicuously folded cuticle at the base of each antenna (Fig. 7.13) functions to increase the angle through which the limb can swing during swimming. They carry arrays of long plumose natatory setae that are typically splayed out to maximize their surface area in contact with the water during the swimming power stroke. The antennae are folded toward the body to minimize their contribution to drag during the recovery stroke (Zaret and Kerfoot 1980). The predatory haplopodan branchiopod *Leptodora kindti* swims continuously in the water column using its large antennae to attain speeds up to 28 mm/s (Browman et al. 1989). The large, powerful antennae are also important swimming limbs in the Laevicaudata and Spinicaudata. The long antennules of planktonic copepods are folded back against the body during swimming, but evidence that they contribute to swimming itself is lacking.

Many malacostracans use their abdomen to perform a powerful tail-flip swimming action. This is an energetically expensive behavior and is usually employed as a startle escape response from an attacking predator. Tail-flip swimming in shrimps such as *Crangon* involves motions of a head fan, formed by the antennal scales, as well as the tail fan, formed from telson and uropods. The antennal scales pivot laterally during body flexion to form an expanded propulsive

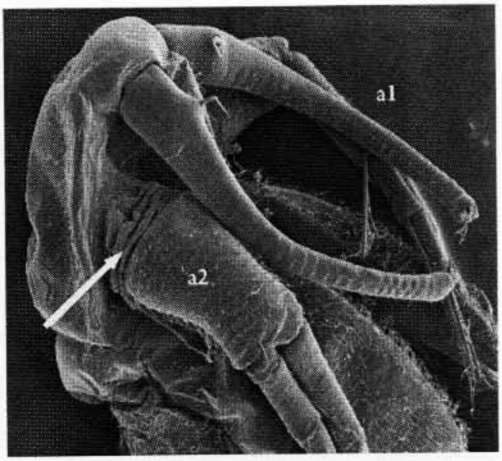

Fig. 7.13.
Scanning electron micrograph of male *Moina* (Branchiopoda) in lateral view, showing the curved form of antennules (a1) and a large biramous antenna (a2) with a robust protopod and proximal zone of highly folded cuticle (arrow).

surface, the head fan, which assists in the generation of thrust during tail-flips (Arnott et al. 1998). In the heavily armored scyllarid lobsters, lift is created during tail-flips, and changes in orientation of the transformed, platelike antennal flagella are used to alter the distribution of this lift to create pitching and rolling movements during maneuvers.

Attachment

Attachment to Substratum

The cyprid larva of cirripedes is a transitional stage marking the end of the planktonic dispersal phase of the life cycle and the beginning of the sessile adult phase. The highly mobile cyprid is specialized for settlement: the task of selecting a site for permanent attachment and metamorphosis, mediated by specific environmental cues (Crisp and Meadows 1962). The paired antennules play a key role in settlement behavior in free-living cirripedes. Cyprid larvae explore surfaces by walking across the substratum in a bipedal fashion, using alternate movements of their antennules (Nott and Foster 1969). The antennules are equipped with an attachment disc and cement gland for temporary adhesion to the substratum during walking, and they also carry an array of sensory elements (Nott and Foster 1969, Walker 1971), almost all of which were considered to be bimodal by Lagersson et al. (2003).

The attachment disc, carried on the third segment of the four-segmented antennule, is a disc-shaped pad, the surface of which is densely covered with cuticular villi (Fig. 7.14). The pad is surrounded by a membranous velum and also contains the opening of the cement gland duct. The cement gland is located in the head, close to the brain, and a long duct with a muscular sac located proximally carries the glycoproteinaceous cement down the antennule into the disc. The mechanism that allows rapidly reversible, temporary attachment via the discs is poorly understood, but a preliminary study of the footprints left by a walking cyprid led Phang et al. (2007) to suggest that a solely viscoadhesive mechanism, with the cement functioning as an adhesive, could not generate sufficient adhesive force to explain the real attachment tenacity of the cyprids.

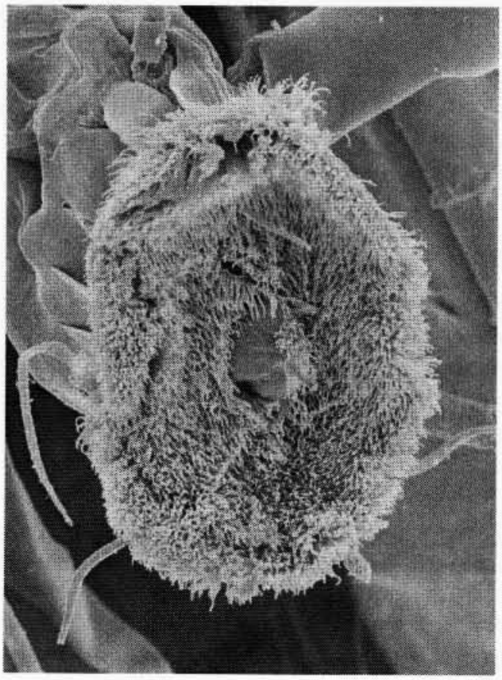

Fig. 7.14.
Scanning electron micrograph of attachment disc on antennule of cypris larva of *Megabalanus* (Cirripedia), showing cuticular villi covering the surface. Photo courtesy of J. Høeg.

In parasitic cirripedes, the Rhizocephala, the antennules play a major role in the unique host invasion process. As with other cirripedes, rhizocephalans typically hatch as a nauplius larva that, after four or five stages, metamorphoses into the cyprid larva. In the Kentrogonida, female cyprids attach to the surface of their crustacean hosts using their antennular cement glands and undergo a postsettlement molt into a flask-shaped, infective kentrogon stage that becomes firmly attached to the host. Internally, the kentrogon forms a stylet that it uses to penetrate the host cuticle and inoculate the next stage, the vermigon larva, into the host. This vermigon develops to form the adult body comprising the interna (the rootlet system within the host) and the externa (the external reproductive body). In the Lernaeodiscidae and Peltogastridae, the release of supplementary cement from the cement gland secures the kentrogon larva onto the host, and the stylet is evaginated through its midventral surface. In contrast, in the Sacculinidae, the kentrogon remains attached only by the cyprid antennules, and the stylet penetrates the host cuticle either via one of the antennules or between the antennules (see Glenner 2001). Again, the host is inoculated with the vermigon larva via the stylet. As do females, male cyprids attach using their antennules, but their postsettlement metamorphosis produces a motile larva, the trichogon, which escapes from the cyprid via one of its antennules at the distal break zone (Høeg 1987) and enters the female externa via its mantle aperture.

Penetration has been observed in only three akentrogonid rhizocephalans. The "female" cyprid of *Clistosaccus* uses its long antennules to permanently attach to the host (Høeg 1990), and then one antennule penetrates the host cuticle. The method of penetration is unknown. The distal region of the penetrating antennule breaks off, allowing the embryonic cells within the cyprid to pass into the host and commence interna formation. The male cyprid uses its antennules in a similar way to inject male generative cells either into the host adjacent to a developing female interna or directly into a newly emerged externa (Høeg 1985).

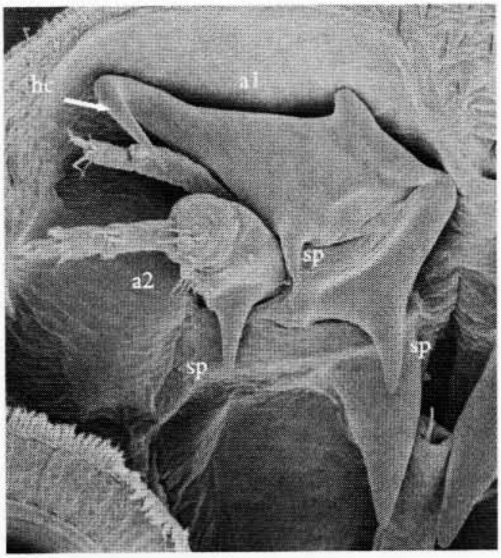

Fig. 7.15.
Scanning electron micrograph of *Argulus* (Branchiura) showing base of antennule (a1) with hooked claw (hc) and spinous processes (sp), and base of antenna (a2) with spinous process (sp). Both limbs have slender, cylindrical distal segments carrying sensory elements.

Attachment to Host

Many crustaceans are parasitic, and several others, in addition to the rhizocephalans, attach to the host using modified antennules. In the Ascothoracida, for example, the antennule is prehensile and used for attachment to the invertebrate host (Grygier 1984). In the majority of parasitic copepods, it is the antennae that form the grasping mechanism by which attachment to the host surface is secured (Huys and Boxshall 1991). They are typically subchelate structures, with a robust protopodal part housing the main musculature, and a clawlike distal subchela that grasps the host. The exopod is typically lost.

In the branchiuran fish lice, the basal part of the antennule is robust, heavily sclerotized, and armed with curved hooklike processes on the segmental margins (Fig. 7.15). In *Argulus* the first segment is drawn out into a hooklike process medially, and the more elongate second segment carries spinous processes anteriorly and posteriorly and terminates in a robust ventral hook. Adduction by extrinsic muscles originating on the dorsal cephalic wall brings these hooks into contact with the host surface (Gresty et al. 1993b). These hooks form part of the multilimb mechanism employed by these ectoparasites to attach to their fish hosts. In branchiurans, the coxa of the five-segmented antenna is heavily sclerotized and carries a stout hooked process proximally. However, since no adduction-abduction motions of the coxa are possible, this process probably only assists in securing the attachment of the parasite by preventing it from being dislodged (Gresty et al. 1993b).

Mating

Sexual dimorphism in antennule morphology reflects differing behavioral roles of the sexes in mating, although the functional significance of structures is not always well understood. For example, in the male of the mysid *Mesopodopsis slabberi*, the third segment of the antennulary peduncle carries, in addition to the two flagella, a large setose lobe referred to as the appendix

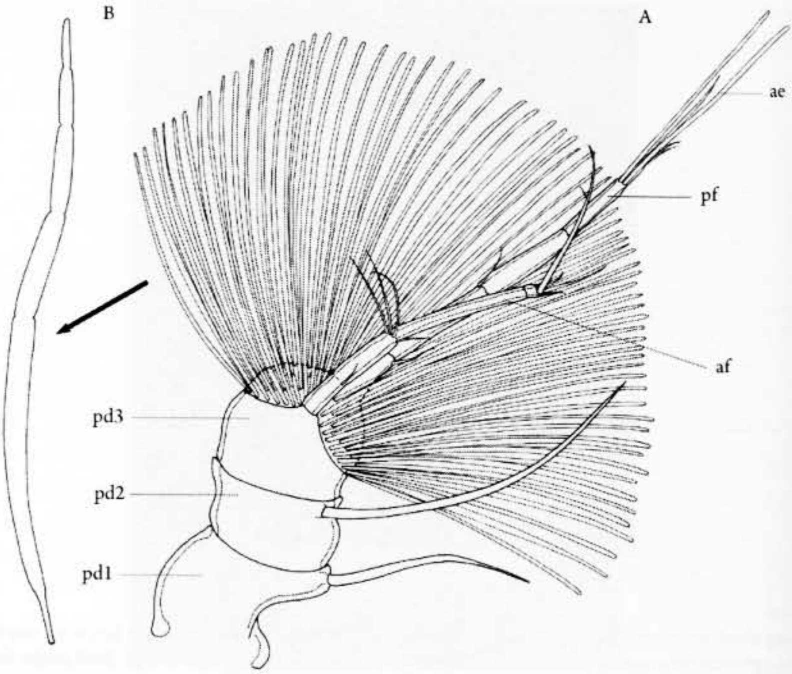

Fig. 7.16.
(A) Antennule of male *Leptostylis longimana* showing three-segmented peduncle (pd1–pd3) bearing primary (pf) and accessory (af) flagella. The proximal annulus of the primary flagellum is flared at its base and carries a dense array of aesthetascs; this flagellum also carries a pair of aesthetascs (ae) distally, as in the female. (B) Isolated aesthetasc from the basal array.

masculine plus an accessory appendix, which is an elongate lobe with a single long apical seta (Tattersall and Tattersall 1951). The function of these lobes is unknown.

Mate Location

In many groups of crustaceans, males actively locate sexually receptive females using chemosensory-mediated behavior based on the detection and localization of pheromone plumes produced by the female (e.g., Doall et al. 1998, Yen et al. 1998, Johnson and Atema 2005). Reflecting this sexual difference in behavioral roles, males commonly carry an enhanced array of aesthetascs compared with conspecific females (Hallberg et al. 1997). For example, the male of the mysid *Neomysis integer* has additional specialized setae on the antennulary peduncle (Guse 1983, Johansson and Hallberg 1992). In some male cumaceans, the proximal annulus of the primary flagellum carries a spectacular array of long aesthetascs (Fig. 7.16) on a flared basal swelling. In the male of *Lophogaster typicus*, the primary flagellum carries several hundred additional slender "male-specific sensilla" in regular arrays on each annulus in the middle and distal parts of the flagellum. Although considerably smaller, these male-specific sensilla do not differ significantly from aesthetascs in fine structure. In decapods, only aesthetascs, not the nonaesthetasc chemosensors, are involved in processing pheromones (Johnson and Atema 2005).

In copepods, the array of chemosensors on the antennules of adult males is often enhanced relative to that of the female (Boxshall and Huys 1998). Enlargement of aesthetascs in the male, rather than higher numbers of aesthetascs, is found in some planktonic copepods such as

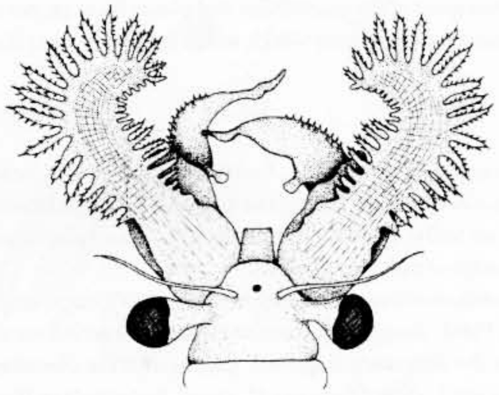

Fig. 7.17.
Dorsal view of head of male *Eubranchipus grubii* (Anostraca) showing species-specific form of antenna that is used for grasping the female during mating. Redrawn from Daday (1910).

Pontoeciella abyssicola. The female carries two aesthetascs; the male has a third located proximally, but the middle aesthetasc is grossly enlarged (1.12 mm long) in an animal with a body length of only 1.10 mm. Outspread, this pair of aesthetascs spans more than 2.2 mm, providing an enormous surface area and enhanced ability to scan the water passing across the antennules for pheromonal signals.

Copulation

Male anostracans clasp onto females during mating using their antennae. In all anostracan families except the Streptocephalidae, the basal and apical parts of the male antennae flex against each other to form a prehensile mechanism that enables them to grasp the female around the genital segment (Linder 1941). The basal part of the antenna carries an array of spinous or digitiform processes and smaller warts, and in some anostracans large elaborate frontal processes form as outgrowths of the basal part (Fig. 7.17). This ornamentation and the frontal processes may function as part of a species-specific mate recognition system (Belk 1984).

All neocopepodan orders primitively have geniculate antennules in adult males that are used for grasping the female during precopulatory and postcopulatory mate guarding, as well as during mating (Boxshall 1990). The specialized geniculation lies between ancestral segments XX and XXI, either side of which there is usually segmental fusion and setal modifications.

Siphonostomatoid copepods exhibit precopulatory mate guarding behavior in which adult males grasp developing females using modified antennae (Boxshall 1990). The dimorphism in antennal form and structure reflects the different behavior patterns during mating. Sexual dimorphism in antennule morphology can also reflect gender differences in feeding biology in copepods with dwarf parasitic males or with nonfeeding adult males. These are reflected in the number and size of sensors on the antennules (Boxshall et al. 1997, Boxshall and Huys 1998).

Offspring Brooding

Some arcturid isopods of the genera *Astacilla* and *Arcturus* provide extended parental care for their developing young by carrying their first stage juveniles on their long antennae (Sars 1899). Similar behavior has been reported for the caprellid amphipod *Pseudoprotella phasma*, in which the mother lifts the young out of the marsupium and places them on her antennae (and gnathopods), where they remain for up to three weeks, until the third instar (Harrison 1940).

Feeding

As a major sensory interface, the antennules function to identify and locate potential food items for many crustaceans. Chemosensors along the antennules allow the animal to detect odorant molecules (often amino acids) emanating from their food, and mechanosensors allow the animal to detect the presence of particles nearby.

Decapods and stomatopods use their antennules to track the chemical signatures of their food (Goldman and Patek 2002). The chemosensors are carried on the primary flagellum (aesthetascs) and on the accessory flagellum (nonaesthetasc chemosensors), and both are involved in detecting food odors (Keller et al. 2003). Antennulary flicking is a well-studied behavior pattern (Schmitt and Ache 1979). The primary flagellum is flicked through the water, a process of sampling the surrounding medium that has been likened to sniffing. In *Panulirus argus*, water flows through the aesthetasc array during the rapid flick downstroke and is retained there during the slower return stroke (Koehl et al. 2001). Intermittent flicking possibly enables the lobsters to take discrete samples of odor-containing fluid (Reidenbach et al. 2008).

Antennae can be used mechanically in deposit and suspension feeding. The amphipod *Corophium*, for example, is a deposit feeder that uses its long antennae to rake surface sediment into the entrance of its burrow, from where it is drawn down to the setose gnathopods by a water current generated by the beating pleopods. Some *Caprella* also use their antennae for scraping food particles from the substrate. The mole crab *Emerita* is a swash rider, burrowing into the sediment repeatedly as it follows the tide up and down the beach. It uses its large setose antennae for suspension feeding on phytoplankton during each wave cycle. Podocerid amphipods are also known to sieve seston from the water using their setose antennae.

The planktonic copepod *Euchaeta* is a specialist predator that detects the presence of prey by means of a three-dimensional array of long setae on the antennules (Yen and Nicoll 1990). It feeds only on live prey, typically other copepods, which it detects by responding to disturbance (shear) in the water column generated by the swimming motions of the prey. The setal array develops through the copepodid stages and reaches the peak of development in the adult female but is atrophied in the adult male, which is a nonfeeding stage with vestigial mouthparts (Boxshall et al. 1997). Small-particle-feeding copepods beat their antennae in opposition to the maxillipeds to create the flow fields that bring food particles within range, so they can be captured by the maxillae (Price et al. 1983).

Excretion

The antennal gland is the primary excretory gland in early crustacean larval stages, but in the adults of most taxa the paired maxillary glands take over this role during development. However, in the Mystacocarida, Eucarida, Amphipoda, Mysidacea, some Myodocopa, and misophrioid copepods, the antennal glands are retained in the adults as the sole functional excretory gland (Hessler and Elofsson 2007, Boxshall 1982). The gland is typically located within the head, and only the excretory duct passes into the antenna. In amphipods, the exit pore of the antennal gland is typically carried at the tip of a conical process located at the base of the antenna. In *Derocheilocaris typica*, the antennal excretory gland is, uniquely, located entirely within the coxa of the limb. It comprises only eight cells and has an excretory duct that opens via a pore on the posterior surface of the coxa (Hessler and Elofsson 2007).

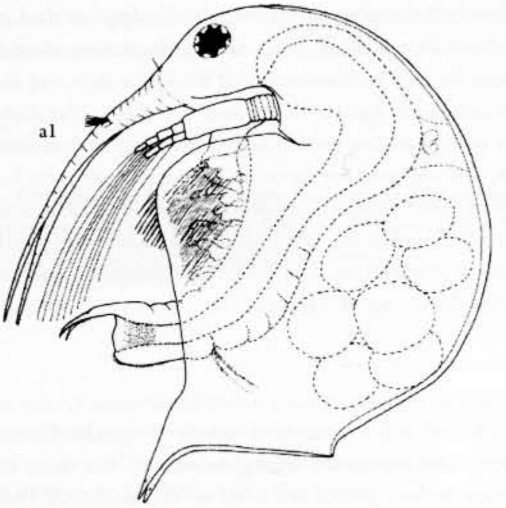

Fig. 7.18.
Lateral view of *Bosmina longispina* (Branchiopoda) showing elongate spinous form of antennules (a1). Redrawn from Lilljeborg (1900).

Defense

Predator Deterrence

The antennules of some cladocerans take the form of curved spinous processes (Fig. 7.18) that, together with carapace spines and crests, help to protect them against predators. Long features, including long antennules, may be selected to reduce predation risk from grasping predators such as copepods and *Leptodora* (Kerfoot 1978). Such long-featured morphs may be replaced by short-featured morphs when predation pressure declines (Kerfoot and Peterson 1980, Tollrian and Dodson 1999). In *Bosmina coregoni gibbera*, feature length seems to be determined by fitness trade-offs between increased protection afforded by the better developed antennules and spines and negative hydrodynamic effects of these structures on swimming performance (Lord et al. 2006).

Migrating spiny lobsters (*Panulirus argus*) exhibit collective defensive behavior when attacked by predatory fish. Under threat, they cluster into outward-facing, rosettelike groups and defend themselves using their spinous antennae. This behavior is effective, with per capita mortality declining with increasing lobster group size. *Panulirus* also produces sound by stridulation. The antenna has an area of ridged membrane, the stridulatory membrane, on a medial process on the proximal antennal segment. When the antennae are raised, the stridulatory membrane moves over the toothed ridge on the adjacent margin of the carapace, generating a rasping sound or a slow rattle. Bouwma and Herrnkind (2009) showed that stridulation in *P. argus* improved the chances of escape from attacking predators such as *Octopus*.

Detection of Incoming Predators

The array of setae on the eight distal (ancestral) segments of copepod antennules is highly conservative (Boxshall and Huys 1998) throughout the copepodid phase of development. This underlying conservatism of the distal array of sensors through ontogeny indicates a requirement for functional continuity. Electrophysiological studies by Yen et al. (1992) demonstrated that these antennulary setae are mechanosensors and that ablation of the distal tip of the antennule in *Pleuromamma* and *Euchaeta* deprives the copepod of its rapid escape response to mechanical signals (Lenz and Yen 1993). The distal array of setae forms the mechanosensory early warning system and is involved in detecting incoming predators. In the water column, the copepod represents a potential prey item for many predators, and the possession of a functional approaching-predator warning system is highly advantageous. The setae of the distal array are already present in late nauplii of planktonic calanoids. This mechanosensory system is operational very early in ontogeny, and functional continuity is maintained throughout the copepodid phase.

Grooming

Antennular grooming behavior is a distinctive and stereotyped behavior in decapods in which the antennulary flagella are repeatedly brought down to the third maxillipeds and drawn through pads of densely packed specialized setae on the endopods (Bauer 1989). In *Panulirus argus*, this behavior is elicited by stimulation with L-glutamate (Barbato and Daniel 1997), and Schmidt and Derby (2005) concluded that it is mediated through the chemoreceptors within the asymmetric setae on the flagella. The long antennal flagellum of most dendrobranchiate, stenopodidean, and caridean shrimps is groomed by specialized brushes of setae located either side of the carpus-propodus articulation of the first pereopod, whereas in most other decapods antennal grooming is performed by the third maxillipeds (Bauer 1989).

Respiration

In the burrowing crab *Corystes*, the long antennae carry linear arrays of setae that interlock when the antennae are closely apposed, thus forming a breathing tube, the tip of which extends to the surface. Inhalant water is filtered and drawn down this tube into the branchial chamber (Hartnoll 1972).

WIDER COMPARISONS

The variation in form and function of the antennules and antennae within the Crustacea is remarkable. The other mandibulatans, hexapods, and myriapods, all lack antennae, but their antennules can also perform a range of roles. With the exception of the Protura, which lack them, the antennules of hexapods and myriapods function primarily as sense organs. The flagellate antennules of insects (winged hexapods) typically carry an array of sensilla that can serve as olfactory receptors, mechanoreceptors, or thermohygroreceptors (Zacharuk 1985). As in the Malacostraca, the modular construction of the antennule provides a basic flexibility since the numbers of modules expressed during development can be adapted to suit changing requirements. Very long antennules, as found in cockroaches, for example, may have a tactile role analogous to that of the long antennal flagellum in *Cherax*.

Even in insects, the antennules can perform additional functions in mating, respiration, or feeding behavior. The terminal annuli of the flagellum in the water beetle *Hydrophilus* are covered in hydrophobic hairs and are involved in the formation of a funnel that carries air down to the layer of trapped air on the ventral surface. Male fleas grasp their mates using their antennules, which are provided with stalked discs, and many male collembolans exhibit similar clasping behavior during mating. The plasticity of form, as it reflects different functional priorities, is apparent in all arthropod limbs, but the sheer structural diversity of the antennules and antennae of the Crustacea is more spectacular than in any other arthropod group.

ACKNOWLEDGMENTS

We thank the editors for their constructive suggestions and improvements to the manuscript. Paul Clark pointed us to important references on decapod morphology. We are grateful to Jens Høeg and Roger Lincoln for providing photographic illustrations.

REFERENCES

Akam, M. 2000. Arthropods: Developmental diversity within a (super) phylum. Proceedings of the National Academy of Sciences of the USA 97:4438–4441.

Anderson, P.A., and B.W. Ache. 1985. Voltage- and current-clamp recordings of the receptor potential in olfactory receptor cells in situ. Brain Research 338:273–280.

Andersson, A. 1975. The ultrastructure of the presumed chemoreceptor aesthetasc "Y" of a cypridid ostracode. Zoologica Scripta 4:151–158.

Arnott, S.A., D.M. Neil, and A.D. Ansell. 1998. Tail-flip mechanism and size-dependent kinematics of escape swimming in the brown shrimp *Crangon crangon*. Journal of Experimental Biology 201:1771–1784.

Atema, J. 1977. Functional separation of smell and taste in fish and Crustacea. Pages 165–174 *in* J. Le Magnen and P. MacLeod, editors. Olfaction and taste, Vol. 6. Information Retrieval, London.

Bacescu, M. 1967. Decapoda. Fauna Republicii Socialiste Romania (Crustacea), Vol. 4, Fasicle 9. Editura Academiei R.S.R., Bucharest.

Ball, E.E., and A.N. Cowan. 1977. Ultrastructure of the antennal sensilla of *Acetes* (Crustacea, Decapoda, Natantia, Sergestidae). Philosophical Transactions of the Royal Society of London Series B 277:429–457.

Barbato, J.C., and P.C. Daniel. 1997. Chemosensory activation of an antennular grooming behavior in the spiny lobster, *Panulirus argus*, is tuned narrowly to L-glutamate. Biological Bulletin 293:107–115.

Barnes, T.G., T.Q. Truong, G.G. Adams, and N.E. McGruer. 2001. Large deflection analysis of a biomimetic lobster antenna due to contact and flow. ASME Journal of Applied Mechanics 68:948–951.

Bauer, R.T. 1989. Decapod crustacean grooming: Functional morphology, adaptive value and phylogenetic significance. Pages 49–73 *in* B.E. Felgenhauer , L. Watling, and A.B. Thistle, editors. Functional morphology of feeding and grooming in Crustacea. Balkema, Rotterdam.

Belk, D. 1984. Antennal appendages and reproductive success in the Anostraca. Journal of Crustacean Biology 4:66–71.

Bielecki, J., B.K.K. Chan, J.T. Høeg, and A. Sari. 2009. Antennular sensory organs in cyprids of balanomorph cirripedes: Standardizing terminology using *Megabalanus rosea*. Biofouling 25:203–214.

Bjørnberg, T.S. 1986. The rejected nauplius: A commentary. Syllogeus 58:232–236.

Bouwma, P.E., and W.F. Herrnkind. 2009. Sound production in Caribbean spiny lobster *Panulirus argus* and its role in escape during predatory attack by *Octopus briareus*. New Zealand Journal of Marine and Freshwater Research 43:1–13.

Boxshall, G.A. 1982. On the anatomy of the misophrioid copepods, with special reference to *Benthomisophria palliata* Sars. Philosophical Transactions of the Royal Society of London Series B 297:125–181.

Boxshall, G.A. 1985. The comparative anatomy of two copepods, a predatory calanoid and a particle feeding mormonilloid. Philosophical Transactions of the Royal Society of London Series B 311:303–377.

Boxshall, G.A. 1990. Precopulatory mate guarding in copepods. Bijdragen tot de Dierkunde 60:209–213.

Boxshall, G.A. 2004. The evolution of arthropod limbs. Biological Reviews 79:253–300.

Boxshall, G.A. 2007. Crustacean classification: On-going controversies and unresolved problems. Zootaxa 1668:313–325.

Boxshall, G.A., and R. Böttger-Schnack. 1988. Unusual ascothoracid nauplii from the Red Sea. Bulletin of the British Museum (Natural History), Zoology Series 54:275–283.

Boxshall, G.A., D.L. Danielopol, D.J. Horne, R.J. Smith, and I. Tabacaru. 2010. A critique of biramous interpretations of the crustacean antennule. Crustaceana 83:153–167.

Boxshall, G.A., T.D. Evstigneeva, and P.F. Clark. 1993. A new interstitial cyclopoid copepod from a sandy beach on the western shore of Lake Baikal, Siberia. Hydrobiologia 268:99–107.

Boxshall, G.A., and R. Huys, 1998. The ontogeny and phylogeny of copepod antennules. Philosophical Transactions of the Royal Society of London Series B 353:765–786.

Boxshall, G.A., and D. Jaume. 2000. Discoveries of cave misophrioids (Crustacea: Copepoda) shed new light on the origin of anchialine faunas. Zoologischer Anzeiger 239:1–19.

Boxshall, G.A., and R.J. Lincoln. 1987. The life cycle of the Tantulocarida (Crustacea). Philosophical Transactions of the Royal Society of London Series B 315:267–303.

Boxshall, G.A., J. Yen, and J.R. Strickler. 1997. Functional significance of the sexual dimorphism in the cephalic appendages of *Euchaeta rimana* Bradford. Bulletin of Marine Science 61:387–398.

Briggs, D.E.G., M.D. Sutton, D.J. Siveter, and D.J. Siveter. 2003. A new phyllocarid (Crustacea: Malacostraca) from the Silurian Fossil-Lagerstätte of Herefordshire, UK. Proceedings of the Royal Society of London Series B 271:131–138.

Browman, H.I., S. Kruse, and W.J. O'Brien. 1989. Foraging behavior of the predaceous cladoceran, *Leptodora kindti*, and escape responses of their prey. Journal of Plankton Research 11:1075–1088.

Bruce, N. 1986. Cirolanidae (Crustacea: Isopoda) of Australia. Records of the Australian Museum, Supplement 6:1–239.

Brusca, R.C., and G.D.F. Wilson. 1991. A phylogenetic analysis of the Isopoda with some classificatory recommendations. Memoirs of the Queensland Museum 31:143–204.

Bruton, D.L., and H.B. Whittington. 1983. *Emeraldella* and *Leanchoilia*, two arthropods from the Burgess Shale, Middle Cambrian, British Columbia. Proceedings of the Royal Society of London Series B 300:553–585.

Cate, H.S., and C.D. Derby. 2002. Ultrastructure and physiology of the hooded sensillum, a bimodal chemo-mechanosensillum of lobsters. Journal of Comparative Neurology 442:293–307.

Cate, H.S., and D.B. Roye. 1997. Ultrastructure and physiology of the outer row statolith sensilla of the blue crab *Callinectes sapidus*. Journal of Crustacean Biology 17:398–411.

Clark, P.F., D.K. Calazans, and G.W. Pohle. 1998. Accuracy and standardisation of brachyuran larval descriptions. Invertebrate Reproduction and Development 33:127–144.

Crisp, D.J., and P.S. Meadows. 1962. The chemical basis of gregariousness in cirripedes. Philosophical Transactions of the Royal Society of London Series B̄ 156:500–520.

Daday, E. 1910. Monographie systématique des Phyllopodes Anostracés. Annales des Sciences Naturelle, Zoologie, Series 9, 9:91–489.

Dahl, E., H. Emanuelsson, and C.V. Mecklenburg. 1970. Pheromone reception in the males of the amphipod *Gammarus duebeni* Lilljeborg. Oikos 21:42–47.

Dahms, H.-U. 1992. Metamorphosis between naupliar and copepodid phases in the Harpacticoida. Philosophical Transactions of the Royal Society of London Series B 335:221–236.

Damen, W.G.M., M. Hausdorf, E.A. Seyfarth, and D. Tautz. 1998. A conserved mode of head segmentation in arthropods revealed by the expression patterns of Hox genes in a spider. Proceedings of the National Academy of Sciences of the USA 95:10665–10670.

Daniel, P.C., M. Fox, and S. Mehta. 2008. Identification of chemosensory sensilla mediating antennular flicking behavior in *Panulirus argus*, the Caribbean spiny lobster. Biological Bulletin 215:24–33.

De Calazans, D.K. 1992. Taxonomy, distribution and abundance of protozoea, mysis and megalopa stages of Penaeidean decapods from the southern Brazilian coast. PhD dissertation, University of London.

Denton, E., and J.A.B. Gray. 1986. Lateral-line-like antennae of certain of the Penaeidea (Crustacea, Decapoda, Natantia). Proceedings of the Royal Society of London Series B 226:249–261.

Derby, C.D. 1982. Structure and function of cuticular sensilla of the lobster *Homarus americanus*. Journal of Crustacean Biology 2:1–21.

Derby, C.D., H.S. Cate, and L.R. Gentilcore. 1997. Perireception in olfaction: Molecular mass sieving by aesthetasc sensillar cuticle determines odorant access to receptor sites in the Caribbean spiny lobster *Panulirus argus*. Journal of Experimental Biology 200:2073–2081.

Diederich, R.J., V.K.L. Merrill, M.A. Pultz, and T.C. Kaufman. 1989. Isolation, structure and expression of *labial*, a homeotic gene of the Antennapedia complex involved in *Drosophila* head. Genes and Development 3:399–414.

Doall, M.H., S.P. Colin, J.R. Strickler, and J. Yen. 1998. Locating a mate in 3D: The case of *Temora longicornis*. Philosophical Transactions of the Royal Society of London Series B 353:681–689.

Elofsson, R., and R.R. Hessler. 1991. Sensory morphology in the antennae of the cephalocarid *Hutchinsoniella macracantha*. Journal of Crustacean Biology 11:345–355.

Foxton, P. 1969. The morphology of the antennal flagellum of certain of the Peneidea (Decapoda, Natantia). Crustaceana 16:33–43.

Ghiradella, H.T., J. Case, and J. Cronshaw. 1968a. Fine structure of the aesthetasc hairs of *Pagurus hirsutiusculus* Dana. Protoplasma 66:1–20.

Ghiradella, H.T., J. Case, and J. Cronshaw. 1968b. Structure of aesthetascs in selected marine and terrestrial decapods: Chemoreceptor morphology and environment. American Zoologist 8:603–621.

Giesbrecht, W. 1893. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna und Flora des Golfes von Neapel 19:1–831 (text), pls. 1–54 (atlas).

Glenner, H. 2001. Cypris metamorphosis, infection and earliest internal development of the rhizocephalan *Loxothylacus panopaei* (Gissler). Crustacea: Cirripedia: Rhizocephala: Sacculinidae. Journal of Morphology 249:43–75.

Goldman, J.A., and S.N. Patek. 2002. Two sniffing strategies in panulirid lobsters. Journal of Experimental Biology 205:3891–3902.

Gresty, K.A., G.A. Boxshall, and K. Nagasawa. 1993a. Antennulary sensors of the infective copepodid larva of sea lice (Copepoda: Caligidae). Pages 83–98 *in* G.A. Boxshall and D. Defaye, editors. Pathogens of wild and farmed fish: Sea lice. Ellis Horwood, Chichester, UK.

Gresty, K.A., G.A. Boxshall, and K. Nagasawa. 1993b. The fine structure and function of the cephalic appendages of the branchiuran parasite, *Argulus japonicus* Thiele. Philosophical Transactions of the Royal Society of London Series B 339:119–135.

Gruner, H.-E., and G. Scholtz, 2004. Segmentation, tagmata, and appendages. Pages 13–57 *in* J. Forest, J.C. von Vaupel Klein and F.R. Schram, editors. The Crustacea. Brill, Leiden, The Netherlands.

Grünert, U., and B.W. Ache. 1988. Ultrastructure of the aesthetasc (olfactory) sensilla of the spiny lobster, *Panulirus argus*. Cell and Tissue Research 251:95–103.

Grygier, M.J. 1984. Comparative morphology and ontogeny of the Ascothoracida, a step towards a phylogeny of the Maxillopoda. PhD dissertation, University of California, San Diego.

Grygier, M.J., and S. Ohtsuka. 1995. SEM observation of the nauplius of *Monstrilla hamatapex*, new species, from Japan and an example of upgraded descriptive standards for monstrilloid copepods. Journal of Crustacean Biology 15:703–719.

Guse, G.-W. 1978. Antennal sensilla of *Neomysis integer* (Leach). Protoplasma 95:145–161.

Guse, G.-W. 1983. Ultrastructure, development and moulting of the aesthetascs of *Neomysis integer* and *Idotea baltica* (Crustacea, Malacostraca). Zoomorphology 103:121–133.

Hallberg, E., K.U.I. Johansson, and R. Elofsson. 1992. The aesthetasc concept: Structural variations of putative olfactory receptor cell complexes in Crustacea. Microscopy Research and Technique 22:325–335.

Hallberg, E., K.U.I. Johansson, and R. Wallén. 1997. Olfactory sensilla in crustaceans: Morphology, sexual dimorphism, and distribution patterns. International Journal of Insect Morphology and Embryology 26:173–180.

Hallberg, E., and M. Skog. 2011. Chemosensory sensilla in crustaceans. Pages 103–121 *in* T. Breithaupt and M. Thiel, editors. Chemical communication in crustaceans. Springer, New York.

Harrison, R.J. 1940. On the biology of the Caprellidae. Growth and moulting in *Pseudoprotella phasma* Montagu. Journal of the Marine Biological Association of the UK 24:483–493.

Hartnoll, R.G. 1972. The biology of the burrowing crab, *Corystes cassivelaunus*. Bijdragen tot de Dierkunde 42:139–155.

Heimann, P. 1979. Fine structure of sensory tubes on the antennule of *Conchoecia spinirostris* (Ostracoda Crustacea). Cell and Tissue Research 202:461–477.

Heimann, P. 1984. Fine structure and molting of aesthetasc sense organs on the antennules of the isopod *Asellus aquaticus* (Crustacea). Cell and Tissue Research 235:117–128.

Hessler, R.R. 1964. The Cephalocarida. Comparative skeletomusculature. Memoirs of the Connecticut Academy of Arts and Sciences 16:1–97.

Hessler, R.R. 1983. A defense of the caridoid facies, wherein the early evolution of the Eumalacostraca. Pages 145–164 *in* F.R. Schram, editor. Crustacean phylogeny. Balkema, Rotterdam.

Hessler, R.R., and R. Elofsson. 2007. An excretory organ in the Mystacocarida (Crustacea). Arthropod Structure and Development 36:171–181.

Hessler, R.R., and H.L. Sanders. 1966. *Derocheilocaris typicus* Pennak and Zinn (Mystacocarida) revisited. Crustaceana 11:141–155.

Heymons, R. 1901. Die Entwicklungsgeschichte der Scolopender. Zoologica 33:1–33, pls. I–VIII.

Høeg, J.T. 1985. Male cypris settlement in *Clistosaccus paguri* Lilljeborg (Crustacea: Cirripedia: Rhizocephala). Journal of Experimental Marine Biology and Ecology 89:221–235.

Høeg, J.T. 1987. Male cypris metamorphosis and a new male larval form, the trichogon, in the parasitic barnacle *Sacculina carcini* (Crustacea: Cirripedia: Rhizocephala). Philosophical Transactions of the Royal Society of London Series B 317: 47–63.

Høeg, J.T. 1990. "Akentrogonid" host invasion and an entirely new life cycle in the rhizocephalan parasite *Clistosaccus paguri* (Thecostraca: Cirripedia). Journal of Crustacean Biology 10:37–52.

Hou, X., and J. Bergström. 1997. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China Fossils and Strata 45:1–116.

Hunt, G., L.E. Park, and M. Labarbera. 2007. A novel crustacean swimming stroke: coordinated four-paddled locomotion in the Cypridoidean ostracode *Cypridopsis vidua* (Müller). Biological Bulletin 212:67–73.

Huys, R., and G.A. Boxshall. 1991. Copepod evolution. Ray Society, London.

Huys, R., G.A. Boxshall, and R.J. Lincoln. 1993. The tantulocaridan life cycle: The circle closed? Journal of Crustacean Biology 13:432–442.

Imms, A.D. 1939. On the antennal musculature in insects and other arthropods. Quarterly Journal of the Microscopical Society 81:273–320.

Jaume, D., G.A. Boxshall, and R.N. Bamber. 2006. A new genus of Hirsutiidae from the continental slope off Brazil and the discovery of the first males in the Bochusacea (Crustacea: Peracarida). Zoological Journal of the Linnean Society 148:169–208.

Jaume, D., and F. Bréhier. 2005. A new species of *Typhlatya* (Crustacea: Decapoda: Artyidae) from anchialine caves on the French Mediterranean coast. Zoological Journal of the Linnean Society 144:387–414.

Jaume, D., J.E. Cartes, and J.-C. Sorbe. 1998. A new species of *Bathymedon* Sars, 1892 (Amphipoda: Oedicerotidae) from the western Mediterranean bathyal floor. Scientia Marina 62:341–356.

Jaume, D., and K. Christenson. 2001. Amphi-Atlantic distribution of the subterranean amphipod family Metacrangonyctidae (Gammaridea). Contributions to Zoology 70:99–125.

Jenner, R. A., C. Ní Dhubhghaill, M.P. Ferla, and M.A. Wills. 2009. Eumalacostracan phylogeny and total evidence: Limitations of the usual suspects. BMC Evolutionary Biology 9:21.

Johansson, K.U.I., L. Gefors, R. Wallén, and E. Hallberg. 1996. Structure and distribution patterns of aesthetascs and male-specific sensilla in *Lophogaster typicus* (Mysidacea). Journal of Crustacean Biology 16:45–53.

Johansson, K.U.I., and E. Hallberg. 1992. Male-specific structures in the olfactory system of mysids (Mysidacea: Crustacea). Cell and Tissue Research 268:369–368.

Johnson, M.E., and J. Atema. 2005. The olfactory pathway for individual recognition in the American lobster *Homarus americanus*. Journal of Experimental Biology 208:2865–2872.

Kaïm-Malka, R.A., S. Maebe, C. Macquart-Moulin, and C. Bezac. 1999. Antennal sense organs of *Natatolana borealis* (Lilljeborg, 1851) (Crustacea: Isopoda). Journal of Natural History 33:65–88.

Kaji, T., and A. Tsukagoshi. 2008. Origin of the novel chemoreceptor Aesthetasc "Y" in Ostracoda: Morphological thresholds and evolutionary innovation. Evolution and Development 10:228–240.

Karanovic, I. 2005. Comparative morphology of the Candoninae antennula, with remarks on the ancestral state in ostracods and a proposed new terminology. Spixiana 28:141–160.

Keller, T.A., I. Powell, and M.J. Weissburg. 2003. Role of olfactory appendages in chemically mediated orientation of blue crabs. Marine Ecology Progress Series 261:217–231.

Kerfoot, W.C. 1978. Combat between predatory copepods and their prey: *Cyclops*, *Epischura* and *Bosmina*. Limnology and Oceanography 23:1089–1102.

Kerfoot, W.C., and C. Peterson. 1980. Predatory copepods and *Bosmina*: Replacement cycles and further influences of predation upon prey reproduction. Ecology 61:417–431.

Kesling, R.V. 1951. The morphology of ostracod molt stages. III. Biological Monographs 21:1–324.

Koehl, M.A.R., J.R. Koseff, J.P. Crimaldi, M.G. McCay, T. Cooper, M.B. Wiley, and P.A. Moore. 2001. Lobster sniffing: Antennule design and hydrodynamic filtering of information in an odor plume. Science 294:1948–1951.

Koenemann, S., F.R. Schram, A. Bloechl, T.M. Iliffe, M. Hoenemann, and C. Held, 2007. Post-embryonic development of remipede crustaceans. Evolution and Development 9:117–121.

Kunze, J. K., 1983. Stomatopoda and the evolution of the Hoplocarida. Pages 165–188 *in* F.R. Schram, editor. Crustacean phylogeny. Crustacean Issues, Vol. 1. Balkema, Rotterdam.

Lagersson, N.C., A. Garm, and J.T. Høeg. 2003. Notes on the ultrastructure of the setae on the fourth antennulary segment of the *Balanus amphitrite* cyprid (Crustacea: Cirripedia: Thoracica). Journal of the Marine Biological Association of the UK 83:361–365.

Laverack, M.S. 1964. The antennulary sense organs of *Panulirus argus*. Comparative Biochemistry and Physiology 13:301–321.

Laverack, M., and M.Q. Hull. 1993. Sensory innervation of the antennule of the preadult male *Caligus elongatus*. Pages 114–122 *in* G.A. Boxshall and D. Defaye, editors. Pathogens of wild and farmed fish: Sea lice. Ellis Horwood, Chichester, UK.

Lenz, P.H., and J. Yen. 1993. Distal setal mechanoreceptors of the first antennae of marine copepods. Bulletin of Marine Science 53:170–179.

Lilljeborg, W. 1900. Cladocera Sueciae oder Beträge zur Kenntniss der in Schweden lebenden Krebsthiere von der Ordnung der Branchiopoden und der Unterordnung der Cladoceren. Akademischen Buchdruckerei, Upsala.

Lincoln, R.J., and D.E. Hurley. 1981. The calceolus, a sensory structure of gammaridean amphipods (Amphipoda: Gammaridea). Bulletin of the British Museum (Natural History), Zoology Series 40:103–116.

Linder, F. 1941. Contributions to the morphology and the taxonomy of the Branchiopoda Anostraca. Zoologiska Bidrag från Uppsala 20:101–302.

Lochhead, J.H. 1968. The feeding and swimming of *Conchoecia* (Crustacea, Ostracoda). Biological Bulletin 134:456–464.

Lord, H., R. Lagergren, J.-E. Svensson, and N. Lindqvist. 2006. Sexual dimorphism in *Bosmina*: The role of morphology, drag, and swimming. Ecology 87:788–795.

Lowry, J.K. 1986. The callynophore, a eucaridan/peracaridan sensory organ prevalent among the Amphipoda (Crustacea). Zoologica Scripta 15:333–349.

Maas, A., D. Waloszek, and K.J. Müller. 2003. Morphology, ontogeny and phylogeny of the Phosphatocopina (Crustacea) from the Upper Cambrian "Orsten" of Sweden. Fossils and Strata 49:1–238.

Maddox, R.F. 2000. The antennule in podocopid Ostracoda: Chaetotaxy, ontogeny and morphometrics. Micropaleontology 4(suppl 2):1–72.

Martin, J. 1992. Branchiopoda. Pages 25–224 *in* F.W. Harrison, editor. Microscopic anatomy of invertebrates, Vol. 9, Crustacea. John Wiley and Sons, New York.

Maruzzo, D., A. Minelli, M. Ronco, and G. Fusco. 2007. Growth and regeneration of the second antennae of *Asellus aquaticus* (Isopoda) in the context of arthropod antennal segmentation. Journal of Crustacean Biology 27:184–196.

McKenzie, K.G., P.-J. Chen, and S. Majoran. 1991. *Almatium gusevi* (Chernyshev 1940): Redescription, shield-shapes, and speculations on the reproductive mode (Branchiopoda, Kazacharthra). Paläontologische Zeitschrift 65:305–317.

Mead, K.S. 2002. From odor molecules to plume tracking: An interdisciplinary, multilevel approach to olfaction in stomatopods. Integrative and Comparative Biology 42:258–264.

Mead, K.S. 2008. Do antennule and aesthetasc structure in the crayfish *Orconectes virilis* correlate with flow habitat? Integrative and Comparative Biology 48:823–833.

Mead, K.S., and M.A.R. Koehl. 2000. Stomatopod antennule design: The asymmetry, sampling efficiency and ontogeny of olfactory flicking. Journal of Experimental Biology 203:3795–3808.

Mead, K.S., and T.M. Weatherby. 2002. Morphology of stomatopod chemosensory sensilla facilitates fluid sampling. Invertebrate Zoology 121:148–157.

Michel, W.C., H.G. Trapido-Rosenthal, E.T. Chao, and M. Wachowiak. 1993. Stereoselective detection of amino acids by lobster olfactory receptor neurons. Journal of Comparative Physiology A 171:705–712.

Nott, J.A., and B.A. Foster. 1969. On the structure of the antennular attachment organ of the cypris larva of *Balanus balanoides* (L.). Philosophical Transactions of the Royal Society of London Series B 256:115–134.

Olesen, J. 2001. External morphology and larval development of *Derocheilocaris remanaei* Delamare-Deboutteville and Chappuis, 1951 (Crustacea, Mystacocarida), with a comparison of crustacean segmentation and tagmosis patterns. Biologiske Skrifter 53:1–59.

Olesen, J., and D. Waloßek. 2000. Limb ontogeny and trunk segmentation in *Nebalia* species (Crustacea, Malacostraca, Leptostraca). Zoomorphology 120:47–64.

Perrier, V., J. Vannier, P.R. Racheboeuf, S. Charbonnier, D. Chabard, and D. Sotty. 2006. Syncarid crustaceans from the Montceau Lagerstätte (Upper Carboniferous; France). Palaeontology 49:647–672.

Peterson, M., B.T. Rogers, A. Popadić, and T.C. Kaufman. 1999. The embryonic expression pattern of *labial*, posterior homeotic complex genes and the *teashirt* homologue in an apterygote insect. Development, Genes and Evolution 209:77–90.

Phang, I.Y., N. Aldred, A.S. Clare, and G.J. Vancso. 2007. Towards a nanomechanical basis for temporary adhesion in barnacle cyprids (*Semibalanus balanoides*). Interface 5:397–402.

Prentiss, C.W. 1901. The otocyst of decapod Crustacea. Bulletin of the Museum of Comparative Zoology 36:167–251.

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

Rainbow, P.S., and G. Walker. 1976. The feeding apparatus of the barnacle nauplius larva: A scanning electron microscope study. Journal of the Marine Biological Association of the UK 56:321–326.

Reidenbach, M.A., N. George, and M.A.R. Koehl. 2008. Antennule morphology and flicking kinematics facilitate odor sampling by the spiny lobster, *Panulirus argus*. Journal of Experimental Biology 211:2849–2858.

Richter, S., and G. Scholtz. 2001. Phylogenetic analysis of the Malacostraca (Crustacea). Journal of Zoological Systematics and Evolutionary Research 39:113–136.

Rossetti, G., and K. Martens. 1996. Redescription and morphological variability of *Darwinula stevensoni* (Brady and Robertson, 1870) (Crustacea, Ostracoda). Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Biologie 66:73–92.

Rushton-Mellor, S., and G.A. Boxshall. 1994. The developmental sequence of *Argulus foliaceus*. Journal of Natural History 28:763–785.

Sandeman, D.C. 1989. Physical properties sensory receptors and tactile reflexes of the antenna of the Australian freshwater crayfish *Cherax destructor*. Journal of Experimental Biology 141:197–218.

Sandeman, R.E., and D.C. Sandeman. 1996. Pre- and postembryonic development, growth and turnover of olfactory receptor neurones in crayfish antennules. Journal of Experimental Biology 199:2409–2418.

Sanders, H.L. 1963. The Cephalocarida. Functional morphology, larval development, comparative external anatomy. Memoirs of the Connecticut Academy of Arts and Sciences 15:1–80.

Sars, G.O. 1899. Isopoda. An account of the Crustacea of Norway. Bergen Museum 2:1–270.

Schmidt, M., and B.W. Ache. 1996. Processing of antennular input in the brain of the spiny lobster, *Panulirus argus*. I. Non-olfactory chemosensory and mechanosensory pathway of the lateral and median antennular neuropils. Journal of Comparative Physiology A 178:579–604.

Schmidt, M., and C.D. Derby. 2005. Non-olfactory chemoreceptors in asymmetric setae activate antennulary grooming behaviour in the Caribbean spiny lobster *Panulirus argus*. Journal of Experimental Biology 208:233–248.

Schmidt, M., and W. Gnatzy. 1984. Are the funnel-canal organs the campaniform sensilla of the shore crab *Carcinus maenas* (Crustacea, Decapoda). 2. Ultrastructure. Cell and Tissue Research 237:81–93.

Schmitt, B.C., and B.W. Ache. 1979. Olfaction: Responses of a decapod crustacean are enhanced by flicking. Science 205:204–206.

Scholtz, G. 2000. Evolution of the nauplius stage in malacostracan crustaceans. Journal of Zoological Systematics and Evolutionary Research 38:175–187.

Scholtz, G., and G.D. Edgecombe. 2005. Heads, Hox and the phylogenetic position of trilobites. Pages 139–165 *in* S. Koenemann and R.A. Jenner, editors. Crustacea and arthropod relationships. Crustacean Issues, Vol. 16. Taylor and Francis, Boca Raton, FL.

Schram, F.R. 1986. Crustacea. Oxford University Press, New York.

Schram, F.R., and C. Hof. 1998. Fossils and the interrelationships of major crustacean groups. Pages 233–302 *in* G.D. Edgecombe, editor. Arthropod fossils and phylogeny. Columbia University Press, New York.

Schutze, M.L.M., C.E.F. da Rocha, and G.A. Boxshall. 2000. Antennular development during the copepodid phase in the family Cyclopidae (Copepoda, Cyclopoida). Zoosystema 22:749–806.

Scourfield, D.J. 1926. On a new type of crustacean from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire)—*Lepidocaris rhyniensis*, gen, et sp. nov. Philosophical Transactions of the Royal Society of London Series B 214:153–186.

Scourfield, D.J. 1940. Two new complete specimens of young stages of the Devonian fossil crustacean *Lepidocaris rhyniensis*. Proceedings of the Linnean Society 152:290–298.

Shakori, A.R. 1968. Morphology and skeletomusculature of *Caenestheria propinqua* (Sars) (Conchostraca; Branchiopoda; Crustacea). Bulletin of the Department of Zoology University of the Panjab 2:1–48.

Siewing, R. 1956. Untersuchungen zur Morphologie der Malacostraca. Zoologische Jahrbücher, Abteilung für Anatomie 75:39–176.

Siewing, R. 1959. Syncarida. Pages 1–121 *in* H.-E. Gruner, editor. Dr. H. G. Bronns Klassen und Ordnungen des Tierreiches, Vol. 5, Band 1. Akademische-Verlagsgesellschaft Geest, Leipzig.

Siveter, David J., Derek J. Siveter, M.D. Sutton, and D.E.G. Briggs. 2007. Brood care in a Silurian ostracod. Proceedings of the Royal Society of London Series B 274:465–469.

Siveter, David J., M.D. Sutton, D.E.G. Briggs, and Derek J. Siveter. 2003. An ostracode crustacean with soft parts from the Lower Silurian. Science 302:1749–1751.

Siveter, David J., M. Williams, and D. Waloszek. 2001. A phosphatocopid Crustacean with appendages from the Lower Cambrian. Science 293:479–481.

Smith, R.J., and T. Kamiya. 2008. The ontogeny of two species of Darwinuloidea (Ostracoda, Crustacea). Zoologischer Anzeiger 247:275–302.

Smith, R.J., and R. Matzke-Karasz. 2008. The organ on the first segment of the cypridoidean (Ostracoda, Crustacea) antennule: Morphology and phylogenetic significance. Senckenbergiana Lethaea 88:127–140.

Smith, R.J., and A. Tsukagoshi. 2005. The chaetotaxy, ontogeny and musculature of the antennule of podocopan ostracods (Crustacea). Journal of Zoology 265:157–177.

Stensmyr, M.C., S. Erland, E. Hallberg, R. Wallén, P. Greenaway, and B.S. Hansson. 2005. Insect-like olfactory adaptations in the terrestrial giant robber crab. Current Biology 15:116–121.

Steullet, P., H.S. Cate, W.C. Michel, and C.D. Derby. 2000. Functional units of a compound nose: Aesthetasc sensilla house similar populations of olfactory receptor neurons on the crustacean antennule. Journal of Comparative Neurology 418:270–280.

Tattersall, W.M., and O.S. Tattersall. 1951. The British Mysidacea. Ray Society, London.

Telford, M.J., and R.H. Thomas. 1998. Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. Proceedings of the National Academy of Sciences of the USA 95:10671–10675.

Thomson, M., K. Robertson, and A. Pile. 2009. Microscopic structure of the antennulae and antennae on the deep-sea isopod *Bathynomus pelor.* Journal of Crustacean Biology 29:302–316.

Tollrian, R., and S.I. Dodson. 1999. Inducible defenses in Cladocera: Constraints, costs, and multipredator environments. Pages 177–202 *in* R. Tollrian and C.D. Harvell, editors. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, NJ.

Tyson, G.E. 1980. Fine structure of the type 2 antennular sensilla of the brine shrimp, *Artemia salina.* American Zoologist 20:816–000.

Vandel, A. 1960. Isopodes terrestres (Première partie). Faune de France 64:1–416.

Van der Ham, J.L., and B.E. Felgenhauer. 2006. Ultrastructure of the peduncular aesthetascs of *Speleonectes tanumekes* (Crustacea, Remipedia) in comparison with crustaceans from stressful environments. Invertebrate Biology 125:256–264.

Walker, G. 1971. A study of the cement apparatus of the cypris larva of the barnacle *Balanus balanoides.* Marine Biology 9:205–212.

Walossek, D. 1993. The Upper Cambrian *Rehbachiella* and the phylogeny of Branchiopoda and Crustacea. Fossils and Strata 32:1–202.

Weatherby, T.M., and Lenz, P.H. 2000. Mechanoreceptors in calanoid copepods: Designed for high sensitivity. Arthropod Structure and Development 29: 275–288.

Weatherby, T.M., K.K. Wong, and P.H. Lenz. 1994. Fine structure of the distal sensory setae on the first antenna of *Pleuromamma xiphias* Giesbrecht (Copepoda). Journal of Crustacean Biology 14:670–685.

Wege, W. 1911. Morphologische und experimentelle Studien an *Asellus aquaticus*. Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere 30:217–320.

Yager, J. 1981. Remipedia, a new class of Crustacea from a marine cave in the Bahamas. Journal of Crustacean Biology 1:328–333.

Yen, J., P.H. Lenz, D.V. Gassie, and D.K. Hartline. 1992. Mechanoreception in marine copepods: Electrophysiological studies on the first antennae. Journal of Plankton Research 14:495–512.

Yen, J., and N.T. Nicoll. 1990. Setal array on the first antennae of a carnivorous marine copepod, *Euchaeta norvegica.* Journal of Crustacean Biology 10:218–224.

Yen, J., M.J. Weissberg, and M.H. Doall. 1998. The fluid physics of signal perception by mate-tracking copepods. Philosophical Transactions of the Royal Society of London Series B 353:787–804.

Zacharuk, R.Y. 1985. Antennae and sensilla. Pages 1–69 *in* G.A. Kerkut and L.I. Gilbert, editors. Comprehensive insect physiology, biochemistry and pharmacology, Vol. 6. Pergamon Press, Oxford.

Zaret, R.E., and W.C. Kerfoot. 1980. The shape and swimming technique of *Bosmina longirostris.* Limnology and Oceanography 25:126–133.

Zhang, D., S. Cai, H. Liu, and J. Lin. 2008. Antennal sensilla in the genus *Lysmata* (Caridea). Journal of Crustacean Biology 28:433–438.